Australian tidal wetlands and their response to sea-level rise

Neil Saintilan

B.Sc (hons), PhD

Professor

School of Natural Sciences, Macquarie University

A thesis submitted in fulfillment of the requirements of the degree of Doctor of Science (D.Sc.)

Faculty of Science

University of Sydney

2025

TABLE OF CONTENTS

STATEMENT 7

CANDIDATE'S ROLE IN THESIS PUBLICATIONS 8

DESCRIPTION OF THE THEMES OF THE PUBLISHED WORK 18

ACKNOWLEDGEMENTS 37

CHAPTER 1: HABITAT DYNAMICS IN MANGROVE AND SALTMARSH ECOSYSTEMS 38

1.1 Rogers, K., Boon, P., Lovelock, C. E., & **Saintilan, N.** (2017). Coastal halophytic vegetation. *Australian vegetation, 3rd edn. Cambridge University Press, Cambridge*, 544-569. 39

1.2 **Saintilan N.** (2009). Biogeography of Australian Saltmarsh Plants. *Austral Ecology* 34, 929-937 65

1.3 **Saintilan N.** and Williams R. 1999. Mangrove transgression into saltmarsh environments in New South Wales, Australia. *Global Ecology and Biogeography* 8 117-124. 74

1.4 **Saintilan N.** and Williams R. 2000. The decline of saltmarsh in eastern Australia *Wetlands (Australia)* 18(2) 49-54. 82

1.5 **Saintilan N.,** and Hashimoto R. 1999. Mangrove-saltmarsh dynamics on a prograding bayhead delta in the Hawkesbury River estuary, New South Wales, Australia. *Hydrobiologia* 413: 95-102. 88

1.6 **Saintilan N.** and Wilton K. 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. *Wetland Ecology and Management* 9: 409-420. 96

1.7 Wilson, N. C. & **Saintilan N.** 2018, 'Reproduction of the mangrove species Rhizophora stylosa Griff. At its southern latitudinal limit', Aquatic Botany, vol. 151, pp. 30–37, doi:10.1016/j.aquabot.2018.07.009 108

1.8 Wilson N.C. and **Saintilan N.** (2012) Growth of the mangroves species Rhizophora stylosa Griff. at it's southern limit in eastern Australia. *Aquatic Botany* 101 8-17 116

1.9 **Saintilan N**., Rogers K. and McKee K. (2009) Saltmarsh-Mangrove interactions in Australasia and the Americas. Chapter 31 in Perillo G.M.E., Wolanski E., Cahoon D.R and Brinson M.M. (eds.) *Coastal Wetlands; an integrated ecosystems approach.* Elsevier pp. 855-883. 126

1.10 **Saintilan, N.,** Rogers, K., & McKee, K. L. (2019). The shifting saltmarsh-mangrove ecotone in Australasia and the Americas. In *Coastal wetlands* (pp. 915-945). Elsevier. 156

1.11 **Saintilan N.,** Rogers K, Wilson N., Rajkaran R. and Krauss K. (2014). Mangrove expansion and saltmarsh decline at mangrove pole-ward limits. *Global Change Biology* 20 147-157 188

1.12 **Saintilan, N**., & Rogers, K. (2015). Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. *New Phytologist*, *205*(3), 1062-1070. 199

CHAPTER 2: TROPHIC DYNAMICS IN MANGROVE AND SALTMARSH ECOSYSTEMS 208

2.1 **Saintilan N.,** (2004). Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine Coastal and Shelf Science* 61: 591-601. 209

2.2 **Saintilan N**., and Wen L. (2012) Environmental predictors of estuarine fish landings along a temperate coastline *Estuarine Coastal and Shelf Science* 113 221-230 220

2.3 **Saintilan N**. and Mazumder D., (2010). Fine scale variability in the dietary sources of grazing invertebrates in a temperate Australian Saltmarsh. *Marine and Freshwater Research*.61 615-620 75. 230

2.4 Alderson, B., Mazumder, D., **Saintilan, N.,** Zimmerman, K., & Mulry, P. (2013). Application of isotope mixing models to discriminate dietary sources over small-scale patches in saltmarsh. *Marine Ecology Progress Series*, *487*, 113-122. 236

2.5 Mazumder D., **Saintilan N.** and Williams R. 2005. Temporal variation in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. *Wetlands Ecology and Management.* 13(4) 457-467 246

2.6 Mazumder, D., **Saintilan, N.,** Williams, R. J., & Szymczak, R. (2011). Trophic Importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. *Marine and Freshwater Research*, *62*(1), 11-19. 257

2.7 Mazumder, D., & **Saintilan, N.** (2010). Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. *Wetlands*, *30*, 375-380. 266

2.8 Mazumder D, **Neil Saintilan,** Yusoff, Fatimah M. & Kelleway, J. J. 2019, 'Equivalence of trophic structure between a tropical and temperate mangrove ecosystem in the Indo-Pacific', Marine and Freshwater Research, vol. 70, no. 10, pp. 1436–1444, doi:10.1071/MF18072 272

2.9 **Saintilan, N**., & Mazumder, D. (2017). Mass spawning of crabs: ecological implications in subtropical Australia. *Hydrobiologia*, *803*(1), 239-250. 281

2.10 **Saintilan N.** Hossain K., and Mazumder D. (2007). Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. *Wetlands Ecology and Management* 15 (4) 277-286. 293

2.11 Mazumder, D., **Saintilan, N.,** Alderson, B. & Hollins, S. 2015, 'Inputs of anthropogenic nitrogen influence isotopic composition and trophic structure in SE Australian estuaries', Marine Pollution Bulletin, vol. 100, no. 1, pp. 217-223 303

2.12 Kelleway, J.J., Cavanaugh, K., Rogers, K., Feller, I.C., Ens, E., Doughty, C. & **Saintilan, N.** 2017, 'Review of the ecosystem service implications of mangrove

encroachment into salt marshes', Global Change Biology, vol. 23, no. 10, pp. 3967-3983 310

CHAPTER 3: RESPONSE OF MANGROVES AND SALTMARSHES TO SEA LEVEL RISE 327

3.1 **Saintilan, N**., Khan, N. S., Ashe, E., Kelleway, J.J., Rogers, K., Woodroffe, C. D., & Horton, B. P. (2020). Thresholds of mangrove survival under rapid sea level rise. *Science*, *368*(6495), 1118-1121. 328

3.2 Woodroffe, C.D., Rogers, K., McKee, K.L., Lovelock, C.E., Mendelssohn, I.A. & **Saintilan, N.** 2016, 'Mangrove Sedimentation and Response to Relative Sea-Level Rise', Annual Review of Marine Science, vol. 8, pp. 243-266 332

3.3 Rogers, K., & **Saintilan, N.** (2008). Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *Journal of Coastal Research*, (24), 63-69. 358

3.4 Rogers K., **Saintilan N.** and Wilton K. 2006. Vegetation change and surface elevation dynamics of the estuarine wetlands of southeast Australia. *Estuarine Coastal and Shelf Science*. 66. 559-569 366

3.5 Rogers K., **Saintilan N.** and Heijnis H. 2005.Mangrove encroachment of saltmarsh in Westernport Bay; the role of sedimentation, subsidence and sea-level rise. *Estuaries*. 28(4)-551-559 377

3.6 Rogers, K., **Saintilan, N.** & Woodroffe, C.D. 2014, 'Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: Implications for coastal wetland response to climate change', Estuarine, Coastal and Shelf Science, vol. 149, pp. 46-56 386

3.7 Rogers, K., Zawadzki, A., Mogensen, L. A., & **Saintilan, N.** (2022). Coastal wetland surface elevation change is dynamically related to accommodation space and influenced by sedimentation and sea-level rise over decadal timescales. *Frontiers in Marine Science*. 397

3.8 **Saintilan, N.,** Sun, Y., Lovelock, C. E., Rogers, K., Goddard, M., Hutley, L. B., ... & Jones, A. (2023). Vertical Accretion Trends in Australian Tidal Wetlands. *Estuaries and Coasts*, 1-14. 417

3.9 Lovelock, C.E., Cahoon, D.R., Friess, D.A., Guntenspergen, G.R., Krauss, K.W., Reef, R., Rogers, K., Saunders, M.L., Sidik, F., Swales, A., **Saintilan, N**., Thuyen, L.X. & Triet, T. 2015, 'The vulnerability of Indo-Pacific mangrove forests to sea-level rise', *Nature*, vol. 526, no. 7574, pp. 559-563 431

3.10 Rogers, K., & **Saintilan, N.** (2021). Processes Influencing Autocompaction Modulate Coastal Wetland Surface Elevation Adjustment with Sea-Level Rise. *Frontiers in Marine Science*, 879. 445

3.11 Sun, Y., Rogers, K., Lal, K. K., & **Saintilan, N.** (2024). Living root contributions dominate vertical accretion, but not carbon burial, in two SE Australian tidal wetlands. *Estuarine, Coastal and Shelf Science*, 108776 474

3.12 **Saintilan N**. Kovalenko K. Guntenspergen G. Rogers K, et al (2022). Constraints on the response of tidal marshes to accelerating sea-level rise. *Science* 377.6605 523-527 484

CHAPTER 4: BLUE CARBON AND SEA LEVEL RISE

4.1 **Saintilan N**. 1997. Above and Below-ground Biomass of two species of Mangrove on the Hawkesbury River Estuary, New South Wales. *Marine and Freshwater Research.* 45 (1) 147-52 489

4.2 **Saintilan N.** 1997. Above and Below-ground Biomass of Mangroves in a Sub-tropical estuary. *Marine and Freshwater Research* 48 601-604. 490

4.3 Lamont, K., **Saintilan, N.,** Kelleway, J.J., Mazumder, D., & Zawadzki, A. (2020). Thirty-year repeat measures of mangrove above-and below-ground biomass reveals unexpectedly high carbon sequestration. *Ecosystems*, *23*(2), 370-382. 497

4.4 **Saintilan N.,** Rogers K., Mazumder D. and Woodroffe C.D., (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands *Estuarine Coastal and Shelf Science*. 128 84-92 502

4.5 Kelleway, J.J., **Saintilan, N**., Macreadie, P.I., Baldock, J.A., Heijnis, H., Zawadzki, A., Gadd, P., Jacobsen, G. & Ralph, P.J. 2017, 'Geochemical analyses reveal the importance of environmental history for blue carbon sequestration', Journal of Geophysical Research:Biogeosciences, vol. 122, no. 7, pp. 1789-1805 515

4.6 Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I., Baldock, J.A. & Ralph, P.J. 2017, 'Sediment and carbon deposition vary among vegetation assemblages in a coastal salt marsh', Biogeosciences, vol. 14, no. 16, pp. 3763-3779 524

4.7 Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I. & Ralph, P.J. 2016, 'Sedimentary Factors are Key Predictors of Carbon Storage in SE Australian Saltmarshes', Ecosystems, vol. 19, no. 5, pp. 865-880 541

4.8 Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I., Skilbeck, C.G., Zawadzki, A. & Ralph, P.J. 2016, 'Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes', Global Change Biology, vol. 22, no. 3, pp. 1097-1109 567

4.9 Rogers K., **Saintilan N.,** Mazumder D. & Kelleway, J.J. 2019, 'Mangrove dynamics and blue carbon sequestration', Biology Letters, vol. 15, no. 3, pp. 1–5, doi:10.1098/rsbl.2018.0471 583

4.10 Rogers, K., Kelleway, J. J., **Saintilan, N**., Megonigal, J. P., Adams, J. B., Holmquist, J. R., ... & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature*, *567*(7746), 91-95. 596

4.11 **Saintilan, N.,** Kelleway, J., & Rogers, K. (2021). Australian mangroves through the Holocene: interactions between sea level, mangrove extent, and carbon sequestration. In *Dynamic Sedimentary Environments of Mangrove Coasts* (pp. 217-234). Elsevier. 601

4.12 Karita Negandhi, Grant Edwards, Kelleway, Jeffrey J., Dean Howard, David Safari & **Neil Saintilan** 2019, 'Blue carbon potential of coastal wetland restoration varies with inundation and rainfall', Scientific Reports, vol. 9, no. 1, pp. 1–9, doi:10.1038/s41598-019-40763-8 617

CHAPTER 5: MODELLING, MONITORING AND MANAGEMENT 645

5.1 **Saintilan N.** and Rogers K. (2013). The significance and vulnerability of Australian saltmarshes: implications for management in a changing climate. *Marine and Freshwater Research* 64 66-79 646

5.2 **Saintilan N.,** Horton B., Tornqvist T., Perry C., Schuerch M., Kopp P., Garner G., Ashe A. Rogers K., Albert S., Kelleway J., Shaw T., Khan N, Woodroffe C. (2023). Widespread retreat of coastal habitat likely at warming levels above 1.5˚C**.** *Nature* 621 (7977) 112-119. 660

5.3 Sandi, S. G., Rodriguez, J. F., Saco, P. M., **N. Saintilan** & G. Riccardi 2021, 'Accelerated sea-level rise limits vegetation capacity to sequester soil carbon in coastal wetlands: a study case in southeastern Australia', Earth's Future, vol. 9, no. 9, pp. 1–24, doi:10.1029/2020EF001901 681

5.4 Rogers, K., Kelleway, J. J., & **Saintilan, N.** (2023). The present, past and future of blue carbon. *Cambridge Prisms: Coastal Futures*, *1*, e30. 705

5.5 **Saintilan, N**., Asbridge, E., Lucas, R., Rogers, K., Wen, L., Powell, M., & Lymburner, L. (2021). Australian forested wetlands under climate change: collapse or proliferation? *Marine and Freshwater Research*. 73 (10), 1255-1262 723

5.6 **Saintilan N**, Lymburner L., Wen L., Haigh I., Ai E., Kelleway J.J, Rogers K., Pham D., Lucas R. The lunar nodal cycle controls mangrove canopy cover on the Australian continent. *Science Advances 8*(37), eabo6602. 731

5.7 Rogers, K., **Saintilan, N.,** & Copeland, C. (2014). Managed retreat of saline coastal wetlands: challenges and opportunities identified from the Hunter River Estuary, Australia. *Estuaries and coasts*, *37*, 67-78. 742

5.8 Rijal, S. S., Pham, T. D., Noer'Aulia, S., Putera, M. I., & **Saintilan, N.** (2023). Mapping Mangrove Above-Ground Carbon Using Multi-Source Remote Sensing Data and Machine Learning Approach in Loh Buaya, Komodo National Park, Indonesia. *Forests*, *14*(1), 94. 754

5.9 Kelleway, J.J., Mazumder, D., Baldock, J.A. & **Saintilan, N.** 2018, 'Carbon isotope fractionation in the mangrove Avicennia marina has implications for food web and blue carbon research', Estuarine, Coastal and Shelf Science, vol. 205, pp. 68-74 774

5.10 **Saintilan, N**., Rogers, K., Kelleway, J.J., Ens, E., & Sloane, D. R. (2019). Climate change impacts on the coastal wetlands of Australia. *Wetlands*, *39*(6), 1145-1154 781

5.11 Rogers, K., Boon, P.I., Branigan, S., Duke, N.C., Field, C.D., Fitzsimons, J.A., Kirkman, H., Mackenzie, J.R. & **Saintilan, N.** 2016, 'The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services', Marine Policy, vol. 72, pp. 139-155 791

5.12 K. Rogers, Macreadie, P. I., Kelleway, J. J. & **N. Saintilan** 2019, 'Blue carbon in coastal landscapes: a spatial framework for assessment of stocks and additionality', Sustainability Science, vol. 14, no. 2, pp. 453–467, doi:10.1007/s11625-018-0575-0 808

STATEMENT

This thesis, "Australian Tidal Wetlands and their response to sea-level rise" is submitted in accordance with the University of Sydney (Higher Degree by Research) Rules 2011 (as amended 13 December 2017), Part 5 Higher Doctorates. I declare that I have been the author or co-author of each of the publications in the thesis. My role in each publication is described in the following section. None of the publications have been previously submitted by me for a degree of The University of Sydney or any other university or institution. All the work is original.

The 60 papers presented in this thesis represent my contribution to coastal wetland science, one of the major themes of my research contribution as an aquatic scientist specialising in wetlands. The work consists of five chapters each of twelve papers across multiple disciplines, spanning biogeography, geomorphology, trophic ecology and environmental management, published since graduating from the University of Sydney in 1996.

Most papers in the thesis have multiple authors, reflecting the common practice of the discipline and my role in the mentoring of young scientists. As the following attribution of roles makes clear, in cases where I am not the lead, first-listed author, this place is usually taken by a junior academic working or having worked under my direct supervision, either as a higher degree research student or postdoctoral fellow, in which case I am listed as the second author or the final author, the latter indicates the program lead.

CANDIDATE'S ROLE IN THESIS PUBLICATIONS

The following table details my role in relation to the conceptualisation, conduct and writing of the publications submitted for application. In the citations, my former higher degree research students and postdoctoral fellows are underlined.

Work	CITATION	CANDIDATES ROLE
1.1	Rogers, K., Boon, P., Lovelock, C. E., & **Saintilan, N.** (2017). Coastal halophytic vegetation. *Australian vegetation, 3rd edn. Cambridge University Press, Cambridge*, 544-569.	The paper was conceived by former PhD student and postdoctoral fellow and (now) Professor Kerrylee Rogers, building on my earlier work in 1.2. I contributed substantially to manuscript preparation.
1.2	**Saintilan N.** (2009). Biogeography of Australian Saltmarsh Plants. *Austral Ecology* 34, 929-937	I was sole author
1.3	**Saintilan N.** and Williams R. 1999. Mangrove transgression into saltmarsh environments in New South Wales, Australia. *Global Ecology and Biogeography* 8 117-124.	I conceived the study, assembled most of the data, and wrote the draft manuscript
1.4	**Saintilan N.** and Williams R. 2000. The decline of saltmarsh in eastern Australia *Wetlands (Australia)* 18(2) 49-54.	I conceived the study, assembled most of the data, and drafted the manuscript.
1.5	**Saintilan N.,** and Hashimoto R. 1999. Mangrove-saltmarsh dynamics on a prograding bayhead delta in the Hawkesbury River estuary, New South Wales, Australia. *Hydrobiologia* 413: 95-102.	I conceived the study, led the field campaign, and drafted the manuscript. Hashimoto completed the stratigraphic analysis
1.6	**Saintilan N.** and Wilton K. 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. *Wetland Ecology and Management* 9: 409-420.	A conceived the study, led the data analysis and drafted the manuscript, supported by PhD student Kylee Wilton.
1.7	Wilson, N. C. & **Saintilan N.** 2018, 'Reproduction of the mangrove species Rhizophora stylosa Griff. At its southern latitudinal limit', Aquatic Botany, vol. 151, pp. 30–37	I conceived the study, led field campaigns and made substantial contributions to the writing by PhD student Nicholas Wilson.

1.8	Wilson N.C. and **Saintilan N.** (2012) Growth of the mangrove species Rhizophora stylosa Griff. at it's southern limit in eastern Australia. *Aquatic Botany* 101 8-17	I conceived the study, led field campaigns and made substantial contributions to the writing by PhD student Nicholas Wilson
1.9	**Saintilan N**., Rogers K. and McKee K. (2009) Saltmarsh-Mangrove interactions in Australasia and the Americas. Chapter 31 in Perillo G.M.E., Wolanski E., Cahoon D.R and Brinson M.M. (eds.) *Coastal Wetlands; an integrated ecosystems approach.* Elsevier pp. 855-883.	I conceived the study and led the writing of this review manuscript.
1.10	**Saintilan, N.,** Rogers, K., & McKee, K. L. (2019). The shifting saltmarsh-mangrove ecotone in Australasia and the Americas. In *Coastal wetlands* (pp. 915-945). Elsevier.	I conceived the study and led the writing of this review manuscript.
1.11	**Saintilan N.,** Rogers K, Wilson N., Rajkaran R. and Krauss K. (2014). Mangrove expansion and saltmarsh decline at mangrove pole-ward limits. *Global Change Biology* 20 147-157	I conceived the project, drawing on data held by colleagues in Australia (Wilson, Rogers), the USA (Krauss), and Africa (Rajkaran). I prepared the manuscript.
1.12	**Saintilan, N**., & Rogers, K. (2015). Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. *New Phytologist*, *205*(3), 1062-1070	I conceived the idea after noticing intriguing parallels between dynamics I had observed in coastal and inland wetlands. I prepared the manuscript with input from Kerrylee Rogers.
2.1	**Saintilan N.,** (2004). Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine Coastal and Shelf Science* 61: 591-601.	I was sole author of this manuscript
2.2	**Saintilan N**., and Wen L. (2012) Environmental predictors of estuarine fish landings along a temperate coastline *Estuarine Coastal and Shelf Science* 113 221-230	This paper provides additional analysis to work 2.1 by incorporating environmental variables including river discharge. Statistical input was provided by Dr Li Wen. I prepared the manuscript.
2.3	**Saintilan N**. and Mazumder D., (2010). Fine scale variability in the	I conceived the project, designed the methods and drafted the manuscript. Field

	dietary sources of grazing invertebrates in a temperate Australian Saltmarsh. *Marine and Freshwater Research*.61 615-620	data collection was led by (then) postdoctoral fellow Debashish Mazumder.
2.4	Alderson, B., Mazumder, D., **Saintilan, N.,** Zimmerman, K., & Mulry, P. (2013). Application of isotope mixing models to discriminate dietary sources over small-scale patches in saltmarsh. *Marine Ecology Progress Series*, *487*, 113-122	I previously developed the methodological approach to this paper as work 2.3. This was subsequently applied in Brisbane Waters by my PhD student Brendan Alderson. I contributed substantially to manuscript preparation.
2.5	Mazumder D., **Saintilan N.** and Williams R. 2005. Temporal variation in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. *Wetlands Ecology and Management.* 13(4) 457-467	I conceived the study including the field methods and experimental design, assisted with the data analysis and made substantial contributions to the writing of the manuscript, led by PhD student Debashish Mazumder.
2.6	Mazumder, D., **Saintilan, N.,** Williams, R. J., & Szymczak, R. (2011). Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. *Marine and Freshwater Research*, *62*(1), 11-19	I proposed the idea of using stable isotopes to better understand trophic interactions in the Towra wetland, and worked with (then) postdoctoral fellow Debashish Mazumder to design and implement the project. I contributed substantially to the preparation of the manuscript.
2.7	Mazumder, D., & **Saintilan, N.** (2010). Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. *Wetlands*, *30*, 375-380	I conceived the study and drafted this paper. Analysis was performed by Debashish Mazumder while under my supervision as postdoctoral fellow.
2.8	Mazumder D, **Neil Saintilan,** Yusoff, Fatimah M. & Kelleway, J. J. 2019, 'Equivalence of trophic structure between a tropical and temperate mangrove ecosystem in the Indo-Pacific', Marine and Freshwater Research, vol. 70, no. 10, pp. 1436–1444	This work extends the insights of works 2.5 and 2.6 to a comparison with mangrove ecosystem structure in Malaysia. I drafted the manuscript.
2.9	**Saintilan, N**., & Mazumder, D. (2017). Mass spawning of crabs: ecological implications in subtropical Australia. *Hydrobiologia*, *803*(1), 239-250	The work provides a synthesis of insights developed in 2.6 and studies subsequently inspired by this pioneering work. The paper was conceived by me and I drafted the manuscript.

2.10	**Saintilan N.** Hossain K., and Mazumder D. (2007). Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. *Wetlands Ecology and Management* 15 (4) 277-286	I conceived the project as a synthesis of data emerging from the theses of higher degree research students Kamal Hossain and Debashish Mazumder. I conducted the data analysis and wrote the manuscript.
2.11	Mazumder, D., **Saintilan, N.,** Alderson, B. & Hollins, S. 2015, 'Inputs of anthropogenic nitrogen influence isotopic composition and trophic structure in SE Australian estuaries', Marine Pollution Bulletin, vol. 100, no. 1, pp. 217-223	The paper was conceived by former PhD student and postdoc Debashish Mazumder. I designed the field program, and drafted the manuscript.
2.12	Kelleway, J.J., Cavanaugh, K., Rogers, K., Feller, I.C., Ens, E., Doughty, C. & **Saintilan, N.** 2017, 'Review of the ecosystem service implications of mangrove encroachment into salt marshes', Global Change Biology, vol. 23, no. 10, pp. 3967-3983	I conceived the project with UCLA-based academic Kyle Cavanaugh, to fill a gap concerning the implications of global shifts in coastal wetland community structure. The paper was prepared my by (then) postdoctoral fellow Jeffrey Kelleway, with my substantial input.
3.1	**Saintilan, N**., Khan, N. S., Ashe, E., Kelleway, J.J., Rogers, K., Woodroffe, C. D., & Horton, B. P. (2020). Thresholds of mangrove survival under rapid sea level rise. *Science*, *368*(6495), 1118-1121.	I conceived the project, and led the data collection and synthesis, with supporting analyses provided by Erica Ashe and Nicole Khan. I wrote the manuscript.
3.2	Woodroffe, C.D., Rogers, K., McKee, K.L., Lovelock, C.E., Mendelssohn, I.A. & **Saintilan, N.** 2016, 'Mangrove Sedimentation and Response to Relative Sea-Level Rise', Annual Review of Marine Science, vol. 8, pp. 243-266	This paper was drafted in a writing workshop led by Colin Woodroffe, with all authors contributing to manuscript development and preparation.
3.3	Rogers, K., & **Saintilan, N**. (2008). Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *Journal of Coastal Research*, (24), 63-69.	I conceived of this project, led the field campaign and contributed substantially to the drafting of the paper with (then) research assistant Kerrylee Rogers..
3.4	Rogers K., **Saintilan N.** and Wilton K. 2006. Vegetation change and surface elevation	This paper conceived by me was prepared in collaboration with (then) PhD students Kylee Wilton and Kerrylee Rogers,

	dynamics of the estuarine wetlands of southeast Australia. *Estuarine Coastal and Shelf Science*. 66. 559-569	providing the first synthesis of the SE Australian Surface Elevation Table network data.
3.5	Rogers K., **Saintilan N.** and Heijnis H. 2005.Mangrove encroachment of saltmarsh in Westernport Bay; the role of sedimentation, subsidence and sea-level rise. *Estuaries*. 28(4)-551-559	I worked with (then) PhD student Kerrylee Rogers to analyse the Westernport Bay Surface Elevation Table data, which we jointly installed. I contributed substantially to manuscript prepration.
3.6	Rogers, K., **Saintilan, N.** & Woodroffe, C.D. 2014, 'Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: Implications for coastal wetland response to climate change', Estuarine, Coastal and Shelf Science, vol. 149, pp. 46-56	This paper provided an analysis of the Tweed River Surface Elevation Table data, a network I established with (then) PhD student Kerrylee Rogers. I contributed substantially to manuscript preparation.
3.7	Rogers, K., Zawadzki, A., Mogensen, L. A., & **Saintilan, N.** (2022). Coastal wetland surface elevation change is dynamically related to accommodation space and influenced by sedimentation and sea-level rise over decadal timescales. *Frontiers in Marine Science*	The paper is derived from a program of surface elevation monitoring I established 20 years prior. I contributed substantially to the field programs and manuscript preparation.
3.8	**Saintilan, N.,** Sun, Y., Lovelock, C. E., Rogers, K., Goddard, M., Hutley, L. B., ... & Jones, A. (2023). Vertical Accretion Trends in Australian Tidal Wetlands. *Estuaries and Coasts*, 1-14.	In this paper I collated the Australian Surface Elevation Table dataset, drawing data contributions from across the continent. I conducted the analysis and prepared the manuscript.
3.9	Lovelock, C.E., Cahoon, D.R., Friess, D.A., Guntenspergen, G.R., Krauss, K.W., Reef, R., Rogers, K., Saunders, M.L., Sidik, F., Swales, A., **Saintilan, N**., Thuyen, L.X. & Triet, T. 2015, 'The vulnerability of Indo-Pacific mangrove forests to sea-level rise', *Nature*, vol. 526, no. 7574, pp. 559-563	This paper was the first regional synthesis of mangrove Surface Elevation Table data. I contributed more than half of the data used in the analysis, assisted with the analysis during the writing workshop, and contributed to the preparation of the manuscript.
3.10	Rogers, K., & **Saintilan, N.** (2021). Processes Influencing	The paper is derived from a program of surface elevation monitoring I established

	Autocompaction Modulate Coastal Wetland Surface Elevation Adjustment with Sea-Level Rise. *Frontiers in Marine Science*, 879.	20 years prior. I contributed substantially to the field programs and manuscript preparation
3.11	Sun, Y., Rogers, K., Lal, K. K., & **Saintilan, N.** (2024). Living root contributions dominate vertical accretion, but not carbon burial, in two SE Australian tidal wetlands. *Estuarine, Coastal and Shelf Science*, 108776	I conceived the project, led the field campaign and drafted the manuscript assisted by higher degree research student Yujie Sun.
3.12	**Saintilan N**. Kovalenko K. Guntenspergen G. Rogers K, et al (2022). Constraints on the response of tidal marshes to accelerating sea-level rise. *Science* 377.6605 523-527	The first global synthesis of the Surface Elevation Table dataset from tidal marshes. I conceived the project, collated the dataset and drafted the manuscript. Katya Kovalenko conducted most of the data analysis.
4.1	**Saintilan N**. 1997. Above and Below-ground Biomass of two species of Mangrove on the Hawkesbury River Estuary, New South Wales. *Marine and Freshwater Research.* 45 (1) 147-52	I was sole author of the manuscript
4.2	**Saintilan N.** 1997. Above and Below-ground Biomass of Mangroves in a Sub-tropical estuary. *Marine and Freshwater Research* 48 601-604.	I was sole author of the manuscript
4.3	Lamont, K., **Saintilan, N.,** Kelleway, J.J., Mazumder, D., & Zawadzki, A. (2020). Thirty-year repeat measures of mangrove above-and below-ground biomass reveals unexpectedly high carbon sequestration. *Ecosystems*, *23*(2), 370-382	I conceived the project, which used my PhD data as a benchmark against which to assess biomass accumulation over time. I developed the methods, led the field campaign, supervised the data analysis, and drafted the paper with the assistance of higher degree research student Karen Lamont.
4.4	**Saintilan N.,** Rogers K., Mazumder D. and Woodroffe C.D., (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands *Estuarine Coastal and Shelf Science*. 128 84-92	I conceived the project inspired by a meeting of the International Blue Carbon Scientific Working Group. I led the collation of data, analysis and drafted the manuscript.

4.5	Kelleway, J.J., **Saintilan, N**., Macreadie, P.I., Baldock, J.A., Heijnis, H., Zawadzki, A., Gadd, P., Jacobsen, G. & Ralph, P.J. 2017, 'Geochemical analyses reveal the importance of environmental history for blue carbon sequestration', Journal of Geophysical Research:Biogeosciences, vol. 122, no. 7, pp. 1789-1805	This project was led by my (then) postdoctoral fellow Jeffrey Kelleway, based on his PhD research which I supervised. I contributed substantially to the design of the project and drafting of the manuscript.
4.6	Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I., Baldock, J.A. & Ralph, P.J. 2017, 'Sediment and carbon deposition vary among vegetation assemblages in a coastal salt marsh', Biogeosciences, vol. 14, no. 16, pp. 3763-3779	This project was led by my (then) postdoctoral fellow Jeffrey Kelleway, based on his PhD research which I supervised. I contributed substantially to the design of the project and drafting of the manuscript
4.7	Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I. & Ralph, P.J. 2016, 'Sedimentary Factors are Key Predictors of Carbon Storage in SE Australian Saltmarshes', Ecosystems, vol. 19, no. 5, pp. 865-880	As above, this project was led by my (then) postdoctoral fellow Jeffrey Kelleway, based on his PhD research which I supervised. I contributed substantially to the design of the project and drafting of the manuscript
4.8	Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I., Skilbeck, C.G., Zawadzki, A. & Ralph, P.J. 2016, 'Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes', Global Change Biology, vol. 22, no. 3, pp. 1097-1109	As above, this project was led by my (then) postdoctoral fellow Jeffrey Kelleway, based on his PhD research which I supervised. I contributed substantially to the design of the project and drafting of the manuscript
4.9	Rogers K., **Saintilan N.,** Mazumder D. & Kelleway, J.J. 2019, 'Mangrove dynamics and blue carbon sequestration', Biology Letters, vol. 15, no. 3, pp. 1–5	The paper presents data from the Homebush Bay Surface Elevation Tables, which I established. I led field campaigns and contributed substantially to manuscript preparation.
4.10	Rogers, K., Kelleway, J. J., **Saintilan, N**., Megonigal, J. P., Adams, J. B., Holmquist, J. R., ... & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level	I contributed several of the key insights of this paper, in particular the idea that wetland organic carbon might reflect paleo sea level conditions. I co-drafted the manuscript with (now) Professor Kerrylee Rogers, and my (then) postdoctoral fellow Jeffrey Kelleway.

	rise. *Nature*, *567*(7746), 91-95	
4.11	**Saintilan, N.,** Kelleway, J.J, & Rogers, K. (2021). Australian mangroves through the Holocene: interactions between sea level, mangrove extent, and carbon sequestration. In *Dynamic Sedimentary Environments of Mangrove Coasts* (pp. 217-234). Elsevier	I conceived the paper and drafted the manuscript with input from Dr Kelleway and Professor Rogers.
4.12	Karita Negandhi, Grant Edwards, Kelleway, Jeffrey J., Dean Howard, David Safari & **Neil Saintilan** 2019, 'Blue carbon potential of coastal wetland restoration varies with inundation and rainfall', Scientific Reports, vol. 9, no. 1, pp. 1–9	I conceived the project, based around a novel eddy covariance experiment which I established in the Hunter estuary. Karita Negandhi and the late Grant Edwards led the data collection and analysis, and I prepared the manuscript for publication.
5.1	**Saintilan N.** and Rogers K. (2013). The significance and vulnerability of Australian saltmarshes: implications for management in a changing climate. *Marine and Freshwater Research* 64 66-79	I conceived the paper and drafted the manuscript with the assistance of former PhD student and postdoctoral fellow and (now) Professor Kerrylee Rogers.
5.2	**Saintilan N.,** Horton B., Tornqvist T., Perry C., Schuerch M., Kopp P., Garner G., Ashe A. Rogers K., Albert S., Kelleway J., Shaw T., Khan N, Woodroffe C. (2023). Widespread retreat of coastal habitat likely at warming levels above 1.5˚C**.** *Nature* 621 (7977) 112-119.	I conceived the manuscript and drafted the paper. Modelling input was provided by Mark Schuerch, Erica Ashe, Greg Garner and Nicole Khan.
5.3	Sandi, S. G., Rodriguez, J. F., Saco, P. M., **N. Saintilan** & G. Riccardi 2021, 'Accelerated sea-level rise limits vegetation capacity to sequester soil carbon in coastal wetlands: a study case in southeastern Australia', Earth's Future, vol. 9, no. 9, pp. 1–24,	The study utilises data from my Surface Elevation Table network in the Hunter River estuary. Modelling was conducted by Steven Sandi, Jose Rodruiguez and Patricia Saco. I contributed substantially to the preparation of the manuscript.
5.4	Rogers, K., Kelleway, J. J., & **Saintilan, N.** (2023). The present, past and future of blue carbon. *Cambridge Prisms: Coastal Futures*, *1*, e30	The paper further developed insights presented in works 3.1 and 4.11. I contributed substantially to the preparation of the manuscript.

5.5	**Saintilan, N**., Asbridge, E., Lucas, R., Rogers, K., Wen, L., Powell, M., & Lymburner, L. (2021). Australian forested wetlands under climate change: collapse or proliferation? *Marine and Freshwater Research*. 73 (10), 1255-1262	I conceived the project, collated the data and drafted the manuscript.
5.6	**Saintilan N**, Lymburner L., Wen L., Haigh I., Ai E., Kelleway J.J, Rogers K., Pham D., Lucas R. The lunar nodal cycle controls mangrove canopy cover on the Australian continent. *Science Advances 8*(37), eabo6602	I conceived the paper, led the data analysis with the assistance of Li Wen, and drafted the manuscript. Data were provided by Geosciences Australia (Leo Lymburner, Emma Ai) and Ivan Haigh.
5.7	Rogers, K., **Saintilan, N.,** & Copeland, C. (2014). Managed retreat of saline coastal wetlands: challenges and opportunities identified from the Hunter River Estuary, Australia. *Estuaries and coasts*, *37*, 67-78.	This paper is based on surface elevation table data from a network I established in the Hunter estuary with former student (and now Professor) Kerrylee Rogers, who led the analysis and modelling. I substantially contributed to manuscript preparation.
5.8	Rijal, S. S., Pham, T. D., Noer'Aulia, S., Putera, M. I., & **Saintilan, N.** (2023). Mapping Mangrove Above-Ground Carbon Using Multi-Source Remote Sensing Data and Machine Learning Approach in Loh Buaya, Komodo National Park, Indonesia. *Forests*, *14*(1), 94	I contributed substantially to the writing of this manuscript, supported by current postdoctoral fellow Tien Dat Pham. Data collection and preparation was led by Indonesian colleague S.S. Rijal.
5.9	Kelleway, J.J., Mazumder, D., Baldock, J.A. & **Saintilan, N.** 2018, 'Carbon isotope fractionation in the mangrove Avicennia marina has implications for food web and blue carbon research', Estuarine, Coastal and Shelf Science, vol. 205, pp. 68-74	This paper was conceived while Kelleway was my postdoctoral fellow, and further develops observations first recorded in work 4.4
5.10	**Saintilan, N**., Rogers, K., Kelleway, J.J., Ens, E., & Sloane, D. R. (2019). Climate change impacts on the coastal wetlands of Australia. *Wetlands*, *39*(6), 1145-1154	I conceived the study and drafted the manuscript, supported by PhD student Sloane, postdoctoral fellow Kelleway and former postdoctoral fellow Rogers
5.11	Rogers, K., Boon, P.I., Branigan,	I made substantial contributions to the

	S., Duke, N.C., Field, C.D., Fitzsimons, J.A., Kirkman, H., Mackenzie, J.R. & **Saintilan, N.** 2016, 'The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services', Marine Policy, vol. 72, pp. 139-155	drafting of the manuscript including figures, in this paper led by former PhD student and postdoctoral fellow (now Professor) Kerrylee Rogers.
5.12	K. Rogers, Macreadie, P. I., Kelleway, J. J. & **N. Saintilan** 2019, 'Blue carbon in coastal landscapes: a spatial framework for assessment of stocks and additionality', Sustainability Science, vol. 14, no. 2, pp. 453–467	I made substantial contributions to the drafting of the manuscript in this paper led by former PhD student and postdoctoral fellow (now Professor) Kerrylee Rogers.

DESCRIPTION OF THE THEMES OF THE PUBLISHED WORK

The thesis is grouped into five chapters, each containing twelve published papers. For each publication, I provide below a paragraph explaining how the paper has provided a unique contribution to knowledge in the field of research. I also highlight where a study has contributed to a change in research direction within the field, or policy and management practice.

Measures of impact in the field of research are generally in the form of citations in peer-reviewed literature, and the impact factor of the journal within which the paper is published. For this purpose I use Google Scholar citation metrics as of June 2024. I also indicate if a paper is within the top 1% of cited papers for the field of research over the previous year (so designed by Web of Science as a "highly cited paper"), or when the paper is within the top 0.1% of papers within the discipline field over the previous two months (a Web of Science "hot paper"). For a small group of high-profile papers Altmetric scores are provided, as a measure of their broader media impact.

Chapter 1: Habitat Dynamics in Mangrove and Saltmarsh Ecosystems

Chapter 1 ***Habitat Dynamics in Mangrove and Saltmarsh Ecosystems*** begins with a consideration of recent changes in the distribution of mangrove and saltmarsh, initially in Australia but then extending to multiple continents. The work includes the first treatment of biogeographic patterns in Australian saltmarsh, and the first demonstration of regional-scale mangrove encroachment into saltmarsh. The section finishes with a demonstration of mangrove proliferation and saltmarsh decline across four continents, and the implication of global climate change drivers.

Paper 1.1 opens the thesis by providing a comprehensive overview of the species considered in this thesis and their habitat dependencies. The paper provides an overview of the ecophysiology of the plants of Australian coastal wetlands, the geomorphic settings

within which they are found, and how these are changing as a result of climate change. The Chapter, appearing in the monography "Australian Vegetation" (Keith D. ed) has been cited 11 times since 2017.

Paper 1.2 is the first treatment of the biogeography of Australian saltmarsh plants in the literature. A comprehensive saltmarsh species list was derived from the literature, and the Australian Virtual Herbarium used to determine the distribution in relation to Australian biogeographic regions. Multivariate analysis was used to identify geographic clustering, and analyses explored relationships between diversity, saltmarsh area and latitude. The paper has been cited 79 times since 2009. (*Austral Ecology*; Journal Impact Factor 1.77).

Paper 1.3 was the first paper drawing together evidence that mangrove encroachment into saltmarsh was a regional phenomenon. The study collated independent observations across multiple estuaries, documented the extent of change and presented a series of hypotheses concerning possible causes. The issue has subsequently become an important research topic in Australia and the United States (including papers 1.9, 1.10, 1.11 and 1.12 in this chapter). The paper has been cited 309 times since 1999. (*Global Ecology and Biogeography*; Journal Impact Factor 6.9)

Paper 1.4 follows on the theme of Paper 1.3, providing more detail on individual studies from the published and grey literature documenting changes in the distribution of mangrove and saltmarsh in Australian estuaries. This paper, along with Paper 1.3, were the first to draw attention to the rapid decline in the extent of coastal saltmarsh in eastern Australia, leading eventually to the listing of Coastal Saltmarsh as an Endangered Ecological Community in New South Wales. The paper has been cited 110 times since 2000. (*Wetlands Australia* was a non-ISI journal).

Paper 1.5 places mangrove encroachment into saltmarsh in the Hawkesbury estuary context of mangrove-saltmarsh interactions during the late Holocene. Preserved mangrove root systems beneath saltmarsh were identified at several locations at 0.3 metres depth. These dated to 500-1700 years before present, suggesting the longer-term trend during the

Holocene high-stand has been of mangrove replacement by saltmarsh as the estuary infills. Recent mangrove encroachment in the estuary is therefore a reversal of this trend. The paper has been cited 51 times since 1999. (*Hydrobiologia*: Journal Impact Factor 2.2).

Paper 1.6 considered a case-study of saltmarsh decline in two relatively pristine estuaries on the NSW South Coast. While mangrove encroachment was found to have occurred in both estuaries, significant seaward encroachment of fringing freshwater forests (Melaleuca and Casuarina species) was also found to have occurred, questioning the role of sea-level rise in this estuary. The study highlighted the complex interactions between sea-level and climate phase in determining the nature and extent of vegetation change in coastal wetlands. The paper has been cited 101 times since 2001. (*Wetlands Ecology and Management*; Journal Impact Factor 1.6).

Paper 1.7 is the first of two papers in this chapter examining the expansion of *Rhizophora stylosa* at its southern limit of distribution in northern New South Wales. This paper considered the reproductive phenology and performance over the southern most 265 km of range. Bud emergence and propagule formation did not differ substantially over the range and were comparable to tropical forests. We concluded that there was no evidence of a physiological limit on reproduction at the southern limit of *R. stylosa* in Australia. The paper has been cited 6 times since 2018. (*Aquatic Botany*: Journal Impact Factor 2.47).

Paper 1.8 the paper considers the leaf phenology of *R. stylosa*, complementing Paper 1.7 over the same latitudinal range. A novel leaf and shoot tracking method was developed to monitor relative growth between trees. There was no evidence of a latitudinal cline in growth rate and phenologies of leaf gain and loss were comparable to tropical latitudes. We concluded on the basis of this paper and Paper 1.7 that *R. stylosa* is not close to physiological limits in New South Wales, and that dispersal barriers are likely to explain the southern limit. The paper has been cited 31 times since 2012**.** (*Aquatic Botany*: Journal Impact Factor 2.47).

Paper 1.9 the first global synthesis of changes observed in mangrove and saltmarsh distributions across the globe. The paper places mangrove and saltmarsh dynamics in long-

term context, considering evidence from shifting distributions through the Holocene before turning to evidence of recent changes. Factors limiting mangrove range are reviewed before considering potential drivers of change recently observed. The chapter has been cited 70 times since publication in 2009.

Paper 1.10 updates Paper 1.9 with a decade of research effort between 2009 and 2019. The paper contrasts drivers of habitat change between the United States, where occasional intense frost delimits mangrove expansion, and Australia, where the southern maritime influence effectively removes this threat. In Australia, mangrove and saltmarsh dynamics are more strongly influenced by interactions between sediment delivery and sea-level. The chapter has been cited 36 times since 2019.

Paper 1.11 this paper established that mangrove encroachment into saltmarsh is a global phenomenon, with evidence presented from five continents. Mangrove expansion is documented as a infilling within the latitudinal range of mangroves with a consistent replacement of tidal marsh with mangrove where these two habitat forms coexist in subtropical and temperate locations. The observations are consistent with increases in global atmospheric CO_2, temperature and sea-level rise. A Web of Science "highly cited paper", cited 634 times since 2014. *Global Change Biology*: Journal Impact Factor 10.8)

Paper 1.12 is the first to draw parallels between mangrove encroachment into saltmarsh and woody encroachment of terrestrial grasslands. Both global shifts have occurred in the context of elevated atmospheric CO_2 concentrations, and a model is presented showing this this mechanism could be at work in both locations. In water limited environments, elevated CO_2 allows carbon fixation to occur with less water loss, potentially expanding the range over which plants utilising the C_3 photosynthetic pathway can grow. In both contexts, this expansion occurs at the expense of grasses utilising the C_4 photosynthetic pathway. The paper has been cited 143 times since 2014. (*New Phytologist*: Journal Impact Factor 9.4)

Chapter 2: Trophic Dynamics in Mangrove and Saltmarsh Ecosystems

Prior to the publication of the papers in Chapter 2, little was known of the ecological significance of Australian saltmarshes. The chapter presents the first detailed surveys of fish communities visiting saltmarshes with the spring tide, and the first examination of the dietary contribution to saltmarshes to small fish that form the foundation of estuarine foodchains. The work revealed the central role played by burrowing crustaceans and grazing molluscs in providing high concentrations of larvae, and the unique feeding opportunity available to planktivorous fish during spring tide cycles.

Paper 2.1 provides a predictive understanding of estuarine fish landings in New South Wales. Data on estuarine geomorphic units is sourced from the OzEstuaries database developed by Geosciences Australia, and data on estuarine fish landings provided in annual reports from NSW Fisheries. Using multivariate analyses, assemblages of species are linked to specific habitat variables, most notably the area of mangrove, seagrass and mudflat. The paper has been cited 92 times since 2004. (*Estuarine Coastal and Shelf Science*: Journal Impact Factor 3.23).

Paper 2.2 extends the analysis of paper 2.1 by incorporating time-series of river discharge, as a test of the hypothesis that environmental flows are an important control over estuarine biota. While riverflow was correlated with the catch of *Platycephalus* and *Mugil* species, there we no further significant relationships. Temperature was a more important predictor of catch, along with the habitat variables identified in Paper 2.1. The paper has been cited 8 times since 2012. (*Estuarine Coastal and Shelf Science*: Journal Impact Factor 3.23).

Paper 2.3 sought to resolve the contribution of saltmarsh plants to estuarine foodwebs by exploring the diet of grazing crabs and snails. The study utilised habitat mosaics of plants utilising the C_3 and C_4 photosynthetic pathways at Towra Point, Sydney (*Sarcocornia quinqueflora/Suaeda australia* and *Sporobolus virginicus* respectively). The study found consistent enrichment in the carbon isotope ratios of invertebrates grazing within *S. virginicus* patches. The paper has been cited 22 times since 2010. (*Marine and Freshwater Research*: Journal Impact Factor 2.26).

Paper 2.4 extended the work of Paper 2.3 by measuring a greater range of potential carbon sources, including microphytobenthos, fine benthic organic matter and saltmarsh plant material, across a similar C3/C4 habitat mosaic in Brisbane Water, New South Wales. The application of a dietary isotope mixing model found microphytobenthos to be a more important dietary source than plant matter, but that microphytobenthos was enriched or depleted corresponding to the dominant macrophytes. This was the first demonstration of leakage of dissolved organic carbon from estuarine macrophytes into microphytobenthic foodchains. The paper has been cited 22 times since 2-13. (*Marine Ecology Progress Series*; Journal Impact Factor 2.5)

Paper 2.5 reported on the first survey of fish populations in tidally flooded saltmarsh in temperate Australia. Buoyant pop nets were used in monthly surveys for 12 months to provide comparable density estimates across mangrove and saltmarsh. While mangrove showed a greater diversity of fish species, saltmarsh had higher densities by volume of water. The paper has been cited 43 times since 2005. (*Wetlands Ecology and Management*; Journal Impact Factor 1.6).

Paper 2.6 sought to resolve an important debate concerning fish utilisation of flooded wetland habitats- whether these were being used for protection from predators or as a feeding opportunity. extended the work of paper 2.5 by determining whether fish were feeding while visiting the saltmarsh. Gut content analysis was used to demonstrate that fish visiting the saltmarsh during the spring tide feed on larvae released from resident crabs and molluscs. This was the first demonstration of this link between saltmarsh and adjacent estuarine fish habitats, and became the model for comparable studies elsewhere in Australia. The paper has been cited 58 times since 2011. (*Marine and Freshwater Research*: Journal Impact Factor 2.26).

Paper 2.7 uses stable isotope mixing models to determine whether mangrove leaves make an important contribution to the diet of grazing crabs in temperate Australian wetlands. Mangrove leaves have high tannin contents and high C/N ratios, making surprising the findings from behavioural studies in tropical latitudes that mangrove leaves are the dominant food source of grazing crabs. Our study refuted this hypothesis as applied to

temperate Australian mangroves. The study has been cited 54 times since 2010. (*Wetlands*: Journal Impact Factor 2.0).

Paper 2.8 compares the trophic structure of mangrove aquatic communities between temperate Australia and tropical Malaysia. While differing substantially in biomass, climate, and biogeographic setting, the two forests show remarkable similarity in the structure of aquatic foodwebs. Common families were represented amongst dominant grazing herbivores, zooplanktivorous fishes, decapod crustaceans and top predators. The findings suggested consistency in trophic interactions despite a degree of evolutionary divergence between the opposite sides of the Indo-Pacific. Cited 5 times since 2019 (*Marine and Freshwater Research*: Journal Impact Factor 2.26).

Paper 2.9 draws together the insights of Papers 2.3, 2.4, 2.5 and 2.6 making the case that the synchronised spawning of crustaceans and molluscs in temperate Australian wetlands on the spring tide is foundational to estuarine foodchains. Crabs utilise the spring tide to maximise larval dispersal, and larval concentrations at these times in the saltmarsh are the highest encountered in the estuary. This unique feeding opportunity is heavily utilised by fish that form the diet of predatory fish important to commercial and recreational fisheries. The paper has been cited 17 times since 2017. (*Hydrobiologia*: Journal Impact Factor 2.5).

Paper 2.10 drew together separate studies conducted at the Towra Point Ramsar site over the same 12-month period, each using common methods to assess fish movements between adjacent seagrass, mangrove and saltmarsh during spring tide cycles. The paper provided firm quantitative evidence that fish moved from the seagrass into the mangrove and saltmarsh during spring tides to take advantage of unique feeding opportunities. The results highlighted the importance of habitat connectivity in wetland restoration and preservation. Cited 58 times since 2007. (*Wetlands Ecology and Management*; Journal Impact Factor 1.6).

Paper 2.11 compared tidal wetland ecosystem structure between relatively pristine and modified estuaries along the New South Wales coast. Carbon and Nitrogen stable isotopes were used to identify whether trophic dependencies were consistent between estuaries, to

identify the influence of anthropogenic Nitrogen, and whether these Nitrogen inputs were influencing food chain length. We found clear evidence of anthropogenic N input. While these had no influence on the sources of dietary carbon utilised by crustaceans and fish, there anthropogenic N was associated with decreases in food chain length. The paper has been cited 26 ties since 2015. (*Marine Pollution Bulletin*; Journal Impact Factor 7.00)

Paper 2.12 draws in the insights of earlier papers in this Chapter and Chapter 1 to deduce possible ecosystem-level implications of mangrove encroachment into saltmarsh. The paper expands the geographic scope of the analysis to continental USA. We conclude that while marsh- to mangrove conversion may enhance carbon sequestration and coastal protection, declines occur in the availability of habitat for several species of waterbird and foraging bats. The paper has been cited 253 times (*Global Change Biology*: Journal Impact Factor 13.2).

Chapter 3: Response of Mangroves and Saltmarshes to Sea Level Rise

Chapter 3 explores key drivers responsible for the changes documented in Chapter 1. The theme highlights the application of the Surface Elevation Table-Marker Horizon (SET-MH) technique in assessing mangrove and saltmarsh responses to sea-level rise. These include site-scale analyses of marsh response to local sea-level and sediment conditions, and regional to global scale assessments of mangrove vulnerability and tidal marsh vulnerability to sea-level rise

Paper 3.1 provides the first global overview of Holocene mangrove response to sea-level rise derived from the paleo record. Observations of peat initiation and development from 79 tropical locations are compared to rates of sea-level rise hindcast from models of glacio-isostatic adjustment. The results suggested that mangrove initiation and sustained vertical adjustment is rare if relative sea-level rise is greater than 7mm per year, and greater than 5mm per year in low sediment settings. The paper featured in an editorial review in *Science* by C.E. Lovelock. A Web of Science “highly cited paper”, with 301 citations since 2020. Altmetric Score 699. (*Science*; Journal Impact Factor 47.7)

Paper 3.2 an invited review written by several of the leading scientists in the field. Detailed consideration is given to bio-geomorphic controls over wetland elevation in relation to sea-level rise, including root morphology and sediment deposition, below-ground productivity, feedbacks with sea-level rise and the influence of other climate drivers. A Web of Science "highly cited paper" with 430 citations since 2016. (*Annual Review of Marine Science*; Journal Impact Factor 17.3).

Paper 3.3 demonstrated the influence of groundwater flux on mangrove surface elevation over a range of timescales. Elevation was monitored using the Surface Elevation Tables at Homebush Bay at regular intervals during the diurnal tide, over fortnightly periods for four months, and annually. The results demonstrated the influence of the tide on surface elevation, and the strong influence of the El Nino Southern Oscillation. The paper has been cited 68 times. (*Journal of Coastal Research*; Journal Impact Factor 1.1).

Paper 3.4 provided the first collation of data from the Southeast Australian network of Surface Elevation Tables. We installed the network in 2000-2002, consisting of 69 installations across 7 estuaries. These were the first in an Australian network now expanded to 289 stations (Paper 3.8). Reporting on the first 4-5 years of the experiment, tidal range was found to be the best predictor of accretion rate. The paper has been cited 222 times since 2006. (*Estuarine Coastal and Shelf Science*: Journal Impact Factor 3.23).

Paper 3.5 utilised the Surface Elevation Table network in Westernport Bay, Victoria to further explore the theme of Paper 3.3. We utilised a phase of the El Nino Southern Oscillation to compare groundwater influences on wetland elevation compared to sea-level rise. The paper found that current rates of sedimentation were consistent with longer-term historic trends determined by ^{210}Pb analysis, and sedimentation rate was inversely related to the rate of mangrove landward encroachment. The paper has been cited 174 times since 2005. (*Estuaries*; Journal Impact Factor 2.3**)**

Paper 3.6 provides an analysis of surface elevation trends in the northernmost estuary in our network of monitoring sites described in Paper 3.4. The paper analyses accretion and elevation 12 years after installation. At this timescale the influence of the El Nino Southern Oscillation is evident at shorter timescales, but the overarching trend of sea-level rise on mangrove encroachment and surface elevation gain become evident. The paper has been cited 80 times since 2014. (*Estuarine Coastal and Shelf Science*: Journal Impact Factor 3.23).

Paper 3.7 the paper drew on two independent datasets to model relationships between accretion rate, elevation gain and accommodation space (the space between the wetland surface and the high-water level). Metre-deep cores were extracted from each of the eight sites in Westernport Bay instrumented with Surface Elevation Tables, and 210Pb chronologies established. These allowed the relationship between elevation gain and accommodation space to be determined, and were consistent across sites and the sedimentary record. These relationships were then used in a predictive model to project wetland dynamics and a range of sea-level rise scenarios. The paper has been cited 5 times since 2022. (*Frontiers in Marine Science*; Journal Impact Factor 2.8).

Paper 3.8 is the first collation of the Australian network of Surface Elevation Tables. Data were compiled from 289 installations, primarily in mangrove forests but extending to saltmarshes and tidal freshwater forests. Mangroves were found to have the highest rates of accretion and elevation gain as might be expected from their lower position within the tidal frame and higher biomass. In common with the global tidal marsh analysis (Paper 3.12), the rate of upper level subsidence was found to be strongly associated with the rate of accretion. Two citations since 2023. (*Estuaries and Coasts*; Journal Impact Factor 2.3).

Paper 3.9 is the first regional synthesis of data from the Surface Elevation Table network, drawing together data on mangrove accretion and elevation gain across the Indo-Pacific region. From these data a model was derived to project mangrove survival across the region. The work highlighted the vulnerability of mangroves to sea-level rise and the risk posed by water resource developments impeding sediment delivery to coastal

environments. A Web of Science “highly cited paper” with 801 citations since 2015. Altmetric Score 316 (*Nature*; Journal Impact Factor 69.5)

Paper 3.10 provides a framework for understanding the relationship between accretion, elevation change and sea-level rise using the high quality data available from the Westernport Bay Surface Elevation Table network and associated stratigraphic data (Paper 3.7). Fundamental changes in soil organic carbon density are associated with changing rates of sea-level rise. The paper also reports on the relationship between accretion rate and the rate of upper level subsidence (or compaction), an idea that we develop further in our analysis of the global tidal marsh Surface Elevation Table network (Paper 3.12). The paper has been cited 13 times since 2021. (*Frontiers in Marine Science*; Journal Impact Factor 2.8).

Paper 3.11 provides a detailed examination of material accumulating above feldspar marker horizons installed in the early 2000’s. Mineral sediment was separated from organic detrital material and living root material across several of the SE Australian sites monitored with Surface Elevation Tables. We found that of all accretion components sampled, living root material made the largest contribution to volume, while detrital organic carbon made a larger contribution to carbon accumulation by mass. 2024 publication yet to be cited. (*Estuarine Coastal and Shelf Science*: Journal Impact Factor 3.23).

Paper 3.12 is the first synthesis of the global Surface Elevation Table network in tidal marshes. Data were collected for 478 monitoring stations distributed along gradients of climate and sea-level history. The analysis demonstrated that while accretion rate (sediment accumulation above an artificial horizon) was keeping pace with sea-level rise, subsidence prevented surface elevation from doing the same. Further, the rate of subsidence increased with the rate of accretion and the rate of sea-level rise, most probably due to the additional weight driving compaction. The paper is a Web of Science “highly cited paper” and “hot paper”, cited 83 times since 2022. Altmetric Score 176. (*Science*; Journal Impact Factor 47.7).

Chapter 4: Blue Carbon and Sea Level Rise

One important mechanism by which mangroves and tidal marshes respond to sea-level rise is through the capture and storage of carbon. Mangrove and tidal marsh are premier "blue carbon" ecosystems, and Chapter 3 ***Blue Carbon and Sea Level Rise*** documents carbon stores within these systems and their response to sea-level rise. Works represented here include the first application of stable isotopes to determine the provenance of tidal wetland carbon, the first global meta-analysis of tidal marsh soil carbon in relation to sea-level history, and the first meta-analysis of mangrove palaeo response sea-level rise, suggesting global-scale atmospheric carbon drawdown.

Paper 4.1 is the first assessment of the influence of environmental controls on above- and below-ground biomass in mangroves. The study demonstrated the importance of salinity as a control over both biomass and biomass partitioning within mangroves, confirming the insights of experiments on seedlings by M.C. Ball. Published long before the current interest in "Blue Carbon", the relevance of this work is receiving new interest as a method for assessment autochthonous carbon stores, and as a benchmark for studies on rates or biomass accumulation (Paper 4.3). The paper has been cited 116 times since 1997. (*Marine and Freshwater Research*: Journal Impact Factor 2.26)

Paper 4.2. Using the techniques developed by me in Paper 4.1, this paper documents mangrove above- and below-ground biomass for the greater range of species encountered in the Mary River, Queensland. The influence of soil water salinity on mangrove biomass and biomass partitioning is demonstrated in common with Paper 4.1. This work has grown in relevance and impact over the 25 years since publication, with half of 62 citations occurring in the past 6 years. (*Marine and Freshwater Research*: Journal Impact Factor 2.26).

Paper 4.3 is to our knowledge the only paper in the literature to provide a long-term repeat measure of mangrove above- and below-ground biomass. Working with Master of Research student Karen Lamont and postdoctoral fellow J.J. Kelleway, we returned to sites sampled by me 30 years previously on the Hawkesbury River (Paper 4.1) and applied the same methods to determine standing and root biomass. We used radiometric techniques (Pb^{210}) to

determine the depth of the prior surface, and estimated new below-ground biomass and carbon accumulation above this horizon. The result returned some of the highest estimates of carbon accumulation in the literature, suggesting other methods used to estimate carbon accumulation may be underestimations. The paper has been cited 38 times since 2020. (*Ecosystems*: Journal Impact Factor 4.35)

Paper 4.4. The idea for this paper came to me during one of the early meetings of the International Blue Carbon Scientific Working Group in 2011. I realised that our network of feldspar horizons associated with the Surface Elevation Tables could be used as a common benchmark to assess rates of carbon accumulation across settings. This study was innovative in two respects (i) it provided the first data on rates of organic carbon accumulation in Australian "Blue Carbon" ecosystems, demonstrating the importance of geomorphic controls, and (ii) the first study to apply stable isotopes to determine the provenance of carbon accumulating in mangrove and saltmarsh, whether allochthonous or autochthonous. The paper demonstrated that these sources can vary with the geomorphic evolution of the site. The paper has been cited 274 times since 2013. (*Estuarine Coastal and Shelf Science*: Journal Impact Factor 3.23)

Paper 4.5 applied ^{13}C nuclear magnetic resonance analysis and stratigraphic analysis to determine the origins of carbon within sediment cores in two New South Wales estuaries. This was important because carbon stores within coastal wetlands are often considered as homogenous, and consistent with contemporary vegetation types. The paper demonstrated that unique geomorphic histories were responsible for down-core carbon, including prior occupation of saltmarsh sites by mangrove, along with phases of char carbon inputs from the catchment. The paper has been cited 53 times since 2017. **(***Journal of Geophysical Research:Biogeosciences*; Journal Impact Factor 3.7)

Paper 4.6 utilised a range of techniques to assess accumulation rates in saltmarsh vegetation communities over different timescales. This innovative combination of techniques was able to identify sedimentation patterns in relation to lunar tide cycles, compare these to long-term rates and determine the contribution of allochthonous carbon to

rates of carbon accumulation. The paper has been cited 61 times since 2017. **(***Biogeosciences*: Journal Impact Factor 5.09)

Paper 4.7 built upon the insights of paper 4.4 but expanded the analysis to 10 cores reporting carbon stores to one metre depth. The study demonstrated that geomorphic setting was a key control over carbon accumulation, with coarse textured marine sediments showing lower organic carbon preservation. The paper has guided thinking about the optimal location of Blue Carbon projects. The paper has been cited 141 times since 2016. (*Ecosystems*: Journal Impact Factor 4.35)

Paper 4.8 used a chrono-sequence of mangrove encroachment of saltmarsh at two sites to determine the time period required to demonstrate an increase in carbon store. This is important for the development of predictive models of carbon flux associated with such vegetation transitions. The space-for-time substitution found that increases in carbon store could only be demonstrated several decades after mangrove establishment. This throws new light on studies from the USA which suggested that mangrove encroachment did not lead to carbon gains, in that insufficient time was allowed to demonstrate this change. The paper has been cited 212 times since 2016. (*Global Change Biology*; Journal Impact Factor 13.1)

Paper 4.9 presented data from the longest-running mangrove Surface Elevation Table experiment in the world, at Homebush Bay. During the period of monitoring, mangrove encroached into the saltmarsh sites, in common with regional and global observations documented in Chapter 1. Rates of carbon accumulation were documented along a transect from mangrove to saltmarsh, and the impact of mangrove encroachment on carbon accumulation documented. The paper has been cited 25 times since 2019. (*Biology Letters*, Journal Impact Factor 3.3)

Paper 4.10 developed through discussions with Kerrylee Rogers about the influence of accommodation space (the space between the wetland surface and the highest tides) on accretion rate and carbon accumulation. We proposed that increases in accommodation resulting from relative sea-level rise might increase the volume and density of organic carbon in wetlands. The model was tested using global observations of wetland carbon

stores in relation to paleo sea-level conditions, and through a meso-scale experiment utilising subsidence beneath a coastal wetland resulting from coal mine abandonment. The paper provided a framework for understanding variability in wetland carbon stores, and proposed that low to moderate rates of sea-level rise can enhance carbon sequestration. A Web of Science "highly cited paper", 358 citations since 2019. Altmetric Score of 616 (*Nature,* Journal Impact Factor 69.5). The work was awarded the Eureka Prize for Environmental Research in 2019.

Paper 4.11 utilised the Surface Elevation Table network in SE Australia to determine processes whereby coastal wetlands responded to sea-level rise. We sampled above feldspar marker horizons laid down in 2000-2002 and determined the volumetric and mass contributions of detrital organic carbon, mineral matter, and living root material. The paper demonstrated the importance of living root material as a control on soil elevation, but the greater importance of detrital organic carbon to carbon accumulation. Published in 2024-yet to be cited (*Estuarine Coastal and Shelf Science*: Journal Impact Factor 3.23)

Paper 4.12 is the first paper to use a BACI (Before-After-Control-Impact) design to test the effect of tidal reinstatement on carbon flux in a coastal wetland. The design incorporated an eddy covariance tower to measure gas flux, while simultaneously measuring water quality depth of inundation, and soil microbial composition. The microbial community changed in response to tidal reinstatement to resemble those encountered in "blue carbon" settings, with a higher representation of sulfur reducing bacteria. However, gas flux was strongly influenced by rainfall conditions, with methane fluxes continuing during high rainfall episodes. The paper has been cited 41 times since 2019 (*Scientific Reports*: Journal Impact Factor 5.0)

Chapter 5: Modelling, Monitoring and Management

The adaptive management of coastal ecosystems under a changing climate requires predictive modelling and a program of monitoring designed to both inform management decisions and refine our understanding of system behaviour. In this chapter the implications of warming scenarios are presented in national and international syntheses. These explore

the implications of climate change and sea-level rise in a range of ecosystem services, with an emerging emphasis on Blue Carbon. Consideration is given to whether current ecosystem shifts and mortality events are consistent with the putative impacts of climate change. Monitoring tools are discussed, highlighting the potential of remote sensing, and landscape-scale modelling. Current policy settings are reviewed in terms of fit-for-purpose, and suggestions made concerning further reforms required to accommodate the dynamism introduced by accelerating climate change drivers.

Paper 5.1 reviews a period of concerted research attention on Australian saltmarshes, hitherto one of the more overlooked ecosystems. The paper explores causes behind the dramatic loss of saltmarsh in southern Australia since the middle of the 20th century, the trophic relay between saltmarshes and estuarine fisheries presented in Chapter 2 of this thesis, and the provision of habitat for migratory birds and threatened species of bats. This body of work, represented in this review, contributed substantially to the decision to list coastal saltmarsh as an endangered ecological community in NSW and as a threatened ecological community south of 23 degrees latitude under the Commonwealth EPBC Act. The paper has been cited 88 times since 2013. (*Marine and Freshwater Research*: Journal Impact Factor 2.26)

Paper 5.2 is the first paper to explore the implications of IPCC temperature limiting scenarios on the survival of mangroves, tidal marshes and coral islands. Utilising adjustment thresholds derived from the paleo record and the Surface Elevation Table observations, the paper maps the vulnerability of coastal ecosystems at a global scale, and demonstrates tipping points if the Paris Agreement targets have been exceeded. The paper was included by the editors of *Nature* in their 12 Research Highlights of 2023. Cited 20 times since 2023, Altmetric score 544. (*Nature*; Journal Impact Factor 69.5)

Paper 5.3 implements an eco-geomorphic model to simulate vegetation dynamics, soil carbon accumulation and changes in soil carbon stock for a restored mangrove-saltmarsh wetland undergoing rapid sea-level rise. The results suggest that under high rates of sea-level rise, losses of biomass at the seaward edge of the wetland are not offset by gains at the

landward edge, due to limited biomass, carbon burial and carbon turn-over in newly created areas. The paper has been cited 10 times since 2021. (*Earth's Future*; Journal Impact Factor 8.2).

Paper 5.4 reviews the potential impacts of sea-level rise on Blue Carbon, using paleo and instrumental observations as a guide. Plant mortality, colonisation, accretion and gas flux characteristics are considered. We argue that antecedent geomorphic history will be important in determining opportunities for adjustment. High intertidal platforms characteristic of far field locations subject to mid-Holocene sea level highstand represent opportunities for colonisation where not impeded by coastal infrastructure. The paper has been cited 2 times since 2023.

Paper 5.5 was written to challenge widely held assumptions concerning dieback events in mangrove and terrestrial wetland forests in Australia. The dieback of the River Redgum *Eucalyptus camaldulensis* in inland Australia and the mangrove mortality event in the Gulf of Carpentaria had been attributed to climate change in review papers. Here we provided original mapping and analysis to demonstrate that climate change is unlikely to have been an important driver of decline in either setting. We demonstrate that *E. camaldulensis* is expanding in the large inland wetlands at the expense of wetland grasslands, and that mangrove expansion into saltmarsh grasslands is also the overarching trend for coastal wetlands. Cited 11 times since 2021. (*Marine and Freshwater Research*: Journal Impact Factor 2.26)

Paper 5.6 The largest reported mangrove dieback event occurred in the Gulf of Carpentaria in 2015-2016, an event hitherto attributed to the El Nino event. This paper provided a highly novel alternative explanation- that the mortality was associated with the coincidence of the El Nino with a phase of the 18.6-year lunar nodal cycle. Evidence is presented that the nodal cycle explains a greater range of observations, including the geographic and geomorphic focus of the dieback. The implication is that climate impacts may be phased in predictable periods of vulnerability and resilience. The paper was widely reported

(Altmetric score=410) and was profiled in Scientific American. The paper has been cited 10 times since 2022. (*Science Advances*, Journal Impact Factor 14.14)

Paper 5.7. The network of Surface Elevation Tables installed in the Hunter River estuary in 2001 provided the basis for the development of accretion models in relation to sea level rise within the estuary. This paper was amongst the first to present a landscape-scale model of vegetation change in relation to sea-level rise as modelled by the IPCC. The paper modelled vegetation change with and without floodgate modification, and estimated the possible carbon sequestration benefits across these two management strategies under different warming scenarios. The work was the first to anticipate the potential of the "Blue Carbon Method" of tidal reinstatement adopted by the Australian Commonwealth government in 2021. The paper has been cited 102 times since 2014. (*Estuaries and Coasts*; Journal Impact Factor 2.3)

Paper 5.8 demonstrated how multiple remote sensing datasets (optical, Synthetic Aperture Radar and Digital Elevation Models) could be combined in extreme gradient boosting and genetic algorithm analyses to predict above-ground biomass in mangroves with a remarkable level of accuracy. The paper has been cited 12 times since 2023. (*Forests*; Journal Impact Factor 2.4).

Paper 5.9 Since the publication of paper 4.4, Carbon isotopes have been commonly used to identify the provenance of organic carbon accumulating in "Blue Carbon" settings. This work develops further an insight originally presented in Paper 4.4, that the isotope ratios of plant parts (leaf, stem, root) may vary on an individual tree. Failure to recognise fractionation at the plant level has led to erroneous attribution of sources, or the conclusion that autochthonous material is contributing little to carbon stores when only leaf isotope ratios are measured. The paper provides guidance to appropriate monitoring design. The paper has been cited 22 times since 2018. (*Estuarine Coastal and Shelf Science*: Journal Impact Factor 3.23)

Paper 5.10 the paper reviews evidence for climate change driving vegetation shifts on the Australian continent, and explores cultural and ecosystem service implications. Evidence is

provided that sea-level rise is causing habitat changes across the continent, leading to mangrove expansion and the decline of saltmarsh and coastal freshwater forests. Importantly, this paper is the first to provide detailed consideration of the implications of *Melaleuca* forest dieback in Northern Australia for indigenous communities. The paper has been cited 97 times since 2019. (*Wetlands*; Journal Impact Factor 2.0).

Paper 5.11 is the first comprehensive assessment of the legislative and policy protections for coastal wetlands in Australia. The paper reviews legislation and policy across all Australian jurisdictions. The emerging threat of climate change requires greater dexterity in policy settings, particularly in relation to the ambulatory nature of vegetation boundaries, and the opportunities represented by tidal reinstatement for emissions reductions. The paper has been cited 122 times since 2016 (*Marine Policy*; Journal Impact Factor 4.31)

Paper 5.12. The paper ustilises the insights of Papers 4.4, 4.5, 4.6 and 4.7 to provide a state-wide framework for the identification of blue carbon priority sites NSW. Innovative use is made of publicly available datasets on coastal sedimentary deposits, geomorphic units and vegetation classes. The paper formed the basis of project selection for the NSW Blue Carbon Strategy 2022, released by the NSW Department of Climate Change, Energy, the Environment and Water, and provides a model for similar frameworks elsewhere. Cited 59 times since 2019. (*Sustainability Science*; Journal Impact Factor 5.1).

ACKNOWLEDGEMENTS

It has been my tremendous good fortune to have encountered colleagues who's creativity, generosity and hard work have enabled me to pursue my own scientific vision. First amongst these is Professor Kerrylee Rogers with whom I established the southeast Australian Surface Elevation Table Network and who has been a constant source of guidance and wisdom for nearly the entirety of my career. Dr Debashish Mazumder has been my partner in all things isotopic, and I am indebted to his support, loyalty, and in opening to my team the wonderful facilities and personnel at ANSTO. Jeffrey Kelleway has worked with me in various iterations as an employee, PhD student and Postdoctoral Fellow, and his superb support over such a long period of time has been instrumental in delivering on many of the programs represented in this thesis.

I am always struck by how willing people working in my field are to share data, insights and encouragement, and it has been a pleasure to work with so many outstanding scientists across the globe. Don Cahoon and Glenn Guntenspergen (US Geological Survey) are thanked for their vision, generosity of spirit and technical know-how. Professor Benjamin Horton and Drs Erica Ashe and Nicole Khan have helped me bring the insights of sea-level studies to mangrove and tidal marsh morphodynamics.

Professor Bruce Thom supervised my honours and PhD research and continues to publish original scientific papers, address conferences and provide policy advice into his ninth decade. Bruce is a wellspring of inspiration to the scientific children and grandchildren who contributed to this thesis.

On a personal note I would like to thank my wife Megan, daughters Phoebe and Chloe, and son Christopher for their steadfast support and love.

Chapter 1: Habitat Dynamics In Mangrove And Saltmarsh Ecosystems

1.1 Rogers, K., Boon, P., Lovelock, C. E., & **Saintilan, N.** (2017). Coastal halophytic vegetation. *Australian vegetation, 3rd edn. Cambridge University Press, Cambridge*, 544-569.

1.2 **Saintilan N.** (2009). Biogeography of Australian Saltmarsh Plants. *Austral Ecology* 34, 929-937

1.3 **Saintilan N.** and Williams R. 1999. Mangrove transgression into saltmarsh environments in New South Wales, Australia. *Global Ecology and Biogeography* 8 117-124.

1.4 **Saintilan N.** and Williams R. 2000. The decline of saltmarsh in eastern Australia *Wetlands (Australia)* 18(2) 49-54.

1.5 **Saintilan N.,** and Hashimoto R. 1999. Mangrove-saltmarsh dynamics on a prograding bayhead delta in the Hawkesbury River estuary, New South Wales, Australia. *Hydrobiologia* 413: 95-102.

1.6 **Saintilan N.** and Wilton K. 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. *Wetland Ecology and Management* 9: 409-420.

1.7 Wilson, N. C. & **Saintilan N.** 2018, 'Reproduction of the mangrove species Rhizophora stylosa Griff. At its southern latitudinal limit', Aquatic Botany, vol. 151, pp. 30–37, doi:10.1016/j.aquabot.2018.07.009

1.8 Wilson N.C. and **Saintilan N.** (2012) Growth of the mangroves species Rhizophora stylosa Griff. at it's southern limit in eastern Australia. *Aquatic Botany* 101 8-17

1.9 **Saintilan N**., Rogers K. and McKee K. (2009) Saltmarsh-Mangrove interactions in Australasia and the Americas. Chapter 31 in Perillo G.M.E., Wolanski E., Cahoon D.R and Brinson M.M. (eds.) *Coastal Wetlands; an integrated ecosystems approach.* Elsevier pp. 855-883.

1.10 **Saintilan, N.,** Rogers, K., & McKee, K. L. (2019). The shifting saltmarsh-mangrove ecotone in Australasia and the Americas. In *Coastal wetlands* (pp. 915-945). Elsevier.

1.11 **Saintilan N.,** Rogers K, Wilson N., Rajkaran R. and Krauss K. (2014). Mangrove expansion and saltmarsh decline at mangrove pole-ward limits. *Global Change Biology* 20 147-157*

1.12 **Saintilan, N**., & Rogers, K. (2015). Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. *New Phytologist*, *205*(3), 1062-1070.

22 Coastal Halophytic Vegetation

KERRYLEE ROGERS, PAUL BOON, CATHERINE LOVELOCK AND NEIL SAINTILAN

Coastal halophytes are plants of the coastal zone that are capable of growing and reproducing under saline conditions. Mostly they occur in areas subject to tidal inundation, though may also occur on headlands where salt spray elevates soil salinity. Mangrove and saltmarsh are the primary plant communities occupying the saline intertidal zone of Australia. Mangrove diversity is greatest in the tropics and saltmarsh diversity greatest in temperate zones. Coastal halophytes are most extensive where tidal conditions facilitate the development of a sedimentary substrate for plant establishment and growth. Over time, strong zonation can develop within the tidal frame. Where mangrove and saltmarsh co-occur saltmarsh is typically positioned higher in the tidal frame and thus is subject to less frequent inundation. Seagrass beds often adjoin mangrove in the lower intertidal and sub-tidal zones where environmental conditions are suitable. Mangrove and saltmarsh plants exhibit unique adaptations that enable them to establish and grow within the harsh conditions created by tidal inundation, conditions typified by recurrent waterlogging, elevated salinity and anaerobic substrate. Common adaptations include mechanisms to exclude, extrude or store salt ions, and unique root morphologies that improve stability and create aerated rhizospheres around the roots. Coastal halophyte communities have responded over geological timescales to fluctuating sea levels by shifting their distribution and by accumulating sediments. More recently, coastal halophytes have increasingly succumbed to habitat change and exploitation, both globally and in Australia, with large areas of former mangrove or saltmarsh lost to development. A shift to ecosystem-based management and policy aims to protect increasingly valued ecosystem services provided by coastal halophytes by reversing their loss and degradation. However, losses of coastal halophyte communities are likely to continue in the 21st century due to the effect of climate change on sea-levels, higher air and sea temperatures, and a suite of related impacts on primary productivity. Adaptation to climate change should aim to limit further losses of coastal halophyte vegetation, and urgently improve or restore ecosystem services provided by these highly valuable coastal plant communities.

22.1 Introduction

Halophytes that live in saline environments are distinguished from glycophytes, which are incapable of growing under saline conditions. This distinction is complex: are conditions saline, brackish or near fresh; what is the ionic composition of the water; are halophytes restricted to saline environments only or can they grow elsewhere? Because of this complexity, attempts to define halophytes have used a range of

Australian Vegetation, Third Edition, ed. David A. Keith. Published by Cambridge University Press. © Cambridge University Press 2017.

Citation: Rogers, K. *et al.* (2017). Coastal Halophytic Vegetation. In D. A. Keith, ed., *Australian Vegetation*, 3rd edn. Cambridge: Cambridge University Press, pp. 544–69.

criteria, from salinity thresholds (e.g. Gorham 1993), edaphic characteristics (e.g. Waisel 1972), chemical characteristics of the plant material itself, or possession of specific physiological mechanisms that promote salt tolerance, such as salt secretion (e.g. Breckle 2002). For this chapter we adopt a pragmatic definition of a halophyte (after Flowers and Colmer 2008): plants able to complete their life cycle in a salt concentration of at least 200 mM NaCl (approx. 12 g l^{-1} NaCl, or roughly one-third ocean-water salinity) under conditions that might be expected to occur in the natural environment. We focus on angiosperms, yet recognise that there are many marine algae that meet the definition of being halophytes.

The exact number of halophytic plant species in Australia is largely unknown for a number of reasons. First, it is dependent upon the tolerance threshold used to differentiate halophytes from the salt sensitive glycophytes. In global analyses ~80 mM of sodium chloride has been used as a salinity threshold between the two plant groups, while other assessments use sodium chloride concentrations much closer to seawater resulting in fewer species identified as halophytic plants (Flowers *et al.* 2010). Second, the salt tolerance of many species still remains unknown (Boon 2012). This is particularly apparent at the upper limit of saltmarsh, where salinity conditions are presumed to be low, but for which there is very little published data. For this reason, we focus on those plants known to occur in association with tidal inundation along low-energy coastlines, as well as some that occur in non-tidal, but still saline, settings. Few angiosperms have adapted to the combination of high salinity and waterlogged sediments (Barrett-Lennard 2003; Kozlowski 1997). While they are a minor component of the global flora, they form distinctive and ecologically important habitats. Mangroves, for example, have colonised such environments through the evolution of specialised anatomical, physiological and reproductive adaptations (Clough *et al.* 1982; Saenger 1982) and provide numerous ecosystem services.

In this chapter, we review the ecology, biogeography and geomorphology of Australian coastal halophytic vegetation, focussing on mangrove and saltmarsh. The relationship between halophytic vegetation, sea level and coastal geomorphology, both current and past, is a unifying theme. We then examine climate change and other human influences, such as coastal development, as pervasive and ongoing threats, and discuss governance and management needed to mitigate them. Finally, we identify knowledge gaps and research needed to advance our understanding of ecosystem services provided by halophytic plant communities associated with the Australian coastline.

22.2 Tidal relationships of halophytic communities

Tidal halophytic plants often grow along coastlines where hydrodynamic energy is low, in conditions that enable sediments to accumulate and provide a suitable substrate in which seedlings can establish and plants develop. The occurrence of halophytes along the Australian coastline varies with latitude (Figure 22.1a); saltmarsh species diversity increases with increasing latitude, in contrast to mangrove species, which are predominantly tropical in distribution (Saenger *et al.* 1977; Adam 1996). The coastline of Australia is somewhat atypical in supporting well-developed sympatric mangrove and saltmarsh communities. In the northern parts of the continent, floristically diverse and extensive mangrove stands are seaward of often floristically poor but extensive saltmarshes and saline mudflats. In the southern parts of the continent, mangroves are less diverse but similarly are seaward of saltmarshes that are not only extensive but often floristically rich. A similar juxtaposition is found on parts of the coastlines of Brazil, Gulf of Mexico, Florida, China and the east coast of Africa (Saintilan *et al.* 2014).

Tidally influenced plant communities often exhibit strong zonation; seagrass is restricted to the subtidal and lower regions of the intertidal zone, while mangrove or saltmarsh occur throughout the upper portion of the intertidal zone

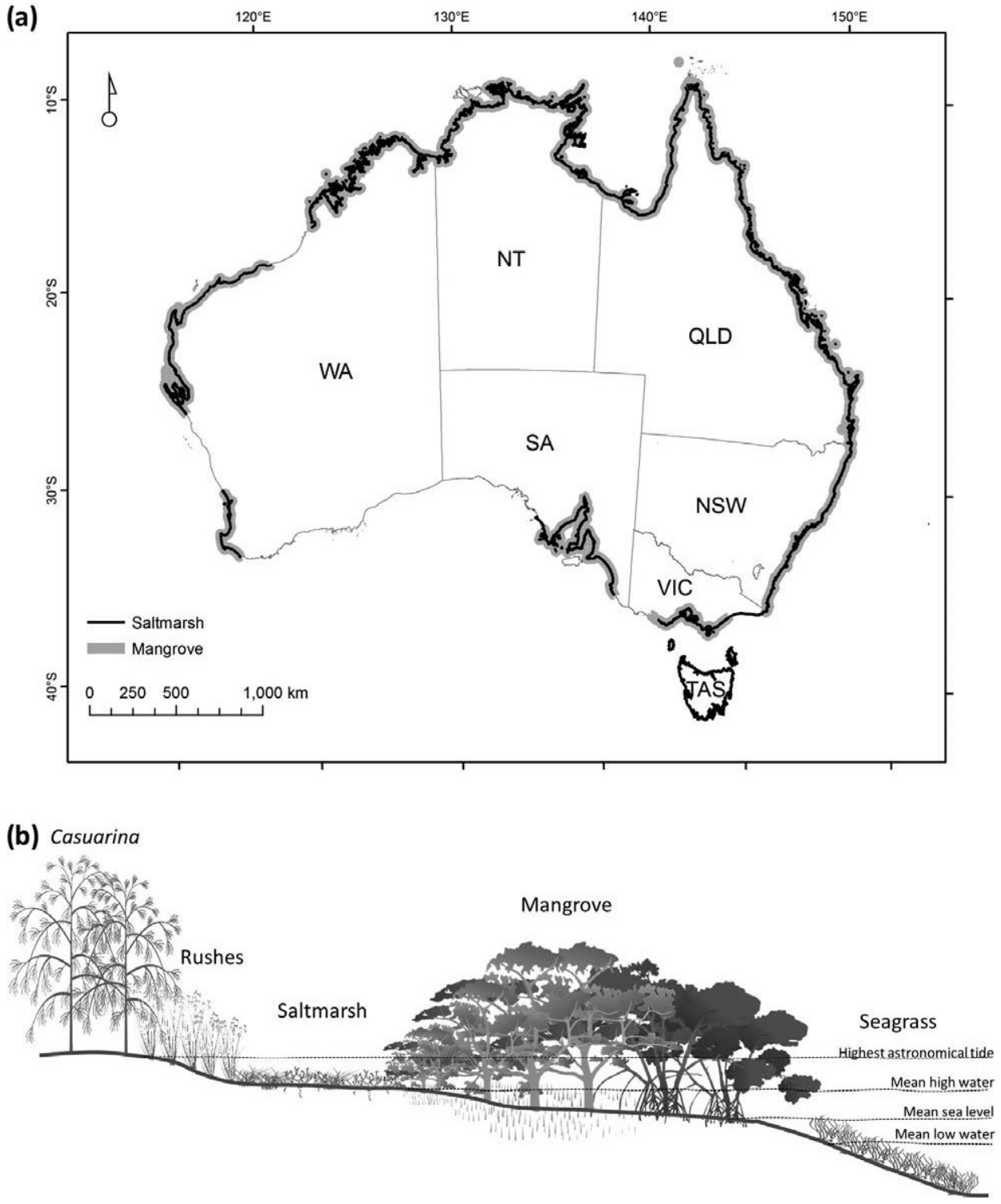


Figure 22.1 Mangrove and saltmarsh halophyte distribution: (a) around the coastline of Australia; and (b) across a tidal gradient, here shown for subtropical and temperate Australia.

above mean sea level (Fig. 22.1b). Seagrasses are ancient flowering plants that exhibit unique adaptations enabling them to complete their life cycle within sheltered coastal and offshore reef environments where salinity conditions are more stable (Sainty *et al.* 2012). Most species grow subtidally, but some may occur lower in the intertidal zone, such as eelgrass (*Zostera* spp.), while *Ruppia* and *Lepilaena* species may occur within pools located within saltmarsh. Where saltmarsh and mangrove co-occur, mangrove forest typically occupies lower elevations (to mean high tide), and saltmarsh occupies high elevations within the tidal frame, usually extending to roughly the limit of the highest astronomic tide. Any simple zonation patterns with increasing distance from the sea are, however, complicated by spatial patterning along the sides of tidal creeks and other waterways that traverse tidal marshes and mangroves. Broad ecotones occur in gently sloping settings and tidal halophytes may merge with 'brackish' ecosystems that may consist of non-woody taxa, such as the sea rush *Juncus kraussii*, as well as trees and shrubs, such as swamp oak *Casuarina glauca*, or paperbarks *Melaleuca* spp. In arid areas, halophytic vegetation may merge with hypersaline mudflats and cyanobacterial mats, sometimes called sabka (Lovelock *et al.* 2010a; Duggan *et al.* 2014). In other areas, where rainfall is high and the elevation gradient over the intertidal is low, freshwater and brackish water wetlands may dominate behind the uppermost levels of the saltmarsh (Catford *et al.*, Chapter 20, this volume).

22.3 Distribution and biogeography

Although there is no single definition of coastal saltmarsh that adequately covers the floristic and structural complexity of this community, mangroves have been defined as trees, shrubs, palms or ferns generally exceeding 0.5 m and which normally grow in the intertidal zone of marine and estuarine environments (Duke 2006). The term 'mangrove' can be used to refer to both the individual tree and to the plant community. For the latter, Macnae (1966) proposed the word 'mangal' be used, but this terminology has not been uniformly adopted by wetland ecologists and managers.

Mangrove forests occupy approximately 18% of the Australian coastline (Duke 2006), with an estimated area of 978 000 ha. Australia has the second largest extent in the world, behind Indonesia (3 113 000 ha) and similar to that of Brazil (963 000 ha) (Giri *et al.* 2011). Six mangrove biogeographic regions have been recognised on a global scale, divided between the Atlantic–East Pacific (AEP) and the Indo-West Pacific (IWP) provinces. Mangrove species diversity is significantly greater in the IWP province, and while Indonesia has the highest mangrove species diversity, Australian species diversity is high on global standards (Duke *et al.* 1998a; Duke 2006). Australia's mangrove flora includes 41 species, drawn from 22 genera and 19 plant families, and this constitutes 57% of the mangrove species in the world. Although mangroves are overwhelmingly dicotylednous angiosperms, Australian mangroves also include one fern (*Acrostichum*, in the family Pteridaceae) and one palm (*Nypa*, in the family Arecaceae).

Despite the high diversity of mangroves in the IWP, mangroves in the region have not evolved and dispersed uniformly (Saenger 1998). Fossil records indicate a much broader distribution of the mangrove palm, *Nypa* than the present-day extant populations of the genus (Plaziat *et al.* 2001), and fossilised *Nypa* pollen has been documented from the Eocene in Tasmania (Pole and Macphail 1996). Unusual occurrences and genetic discontinuities in the current distribution indicate that mangrove evolution was complex (Duke *et al.* 1998b; Duke 2002). Debate about mangrove evolution (Duke 1995; Saenger 1998; Ellison *et al.* 1999) is perhaps unsurprising as mangroves occur in many different plant families, including the Avicenniaceae, Combretaceae, Euphorbiaceae, Meliaceae, Rhizophoraceae, Sonneratiaceae and Sterculiaceae.

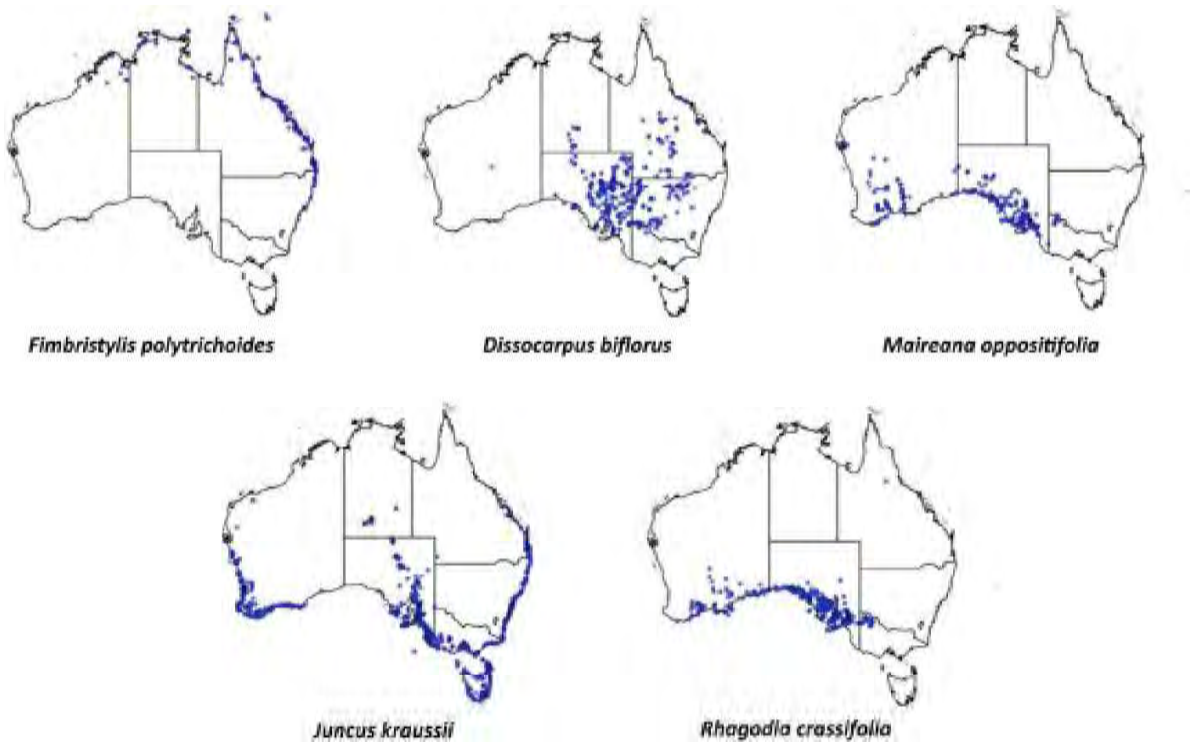


Figure 22.2 Distribution patterns of selected saltmarsh species, being illustrative of predominantly inland distribution (*D. biflorus*), predominantly coastal southern and northern (*J. kraussii* and *F. polytrichoides*, respectively) and arid zone chenopods (*M. oppositifolia* and *R. crassifolia*). *Data and base-maps derived from the Australian Virtual Herbarium (n.d.).*

As mangroves are predominantly tropical in distribution, species diversity is greatest along the wet tropical coastlines of the Indonesian–New Guinea Archipelago and of Northern Australia. Diversity diminishes with increasing latitude, with mangrove distribution broadly corresponding to shorelines where the average sea surface temperature exceeds 20°C (Duke *et al.* 1998a). There is only one species of mangrove, *Avicennia marina* at the highest latitudinal limit (i.e. Corner Inlet, 38°54′25″S); this species has the greatest latitudinal distribution of any mangrove globally (Saintilan *et al.* 2014). The truncated latitudinal distribution of mangroves on the western coasts of continents in the southern hemisphere suggests that aridity may be an important determinant of distribution in these regions (Ball and Sobrado 1998). This pattern is particularly evident along the coastline of north-western Australia, where species diversity declines with increasing aridity (Semeniuk 1983).

Unlike mangrove, the status of many saltmarsh species as either native or introduced to Australia is unknown and still questioned among botanists (Adam 1990; Boon *et al.* 2015). Further complexity arises from occurrence of saltmarsh in both coastal and inland settings, the former with a wide suite of environmental conditions and the latter most often associated with endorheic basins (De Deckker 1983). Saltmarsh taxa may be predominantly inland with some coastal representation (e.g. *Dissocarpus biflorus* in Figure 22.2), predominantly coastal though with inland occurrence (e.g. *Samolus repens*, some species of *Fibristylus*), and more rarely exclusively coastal (e.g. *Austrostipa stipoides*, *Limonium solanderi*). The conditions required for growth, that is, saline habitat periodically freshened while competition with salt-intolerant vegetation is excluded, are similar between upper intertidal environments and salt lakes. Birds migrating between inland and coastal habitats provide an effective dispersal mechanism between coastal saltmarsh and their inland counterparts. Additionally, salt spray, sometimes combined with groundwater seepage, can facilitate the growth of halophytic plant communities on cliffs, bluffs and rock shelves well above tidal reach.

Notwithstanding the transcontinental distribution of many species and the possible non-native status of some species, clear biogeographic patterns in saltmarsh taxa are noticeable at continental and subcontinental scales. The primary biogeographic division of Australia's saltmarsh flora is between northern and southern bioregions, separated at 23° latitude (Saintilan 2009). The two halves of the continent have less than 25% of species in common. Species occurring primarily in the northern regions include *Tecticornia australasica*, *Fimbristylis polytrichoides*, *Portulaca bicolour*, *Fimbristylis ferruginea*, *Batis agrillicola*, *Xerochloa imberbis* and *Sesuvium portulacastrum*. Species occurring primarily in the southern bioregions include *Samolus repens*, *Atriplex cinerea*, *Apium prostratum*, *Centaurium erythraea*, *Myoporum insulare*, *Parapholis incurva* and *Cotula coronopifolia* (Saintilan 2009).

Three bioregions in each of the northern and southern continental divisions have distinct saltmarsh floras (Figure 22.3). In both divisions, about two-thirds of the flora is shared with the remainder of the division. Within the southern division, the Gawler, Nullarbor and Hampton bioregions, all largely characterised by the absence of estuaries, because of the arid climate or the cliffed coastline. This would suggest that saltmarsh occurrences are either open coast or (as is more likely) cliff top. For example, no estuarine saltmarshes are recorded on the Great Australian Bight between Fowler's Bay, SA (33°14'S, 124°02'E) and Point Dempster WA (32°11'S, 133°28'E). Sedges and rushes are largely absent from these bioregions and the characterising species are of the Amaranthaceae family (see for example the distribution of *Maireana oppositifolia* in Figure 22.2). In the northern division, species found consistently in humid areas include *Tecticornia australasica*, the sedges *Fimbristylis ferruginea*, and *Fimbristylis polytrichoides* and *Batis agrillicola*. Species found predominantly in the more arid Pilbara, Dampier and Kimberly coastlines

Figure 22.3 Saltmarsh diversity around the Australian coastline varies at a range of spatial scales. At the regional scale, the most diverse communities occur in temperate south-eastern Australia, such as (a) French Island, Western Port Bay, Victoria, where *Tecticornia* spp. form a shrub-dominated zone near the lower intertidal mangrove and herbfields, with mosaics of species occupying the upper intertidal zone (photo: Kerrylee Rogers). Where freshwater contributions from adjacent catchments are high, diversity may be locally limited in temperate zones to those species tolerant of brackish conditions, as seen in (b) with monospecific stands of the rush *Juncus kraussii* on the middle reaches of the Hawkesbury River, NSW (photo: Kerrylee Rogers). In subtropical and tropical Australia, species diversity diminishes and intertidal zones landward of mangrove may be dominated by few species. Saltmarsh in (c) at Ukerebagh Island, Tweed River, NSW, is dominated by *Sporobolus virginicus* (photo: Kerrylee Rogers), and at (d) Moreton Bay, Qld, is dominated by *Sarcocornia quinqueflora* (photo: Catherine Lovelock).
(A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

are *Tecticornia auriculata*, *Frankenia ambita* and *Neobassia astrocarpa*.

In general, there is little relationship between the intertidal area available to saltmarsh plants and saltmarsh floristic diversity. Northern Australia supports a low diversity of saltmarsh, commonly dominated by grasses including *Sporobolus virginicus*, in spite of the large intertidal area available for saltmarsh colonisation. To some degree, this may be related to climatic constraints, with hypersaline conditions developing during the dry season in many parts of Northern Australia and prolonged inundation in the wet season (Duggan *et al.* 2014). Wide intertidal areas will be devoid of saltmarsh in these situations. Notwithstanding, Tasmania, Victoria, South Australia and New South Wales contain less than 2.5% of the total saltmarsh/saltpan area yet together support 90% of the saltmarsh flora of Australia (Saintilan 2009).

22.4 Ecology, physiology and adaptations

Mangrove more typically grow at mid-tidal elevations where frequent tidal inundation destabilises sediments, reduces soil aeration and exposes soil to seawater salinities. Consequently, mangroves have evolved a number of distinctive adaptations for countering saline and anaerobic soil conditions. Salt tolerance in particular is associated with mechanisms to exclude, extrude, or store salt ions, which is supported by efficient use of water during photosynthesis (Ball 1988; Saenger 2002). Some mangrove species exclude salt more effectively than others, but approximately 80–99% of salt is excluded at the roots (Clough *et al.* 1982; Saenger 2002), and frequent tidal inundation is essential to flush the excluded salt ions and limit the development of hypersaline conditions around the roots. The remaining salt ions that are not excluded are subsequently stored in the vacuoles of cells, with some species extruding salt through salt glands in leaves. Storage of salt ions within leaves is typically accompanied by succulence to dilute salt concentrations; succulence is likely to be an adaptive response to salinity that is absent under freshwater conditions (Saenger 2002).

The high metabolic cost of salt tolerance limits the use of water in mangroves. Many mangroves therefore display traits such as xeromorphy, steep leaf angles and low transpiration rates that promote water-use efficiency and minimise water loss during photosynthesis (Ball 1988). Many mangroves are also strongly dependent on fresh water sources, with evidence for preferential uptake of fresh water sources when available (Santini *et al.* 2015).

Mangroves exhibit a range of root morphologies that improve stability and oxygen transport in anaerobic soils. In *Avicennia marina*, root systems typically consist of laterally spreading cable roots with smaller vertical anchor roots, fine nutritive roots and pneumatophores that increase root aeration, and trap and stabilise sediments (Figure 22.4). Despite generally being restricted to the upper 1–2 m of sediment, the complexity of the mangrove root system is such that the ratio of above-ground to below-ground biomass is lower than in other forests (Saintilan 1997a,b). Above-ground root morphology is equally complex among different mangrove species, with a range of aerial structures present in various genera including pneumatophores – conical root extensions from the cable root system (typical of *Avicennia* and *Sonneratia*); knee roots – cable roots that extend above the soil surface before protruding downward (typical of *Bruguiera*); stilt roots – roots protruding from the trunk before extending into the substrate (typical of *Rhizophora* or *Ceriops*); buttress roots – flattened roots extending laterally from the main trunk (typical of *Heritiera littoralis*); and aerial roots – that descend from branches or the trunk (typical of *Rhizophora* and *Avicennia*). Lenticels on roots facilitate gas exchange by regulating oxygen availability and pressure during tidal inundation and subsequent shifts in pressure as tides recede (Allaway *et al.* 2001). Leakage of oxygen from roots of some species may improve soil oxidation and enhance nutrient availability (Reef *et al.* 2010), though not in all cases (Boon 2006).

Mangrove reproduction takes place in an environment where tidal inundation transports seeds, yet might also limit seedling establishment. Many

Figure 22.4 Some examples of complex root morphology of mangrove in Australia: (a) cone-shaped pneumatophore roots of *Sonneratia alba* in Darwin Harbour, Northern Territory (photo: Kerrylee Rogers); (b) pneumatophores of dwarf *Avicennia marina* in Corner Inlet, Victoria (photo: Paul Boon); (c) exposed cable roots and pneumatophores of a mature *Avicennia marina* at Carama Inlet, Jervis Bay, NSW (photo: Kerrylee Rogers); and (d) complex stilt roots of *Rhizophora stylosa* at Low Isles, north Queensland (photo: Catherine Lovelock).
(A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

mangrove species possess viviparous seeds, where the seed or propagule germinates while attached to the parent tree to the extent that the embryo ruptures the pericarp, or possess cryptoviviparous seeds, which germinate without the pericarp rupturing. How either is an adaptation to inundation, salinity, low-nutrient availability or waterlogging is not clear, although the peculiar timing of germination of mangrove seeds does improve seed anchoring, establishment and nutrient availability (Saenger 1982). Mature seedling or propagule production typically occurs in the later summer months of February to March, coinciding with the end of the rainy season in the tropics (Duke *et al.* 1984). Studies on *Avicennia marina* in southern New South Wales show it flowers in late summer too (Clarke and Myerscough 1993). Many mangrove propagules are buoyant, aiding dispersal on tides well beyond the parent tree; however the dispersal distance appears to be variable. The vast majority of *Avicenna marina* propagules were reportedly stranded within 50 m of the parent tree in south-eastern Australia (Clarke 1993) and *Ceriops tagal* propagules were stranded within 3 m of the parent tree in Northern Australia (McGuinness 1996), although long-distance dispersal is presumably possible. Some seeds are not buoyant or viviparous (e.g. *Sonneratia*), implying that vivipary and seed buoyancy are not always required as an adaptation to the coastal environment.

Whereas mangroves are often limited to the mid-tide zone, coastal saltmarsh can extend to the very highest levels of tidal inundation, the level set under normal conditions by the highest astronomical tide. In the most landward areas, soil salinities can be highly variable: tidal inundation in some locations can be so rare that hypersalinity often develops due to evaporation, but in others periodic freshening by runoff from local catchments or from adjacent floodplain rivers can result in recurrent periods of low salinity. Plants occupying these environments have strategies for tolerating the highly variable salinity and flooding regimes (Clarke and Hannon 1969). In the upper intertidal environment, nitrogen limitation may also be an important control on plant growth (Feller *et al.* 2003), as it is for many coastal marine systems. Strategies for the fixation and preservation of nitrogen in Australian saltmarshes include plant–plant interactions with nearby nitrogen fixers *Casuarina glauca* (Wei *et al.* 2015).

Given the wide range in plant morphologies occurring in saltmarsh, it is not surprising that saltmarsh plants exhibit a very wide range of salt tolerances and adaptations to living in environments that are variously saline or fresh and inundated or desiccated (Morrisey 1995). In hypersaline areas of Victoria only a few angiosperm species can exist and the wetland is typically a low shrubland dominated by succulent Amaranthaceae such as *Tecticornia pergranulata* and *T. halocnemoides* (Boon *et al.* 2015). Elsewhere, extremely high soil salinities may favour the growth of resilient cyanobacterial mats, particularly along the arid coastline of Western Australia (Paling and McComb 1994; Lovelock *et al.* 2010a). Conversely, the rear parts of coastal wetlands are often subject to localised freshwater flows, and may support a wide range of salt-tolerant taxa such as *Bolboschoenus caldwellii* and *Schoenoplectus pungens* and semi-aquatic species tolerant of at least moderate salinity. In other places, rushland/sedgeland vegetation, typically dominated by *Juncus kraussii*, occasionally with *Phragmites australis* or species of Cyperaceae with components of small halophytic herbs, occur in coastal areas where freshwater flows augment otherwise saline environments (Boon *et al.* 2015). Although limited in extent these habitats are some of the most carbon-rich sediments in the intertidal zone (Lovelock *et al.* 2014; Saintilan *et al.* 2013).

Temperature is a critical determinant of competitive interactions between mangrove and saltmarsh. The winnowing of mangrove species with increasing latitude is thought to be primarily an outcome of different cold tolerance among species (Hutchings and Saenger 1987). On the Gulf Coast of the United States, periodic heavy frost is the primary factor that limits encroachment of *Avicennia germinans*

into marsh habitats. In eastern Australia, *Avicennia marina* has a greater tolerance of mild frost, possibly resulting from the higher incidence of mild and lower incidence of heavy frost compared with southern United States (Stuart *et al.* 2007), and in this context frost is a less important limitation in competition with saltmarsh. However, warming may increase the vigour of mangrove growth at higher latitudes, and this may explain the proliferation of mangrove at the expense of saltmarsh at higher latitudes across several continents, Australia included (Saintilan *et al.* 2014). Conversely, the high inverse correlation between minimum monthly temperature and the diversity of saltmarsh species (r^2 = -0.78; Saintilan 2009) suggests that warmer temperatures may limit the germination and growth of some saltmarsh species. Limited experimental research on temperature effects on germination of saltmarsh species provides some preliminary support (Greenwood and MacFarlane 2006).

22.5 Zonation

The distribution of coastal halophytes at local scales is strongly influenced by the effect of tidal inundation on soil salinity, anoxia and nutrient availability, and this often leads to conspicuous zonation in those places where more than one species of halophyte coexist. As noted earlier, mangroves and saltmarshes share the intertidal zone over most of the Australian continent, with mangrove typically in the lower portion and saltmarsh adjacent in the upper portion of the tidal frame. The introduced *Spartina* and native *Phragmites australis* may colonise mudflats seaward of mangrove. Only in Tasmania do saltmarshes grow without competition from mangrove.

The earliest ecological descriptions conceptualised succession from mudflats to mangrove (Curtiss 1888; Davis 1940) and from mangrove to saltmarsh in Clementsian terms (Pidgeon 1940). In this model, the colonising mangroves built sediment elevation and were thereby eventually replaced by saltmarsh, which took advantage of the less frequent tidal inundation. According to this explanation, continuing accretion and increasing substrate elevation creates conditions favourable for species replacement, while 'land building' by pioneer species continued at seaward margins. This sequence concords with several stratigraphic studies in south-eastern Australia (e.g. Saintilan and Hashimoto 1999), although can be equally interpreted as a response to geomorphic evolution of the intertidal substrate over the Holocene as sea level stabilised.

Traditional successional hypotheses for the zonation observed in coastal vegetation communities have been challenged on a number of fronts. First, extensive peats beneath mangrove (presumed to be from pioneer species) have been found in some instances to indicate the inverse pattern of colonisation, with mangrove now occupying areas that were previously landward freshwater environments (Scholl 1964). Second, a considerable body of work in Northern Australia on the spatial pattern of mangrove found species distributions that could not be explained by successional hypotheses (Thom *et al.* 1975; Stoddart 1980; Woodroffe 1987). For example, on the Ord River, Western Australia, the distribution of *Rhizophora*, a so-called pioneer species, did not reflect its role as a 'land builder', as the species occurred at both the seaward margin and at the landward fringe where inundation frequency appeared to create soil salinities close to seawater (Thom *et al.* 1975). The occurrence of mangrove on eroding shorelines at King Sound in north-western Australia similarly indicates an absence of successional seaward advancement of mangrove (Semeniuk 1980).

In recent decades, a trend has been observed of saltmarsh being replaced by mangrove or mangrove invading into areas from which they were formerly absent (Saintilan and Hashimoto 1999; Saintilan *et al.* 2014). Relative sea-level rise (Rogers *et al.* 2006) and altered rainfall patterns (Eslami-Andargoli *et al.* 2009), both factors that prevent desiccation of mangrove propagules and reduce soil salinities within saltmarshes, are often proposed

as the explanation. Disaggregating these factors is difficult because of the compounding effects of the El Niño Southern Oscillation on rainfall and on sea level, and their subsequent co-correlation in south-eastern Australia (Rogers *et al.* 2014).

The expansion of mangroves into coastal saltmarsh has been reported for five continents; purported mechanisms favour geomorphic control on zonation, with expansion of mangrove influenced by interactions between hydroperiod, sedimentation, elevation and salinity, while nutrients play a role in some settings (Saintilan *et al.* 2014). In Tasmania, where mangroves are absent and saltmarsh occupies a greater portion of the intertidal zone, conversion of shrubland to herbfield is reported to be consistent with changes in relative sea level (Prahalad *et al.* 2011; Saintilan and Rogers 2013).

Landward expansion of mangrove is occurring at the same time as seaward mangrove expansion as sediments reach mean sea level (e.g. Mitchell *et al.* 2007). In addition, as forests mature they follow trends of increasing tree size, increasing carbon stores in sediments and declining nutrient availability (Lovelock *et al.* 2010b), but successional turnover in species composition is not necessarily observed. Because of all these factors, support is growing for the notion that the zonation of coastal halophytic vegetation reflects opportunistic responses to geomorphic changes. These involve complex interactions among tidal inundation and soil salinity, substrate subsidence and compaction, changes to freshwater discharge, and sediment deposition and erosion, the latter mediated by sediment availability and changes in sea level, both eustatic and storm-surge related.

Trans-specific zonation patterns can be relatively easy to distinguish along a mangrove tidal profile, particularly on low-energy open coasts. Macnae (1966), for example, identified parallel zones in north-eastern Australia that were characterised by first a landward *Avicennia* zone; *Ceriops* thickets, *Brugiera* forests; *Rhizophora* forests, and finally a seaward fringe of *Avicennia* or *Sonneratia*. In a large study of 17 estuaries in northern Australia, zonation was affected by the biogeographic influence of temperature and rainfall on species occurrence within estuaries and the distinctive tolerance of species to environmental variables that varied along the length of an estuary (Bunt 1996). The influence of tides diminished up-river, and some mangrove species, such as *Avicennia marina*, *Sonneratia alba* and *Rhizophora stylosa*, preferentially occupied the downstream and more saline reaches, where tidal effects were greater. Some species, however, occurred at typically lower salinities in the upstream reaches of coastal rivers, such as *Heritiera littoralis* and *Aegiceras corniculatum* (Duke 2006). Confounding this patterning is the fact that mangroves are often long-lived trees, and zonation patterns can persist for decades, even when environmental conditions that led to their establishment may have changed (Lovelock *et al.* 2011).

Like mangrove, saltmarsh zonation is commonly characterised by distinct growth forms that correlate with gradients of salinity and inundation, such as low grasslands (e.g. *Distichlis distichophylla*, *Sporobolus virginicus*), herbfields (*Samolus repens*, *Wilsonia backhousei*), rhizomatous or stoloniferous sedges (e.g. *Gahnia filum*, *Juncus* spp. such as *J. kraussii*), large clumped grasses (e.g. *Austrostipa stipoides*) and shrubs (e.g. *Atriplex paludosa* subsp. *paludosa*, *Tecticornia arbuscula*, *Tecticornia halocnemoides* and *Tecticornia pergranulata*) (Kirkpatrick and Glasby 1981). These environmental gradients broadly correspond to position in the landscape, with some distinction in species composition between 'upper' and 'lower' saltmarsh, brackish and fringing marsh (Sainty *et al.* 2012). Within subtropical settings, saltmarshes are predominantly grasslands and herbfields, with sedges dominating brackish environments. In temperate Australia, shrubs of the genus *Tecticornia* occupy mid-intertidal environments giving way to herbfields at upper intertidal elevations, which may be particularly diverse (Saintilan 2009).

With the development of elevation models using light detection and ranging (Lidar)

technology, there has been increasing interest in modelling zonation, using elevation as a proxy for environmental gradients. In Darwin Harbour, inundation regime was identified as the most important factor influencing the distribution of *Rhizophora stylosa*, *Sonneratia alba* and *Ceriops tagal*, followed by salinity (Crase *et al.* 2013). Similar correlations between species zonation and inundation regimes have also been established for saltmarsh at Botany Bay (Hickey and Bruce 2010). Clarke (2014) cautioned that the inter-correlated nature of abiotic and biotic variables is poorly accounted for in statistical models; hence, identifying causal factors of zonation is problematic in the absence of experimental manipulation.

22.6 Geomorphic evolution and geomorphological settings

Mangrove and coastal saltmarsh generally occupy low-energy intertidal shorelines above mean sea level, and the influence of sea level on their distribution is profound (Adam 1990; Lovelock *et al.* 2015b; Woodroffe *et al.* 2015). Saltmarsh on headlands are associated with land receiving sufficient salt spray to encourage halophytic plant growth and establishment; in contrast, non-tidally influenced mangrove in Australia are likely to be relict populations where tidal exchange has been lost during the Quaternary period. Sedimentary enclosure is the prevailing explanation for relict inland mangroves at Lake MacLeod (Ellison and Simmonds 2003) and Mandora Marsh, Western Australia (Beard 1967), whereas post-glacial uplift of a shore terrace may explain the occurrence of an elevated *Brugiera* forest on Christmas Island (Woodroffe 1988).

Closure of barriers at estuary entrances along wave-dominated coastlines can significantly reduce tidal exchange between saltmarshes and the ocean. Estuary entrances may close seasonally, as is the case in south-west Australia (Hodgkin and Hesp 1998), or more intermittently, as is the case in many parts of south-eastern Australia. Salinity of inundating waters can fluctuate from hypersaline conditions when closed and hydrological flows from catchments are low, to that of sea waters when tidal exchange with the ocean is not impeded, to freshwater conditions when estuary entrances are closed and rainfall/runoff from catchments is substantial.

Peats derived from halophytic material are useful paleo-indicators of sea level because mangrove and saltmarsh occurrence and zonation are very sensitive to tides. Substantial evidence of mangrove and saltmarsh habitat evolution during the Holocene, the most recent period of sea-level rise, has been extracted from sedimentary cores from the South Alligator River, Northern Territory (Woodroffe *et al.* 1993).

In Australia, sea level over this period was characterised by a low stand at approximately 120 m below present mean sea level (PMSL) at 18 000–20 000 yr BP (Before Present), rising to approximately present level (or up to 2 m above PMSL) about 7000 yr BP. After this period sea level remained relatively stable, although there remains some conjecture about when present levels were attained following highstands that may have been up to 2 m above PMSL (Lewis *et al.* 2013). Three phases of estuarine infill are recognisable from paleo-distributions of halophytic vegetation. The transgressive phase (~8000 yr BP) was dominated by landward transgression of mangrove as the sea drowned the valley of the South Alligator River. Mangrove would not have been able to accumulate sediments at rates equivalent to the high rate of sea-level rise and was restricted to the narrow intertidal margins of the flooded valley. The deceleration in sea-level rise that started approximately 7000 years ago marked the commencement of the 'big swamp' phase in this part of northern Australia. During this period, sediments were able to infill the valley to depths of 10–15 m, creating an expansive intertidal substrate that mangroves colonised. This phase was marked in sediment cores by a dominance of *Rhizophora* pollen, with smaller quantities of pollen from species

typical of high intertidal zones such as *Sonneratia*, *Avicennia* and floodplain sedges. The high rate of infill slowed because of reduced tidal inundation, and during the sinuous/cuspate phase, from 5300 years BP, the mangrove dominance gave way to grasses and sedges on saline mudflats and fresher backwater swamps.

The sequence of infill of the tidally dominated South Alligator estuary is probably typical of the tide-dominated estuarine valleys of northern, western and eastern Australia, with similar Holocene evolution described for the Adelaide, Daly, Mary, Ord, King, Richmond and Hawkesbury Rivers, and Lizard Island (Thom *et al.* 1975; Chappell 1993; Woodroffe *et al.* 1993; Saintilan and Hashimoto 1999; Hashimoto *et al.* 2006; Proske and Haberle 2012). The dominance of mangrove on coastal floodplains in the mid-Holocene has led to the development of large carbon pools in the soils of mangrove, saltmarsh and coastal floodplains. Some of the carbon in these pools has been implicated in the generation of pyrites and acid sulfate soils (Sammut *et al.* 1995, 1996; Lin and Melville 2010).

As intertidal halophytes share the intertidal zone, they also share common geomorphic units for much of their distribution along the Australian coastline. Mangrove development along the tide-dominated coasts typical of northern Australia is generally restricted to two primary geomorphological settings: mangrove may occupy the intertidal zone of tide-dominated estuaries, or deltaic environments where the degree of valley infill is greater and mangrove development tends to be most extensive (Figure 22.5a, b). Where rainfall is high, mangrove may occupy the entire intertidal zone and merge with rainforest and woodlands in the hinterland. Saltmarsh, however, may develop in the upper intertidal zone where mangrove expansion is limited by hypersaline conditions. This occurs around Townsville in Northern Queensland. In contrast, cyanobacterial mats occupy the upper intertidal zone on the arid coastline of north-western Australia, where infrequent tidal inundation and high evaporative demand generate hypersaline conditions and likely severe nutrient limitation (Lovelock *et al.* 2010a).

The wave-dominated rocky coastlines of southern Australia do not provide an ideal substrate for extensive development of coastal halophytes but, there are some places where mangrove occurs on rock platforms or other rocky substrates. Examples include Crackneck Point (New South Wales), basalt at The Jawbone Marine Sanctuary, granite at Millers Landing, sedimentary rocks south of Hastings in Western Port (all in Victoria). These rocky shores are often broken up by extensive beach ridges and sand barriers. As a consequence, the tidally restricted estuarine valleys are more lagoon-like (Figure 22.5c–e). Mangrove may also grow in carbonate geomorphological settings on the Great Barrier Reef (Buckley 1983), typically located in low-energy conditions behind fringing coral reefs (Figure 22.5i).

Within wave-dominated estuaries in south-eastern and south-western Australia, intertidal substrates on which mangrove and saltmarsh establish are most extensive on fluvial and flood-tide deltas. Saltmarsh dominates and mangrove tend to be absent from intermittent estuaries where the estuary entrance is usually closed. The primary cause of exclusion is unknown, but may relate to variable salinity and inundation dynamics associated with transitions between opening and closing. Along the New South Wales coastline, training of estuary entrances using seawalls to reinstate daily tidal flushing appears to promote establishment of mangrove along the shorelines (e.g. Lake Illawarra). Some colonisation and growth of coastal halophytes may occur along low-energy shorelines of drowned river valleys where the geomorphology reduces wave energy and elevates the influence of tides on substrates (e.g. the Hawkesbury River, Figure 22.5f). Tides are even more important along coasts where wave energy is diminished, such as coastal embayments (e.g. Western Port, Figure 22.5g) and the open coast where freshwater inputs from catchments are diminished (Figure 22.5h).

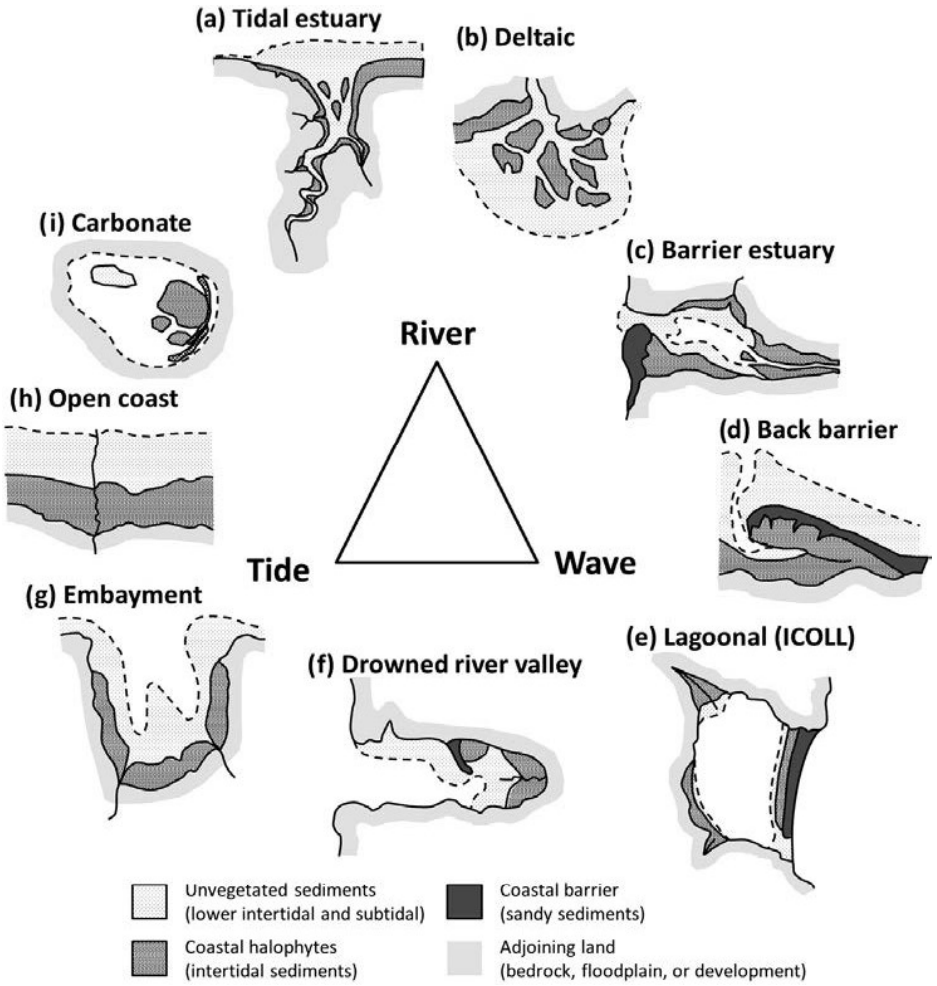


Figure 22.5 Geomorphological settings in which mangrove and saltmarsh are found in Australia. These settings are differentiated on the basis of the influence of wave, tide and river power on sedimentary dynamics within estuarine environments. Conceptualisation of the geomorphic settings of mangrove and saltmarsh in Australia builds upon the ternary classification of estuaries by Boyd *et al.* (1992) and Dalrymple *et al.* (1992); and its application to estuaries of Australia (Harris *et al.* 2002; Heap *et al.* 2004); and integrates the classical geomorphological settings of mangrove (adapted from Thom 1982; Woodroffe 1992) and saltmarsh (Woodroffe 2003).

22.7 Sedimentation and morphodynamic feedbacks

Coastal halophytic vegetation is strongly influenced by sea level. Over extended time periods, eustatic and relative sea level are not stable and as a result intertidal plant communities are dependent upon the supply and accumulation of material to maintain their position within the tidal frame. Once vegetation becomes established in the intertidal zone, further sedimentation is facilitated by organic matter contributions from *in situ* and neighbouring vegetation. Recent analyses using carbon isotopes suggests that *in situ* vegetation is the primary source of organic matter in mangrove and saltmarsh sediments in south-eastern Australia (Saintilan *et al.* 2013).

Once established, the vegetation baffles tides, decreasing flow velocities and enabling entrained sediments to be deposited and trapped (Furukawa *et al.* 1997; Mazda *et al.* 1997; Rogers and Woodroffe 2014). For mangrove in tropical Northern

Australia, the mineral component of sediments may be derived from the considerable mud reserves located offshore and transported onshore by waves, wind and tide (Wolanski 2006). Critical in the deposition process are the drag force of the sediment surface and the complex array of aerial roots, both of which facilitate sedimentation of suspended particles (Mazda *et al.* 1997). Empirical studies emphasise the efficiencies of the aerial components of mangrove in trapping sediments in tropical (Furukawa *et al.* 1997) and subtropical settings (Adame *et al.* 2010). In a microtidal temperate estuary in New South Wales, tidal flow velocity declined from the river through the mudflat and mangrove to the upper intertidal saltmarsh, and varied with distance from the river and suspended particulate matter concentrations (Howe *et al.* 2005). Intertidal halophytic vegetation, therefore, facilitates sediment deposition and stability in a number of ways: the fine mat of surface roots and deeper rhizomes bind sediment and prevent erosion; emergent shoots and roots decrease current velocities and promote deposition of fine particles; and plants add organic matter to sediments via primary production, thus building up the sediment surface.

Saltmarshes in the northern hemisphere commonly exhibit strong relationships between sediment supply, distance to the source of sediment (such as tidal creeks), elevation and deposition (Allen 2000). On the basis of these patterns, Adam (1990) proposed that sediment accumulation was inversely proportional to the time the sediment surface was inundated, known as the hydroperiod. This hypothesis has not been tested in Australia, but analyses of vertical accretion, surface elevation changes and subsidence using surface elevation tables and feldspar marker horizons (i.e. the SET-MH approach) across the intertidal zone consistently showed higher rates of sedimentation in lower intertidal mangrove than upper intertidal saltmarsh in a number of sites in south-eastern Australia (Rogers *et al.* 2006). In most instances, the magnitude of vertical accretion, subsidence and surface elevation increase was mediated by several variables, including sea level (Rogers *et al.* 2005, 2014; Lovelock *et al.* 2015a), turbidity (Lovelock *et al.* 2015a), climatic factors (Rogers *et al.* 2006; Rogers *et al.* 2014), and the effect of climate on groundwater availability (Rogers and Saintilan 2009). Storms were found to have only limited influence on surface elevation trends in vegetated intertidal habitats in south-eastern Australia (Rogers *et al.* 2013b), in contrast with trends reported in North America (Cahoon 2006). In much of south-eastern and south-western Australia, mangrove and saltmarsh occur within barrier estuaries where they are afforded some protection from storm surges.

Established relationships between sedimentation, sediment supply and distance from sediment sources have been the foundation for models of mangrove and saltmarsh evolution in Australia (Akumu *et al.* 2011; Traill *et al.* 2011; McKee *et al.* 2012; Rogers *et al.* 2012) and globally (Fagherazzi *et al.* 2012). With increasing concern about the vulnerability of intertidal vegetation to sea-level rise, models have demonstrated limitations to self-regulation of elevation, with projections indicating that relative sea-level rise will likely lead to declines in mangrove and saltmarsh health and extent unless the rates of sediment supply and accumulation increase (Rogers *et al.* 2013a; Lovelock *et al.* 2015b).

22.8 Current status and trends in extent

The extent of coastal halophytic vegetation is declining across the world, due largely to conversion of halophytic habitats to alternative land uses within the coastal zone (Gedan *et al.* 2009; Polidoro *et al.* 2010). The trend is most rapid in developing countries, but Australia has not been immune to such losses. One of the best indications of declines in extent of halophytic vegetation comes from comparisons of current extents with the estimates of coastal wetland extent prior to extensive drainage of wetlands in the 1970s. In New South Wales, mangrove and saltmarsh is estimated to have declined from 337 km^2 prior to 1969 (Goodrick 1970), to approximately 179 km^2

following the last statewide survey (OzCoasts 2009). Similarly, declines in mangrove and saltmarsh extent in Victoria is estimated to be in the order of 5–20% since the mid-nineteenth century across different sectors of the coast, with some regions having lost as much as 50% of their coastal saline wetland since European colonisation in the early nineteenth century (Sinclair and Boon 2012). In Queensland, there has been widespread conversion of saline habitat to ponded pasture for beef production and other agricultural uses including sugar cane (Holmes *et al.* 2013). In South Australia, anecdotal evidence of mangrove and saltmarsh distribution at the time of European settlement indicates significant habitat loss, particularly around Gulf St Vincent (Fotheringham and Coleman 2008) where approximately 80% of tidal saltmarsh and 100% of saltwater tea tree (*Melaleuca* spp.), reed beds and native coastal grasslands have been lost to urbanisation (Edyvane 1999).

The losses of mangrove and saltmarsh in Australia are largely attributed to land infilling and drainage for coastal developments, solar evaporative ponds for salt production, aquaculture, agriculture and flood mitigation purposes. In New South Wales, Williams and Watford (1997) estimated that approximately 4200 structures prevent tidal flow across coastal floodplains. These facilitated conversion of coastal halophytic vegetation to grazing land or other land uses. Similar impacts on coastal halophytic vegetation have occurred on floodplains across all of the eastern states of Australia (Sinclair and Boon 2012; Boon *et al.* 2015). Flow-on effects from drainage includes the conversion of highly efficient carbon sinks to greenhouse gas sources (Poffenbarger *et al.* 2011), discharge of acid into estuarine waters from pyritic soils associated with halophytes (Sammut *et al.* 1995), habitat fragmentation (Laegdsgaard 2006) and eutrophication (Lovelock *et al.* 2009). Greater governance and community awareness of the value of mangrove and saltmarsh have limited the impact of threatening processes on mangrove and saltmarsh, though resource exploration and infrastructure development remain significant threats.

Despite mounting evidence of the ecosystem services provided to society by coastal communities of halophytic plants (Barbier *et al.* 2011), smaller scale threats are still ongoing and difficult to manage. Vehicle and foot access to adjacent waterways have had a profound effect on saltmarsh extent in urbanised areas. For example, recreational vehicle use on saltmarsh was responsible for the loss of more than 2 ha of restricted saltmarsh along the Georges River in Sydney (Kelleway 2005), and destruction of large stands of the Vulnerable *Wilsonia backhousei* (listed under the New South Wales *Threatened Species Conservation Act 1995*) on the Parramatta River (Kelleway *et al.* 2007). Ongoing disturbance such as mowing, dumping of litter, discharge of stormwater and pollution (Laegdsgaard 2006), trampling by livestock and grazing have reduced the cover and susceptibility of halophyte communities to displacement by specialised exotic species. *Juncus acutus*, of Mediterranean origin, is known to outcompete the native rush *Juncus kraussii*, particularly in highly urbanised estuaries, such as Homebush Bay (Paul and Young 2006). Infestations of the invasive common cord grass (*Spartina* x *townsendii* and *Spartina anglica*), originally introduced to stabilise mudflats and limit erosion of coastal saltmarshes in Tasmania and Victoria, have required significant management efforts (Kriwoken and Hedge 2000). Weed invasions particularly associated with salt-tolerant agricultural plants (e.g. Tall wheat grass, *Lophopyrum ponticum*) are often unrecognised as a major threat to coastal halophytic plant communities (Boon *et al.* 2015; Leishman *et al.*, Chapter 9 this volume).

22.9 Climate change: sea level rise, changing rainfall patterns, increasing temperature, increasing carbon dioxide

Elevated atmospheric carbon dioxide concentration and its effect on temperature, eustatic sea level, storms and rainfall patterns is an ongoing and poorly managed threat. Observed mangrove

expansion and saltmarsh contraction has been linked to multiple factors associated with climate change: sea-level rise (Rogers *et al.* 2006); altered rainfall patterns (Eslami-Andargoli *et al.* 2009); and elevated carbon dioxide concentrations (Reef and Lovelock 2014; Saintilan and Rogers 2015). An explanation of the changes in vegetation lies in the unique niche of coastal halophytes, defined closely by (largely unknown) tolerances to inundation and salinity. Alterations to these processes, facilitated by climatic drivers, induce changes in the extent of mangrove and saltmarsh.

Adaptation to sea-level rise is essential for the long-term future of coastal halophytes and their provision of ecosystem services. In this regard Northern Australia is fortunate to have long stretches of coastline and vast coastal floodplains that have not yet been exposed to significant development pressures, and where mangrove and saltmarsh can retreat from rising seas into a largely undeveloped hinterland. In temperate and subtropical areas of Australia, where coastal development pressures are markedly greater and have longer historical legacies, constraints on shoreward retreat are more significant.

Models are important tools for planning the adaptation of halophytic communities and their ecosystem services along the developed coastlines of Australia (Rogers *et al.* 2016). Simple approaches that employ bath-tub modelling techniques provide a first-order indication of the vulnerability of coastal ecosystems to sea-level rise (e.g. DCC 2009). They, however, do not account well for the many internal processes that alter elevations of the land relative to water levels, such as sedimentation, plant productivity and root expansion, autocompaction and organic matter decomposition (Rogers *et al.* 2012). More complex models account for internal processes and for possible management interventions, allowing the adaptive capacity of coastal halophytic communities to be evaluated. Under low rates of sea-level rise, these models predict existing mangrove and saltmarsh communities to shift across the intertidal zone to higher elevations while maintaining their position within an altered tidal frame (Traill *et al.* 2011; Rogers *et al.* 2013a). Under high rates of sea-level rise, however, the resilience of halophytic communities may become exhausted, resulting in significant declines in extent. The models also predict declines in extent where there are physical barriers to landward retreat, such as seawalls, levee banks, floodgates, roads and buildings are not major impediments to retreat (Rogers *et al.* 2013a). This suggests that climate adaptation requires management intervention to reduce barriers in many areas of south-eastern Australia that have been turned over to urban, industrial or agricultural land uses.

22.10 Governance and management

Governance and management of halophytic vegetation in Australia is implemented within both marine and terrestrial environments governance structures across all levels of government (federal, state and local) (Rogers *et al.* 2016). While this approach has successfully reduced large-scale reclamation and flood mitigation works, it has led to a complex system of conservation and management that varies significantly between localities. Many legislative and policy instruments are generated on the basis of geographically defined boundaries that are usually delineated as polygons on maps. For example in New South Wales, coastal wetlands are protected under State Environmental Planning Policy No. 14 (SEPP14), a planning instrument under the New South Wales Environmental Planning and Assessment Act (1979), which affords protection from threatening processes to mapped coastal halophytic vegetation outside the Sydney–Newcastle–Wollongong area. However, the mapping of protected wetlands is based on aerial photography captured in the early 1980s, and may thus fail to protect ecological communities that migrate beyond existing conservation and management

boundaries in the context of a changing climate and other drivers (Rogers *et al.* 2013a; Mills *et al.* 2015). More recently, floristic based approaches under the New South Wales *Fisheries Management Act 1994* (amended 2010) and *Environmental Protection and Biodiversity Conservation Act 1999* enable protection of listed saltmarsh communities without the accuracy limitations and temporal constraints imposed by statutory maps.

Climate change may also prompt diversification of conservation priorities and management approaches from traditional measures to achieve comprehensive, adequate and representative conservation of ecosystems (National Biodiversity Strategy Review Task Group 2010), to off-reserve maintenance of the ecosystem services provided by coastal halophytic vegetation. For example, in New South Wales, programmes have been established in selected sites to control expansion of mangrove into adjacent saltmarsh, and in Victoria regional Catchment Management Authorities run a process of single-bid auctions to determine reimbursements to landholders for managing saltmarsh on private land for a minimum of five years according to a pre-existing management plan (Rogers *et al.* 2016). These programmes emphasise the ecological contribution of saltmarsh to fisheries (Mazumder *et al.* 2011) and waterbirds (Spencer *et al.* 2009).

Increasing evidence suggests that mangrove contribute to mitigating the effects of climate change by sequestering carbon from the atmosphere within soils and biomass at a faster rate than saltmarsh (Lovelock *et al.* 2014; Saintilan *et al.* 2013). Balancing the various ecosystem services provided by mangrove and saltmarsh, particularly in the context of a changing climate, might require prioritisation of ecosystem values for conservation and management. Projects and proposals to reinstate tidal exchange across coastal floodplains demonstrate the ecosystem services gained by conversion of low-lying coastal floodplain from marginal agricultural or grazing land, to healthy halophytic communities. Key services include improvements to carbon sequestration, fisheries, biodiversity, reductions in flooding, and improved nutrient cycling (e.g. Creighton *et al.* 2015).

References

Adam, P. (1990) *Saltmarsh Ecology*. Cambridge University Press: Cambridge.

Adam, P. (1996) Saltmarsh. In *State of the Marine Environment Report for Australia. Technical annexe 1*, ed. L.P. Zann and P. Kailola. Department of Environment, Sport and Territory: Canberra, pp. 97–106.

Adame, M.F., Neil, D., Wright, S.F. and Lovelock, C.E. (2010) Sedimentation within and among mangrove forests along a gradient of geomorphological settings. *Estuarine, Coastal and Shelf Science* 86, 21–30.

Akumu, C., Pathirana, S., Baban, S. and Bucher, D. (2011) Examining the potential impacts of sea level rise on coastal wetlands in north-eastern NSW, Australia. *Journal of Coastal Conservation* 15, 15–22.

Allaway, W., Curran, M., Hollington, L. *et al.* (2001) Gas space and oxygen exchange in roots of *Avicennia marina* (Forssk.) Vierh. var. *australasica* (Walp.) Moldenke ex N. C. Duke, the grey mangrove. *Wetlands Ecology and Management* 9, 221–228.

Allen, J.R.L. (2000) Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. *Quaternary Science Reviews* 19, 1155–1231.

Australian Virtual Herbarium (n.d.) Available at: http://avh.chah.org.au.
Ball, M. (1988) Ecophysiology of mangroves. *Trees* 2, 129–142.
Ball, M.C. and Sobrado, M. (1998) Ecophysiology of mangroves: challenges in linking physiological proceses with patterns in forest structure. In *Physiological Plant Ecology*, ed. M. Press, J. Scholes and M. Barker. Springer: New York, pp. 331–346.
Barbier, E.B., Hacker, S.D., Kennedy, C. *et al.* (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81, 169–193.
Barrett-Lennard, E.G. (2003) The interaction between waterlogging and salinity in higher plants: causes, consequences and implications. *Plant and Soil* 253, 35–54.
Beard, J. (1967) An inland occurrence of mangrove. *Western Australian Naturalist* 10, 112–115.
Boon, P. (2006) Biogeochemistry, ecology and management of hydrologically dynamic wetlands. In *The Ecology of Freshwater and Estuarine Wetlands*, ed. D.P. Batzer and R.R. Sharitz. University of California Press: Berkeley, pp. 115–176.
Boon, P.I. (2012) Coastal wetlands of temperate eastern Australia: will Cinderella ever go to the ball? *Marine and Freshwater Research* 63, 845–855.
Boon, P.I., Allen, T., Carr, G. *et al.* (2015) Coastal wetlands of Victoria, south-eastern Australia: providing the inventory and condition information needed for their effective management and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25, 454–479.
Boyd, R., Dalrymple, R. and Zaitlin, B.A. (1992) Classification of clastic coastal depositional environments. *Sedimentary Geology* 80, 139–150.
Breckle, S.-W. (2002) Salinity, halophytes and salt affected natural ecosystems. In *Salinity: Environment–Plants–Molecules*. Springer: Netherlands, pp. 53–77.
Buckley, R. (1983) Biogeography of mangroves on northern Great Barrier Reef Islands. *Bulletin of Marine Science* 33, 767–776.
Bunt, J.S. (1996) Mangrove zonation: an examination of data from seventeen riverine estuaries in tropical Australia. *Annals of Botany* 78, 333–341.
Cahoon, D. (2006) A review of major storm impacts on coastal wetland elevations. *Estuaries and Coasts* 29, 889–898.
Chappell, J. (1993) Contrasting Holocene sedimentary geologies of lower Daly River, northern Australia, and lower Sepik-Ramu, Papua New Guinea. *Sedimentary Geology* 83, 339–358.
Clarke, L.D. and Hannon, N.J. (1969) The mangrove swamp and salt marsh communities of the Sydney district: II. The Holocoenotic complex with particular reference to physiography. *Journal of Ecology* 57, 213–234.
Clarke, P.J. (1993) Dispersal of grey mangrove (*Avicennia marina*) propagules in south-eastern Australia. *Aquatic Botany* 45, 195–204.
Clarke, P.J. (2014) Seeking global generality: a critique for mangrove modellers. *Marine and Freshwater Research* 65, 930–933.
Clarke, P.J. and Myerscough, P. (1993) The intertidal distribution of the grey mangrove (*Avicennia marina*) in southern Australia: the effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. *Australian Journal of Ecology* 18, 307–315.
Clough, B., Andrews, T. and Cowan, I. (1982) Physiological processes in mangroves. In *Mangrove Ecosystems in Australia: Structure, Function and Management*, ed. B.F. Clough. National University Press: Canberra, pp. 193–210.
Crase, B., Liedloff, A., Vesk, P.A. *et al.* (2013) Hydroperiod is the main driver of the spatial pattern of dominance in mangrove communities. *Global Ecology and Biogeography* 22, 806–817.

Creighton, C., Boon, P.I., Brookes, J.D. and Sheaves, M. (2015) Repairing Australia's estuaries for improved fisheries production: what benefits, at what cost? *Marine and Freshwater Research* 66, 493–507.

Curtiss, A. (1888) How the mangrove forms islands. *Garden and Forest* 1, 100.

Dalrymple, R.W., Zaitlin, B.A. and Boyd, R. (1992) Estuarine facies models; conceptual basis and stratigraphic implications. *Journal of Sedimentary Research* 62, 1130–1146.

Davis, J.H. (1940) *The Ecology and Geologic Role of Mangroves in Florida*. Carnegie Institution of Washington: Washington.

DCC (2009) *Climate Change risks to Australia's Coast: A First Pass National Assessment*. Department of Climate Change: Canberra.

De Deckker, P. (1983) Australian salt lakes: their history, chemistry, and biota: a review. *Hydrobiologia* 105, 231–244.

Duggan, M., Connolly, R., Whittle, M. *et al.* (2014) Effects of freshwater flow extremes on intertidal biota of a wet–dry tropical estuary. *Marine Ecology Progress Series* 502, 11–23.

Duke, N. (1995) Genetic diversity, distributional barriers and rafting continents: more thoughts on the evolution of mangroves. *Hydrobiologia* 295, 167–181.

Duke, N., Bunt, J. and Williams, W. (1984) Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Australian Journal of Botany* 32, 87–99.

Duke, N.C. (2002) Global distribution and genetic discontinuities of mangroves - emerging patterns in the evolution of *Rhizophora*. *Trees* 16, 65–79.

Duke, N.C. (2006) *Australia's Mangrove*. University of Queensland: Brisbane.

Duke, N.C., Ball, M.C. and Ellison, J.C. (1998a) Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters* 7, 27–47.

Duke, N.C., Benzie, J.A.H., Goodall, J.A. and Ballment, E.R. (1998b) Genetic structure and evolution of species in the mangrove genus *Avicennia* (Avicenniaceae) in the Indo-west Pacific. *Evolution* 52, 1612–1626.

Edyvane, K.S. (1999) Coastal and marine wetlands in Gulf St. Vincent, South Australia: understanding their loss and degradation. *Wetlands Ecology and Management* 7, 83–104.

Ellison, A.M., Farnsworth, E.J. and Merkt, R.E. (1999) Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography* 8, 95–115.

Ellison, J.C. and Simmonds, S. (2003) Structure and productivity of inland mangrove stands at Lake MacLeod, Western Australia. *Journal of the Royal Society of Western Australia* 86, 25–30.

Eslami-Andargoli, L., Dale, P., Sipe, N. and Chaseling, J. (2009) Mangrove expansion and rainfall patterns in Moreton Bay, southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science* 85, 292–298.

Fagherazzi, S., Kirwan, M.L., Mudd, S.M. *et al.* (2012) Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. *Reviews of Geophysics* 50, RG1002.

Feller, I.C., McKee, K.L., Whigham, D.F. and O'Neill, J.P. (2003) Nitrogen versus phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 62, 145–175.

Flowers, T.J. and Colmer, T.D. (2008) Salinity tolerance in halophytes. *New Phytologist* 179, 945–963.

Flowers, T.J., Galal, H.K. and Bromham, L. (2010) Evolution of halophytes: multiple origins of salt tolerance in land plants. *Functional Plant Biology* 37, 604–612.

Fotheringham, D. and Coleman, P. (2008) Salt marshes in SA. In *Natural History of Gulf St Vincent*, ed. S. Shepherd. Royal Society of South Australia: Adelaide.

Furukawa, K., Wolanski, E. and Mueller, H. (1997) Currents and sediment transport in mangrove forests. *Estuarine, Coastal and Shelf Science* 44, 301–310.

Gedan, K.B., Silliman, B.R. and Bertness, M.D. (2009) Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science* 1, 117–141.

Giri, C., Ochieng, E. and Tieszen, L.L. *et al.* (2011) Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography* 20, 154–159.

Goodrick, G.N. (1970) *A Survey of Wetlands of Coastal New South Wales*. CSIRO Division of Wildlife Research: Canberra.

Gorham, J. (1993) Genetics and physiology of enhanced K+/Na+ discrimination. In *Genetic Aspects of Plant Mineral Nutrition*, ed. P.J. Randall, E. Delhaize, R.A. Richards and R. Munns. Kluwer Academic Publishers: Canberra, pp. 151–158.

Greenwood, M.E. and MacFarlane, G.R. (2006) Effects of salinity and temperature on the germination of *Phragmites australis*, *Juncus kraussii*, and *Juncus acutus*: implications for estuarine restoration initiatives. *Wetlands* 26, 854–861.

Harris, P.T., Heap, A.D., Bryce, S.M., *et al.* (2002) Classification of Australian clastic coastal depositional environments based upon a quantitative analysis of wave, tidal, and river power. *Journal of Sedimentary Research* 72, 858–870.

Hashimoto, T.R., Saintilan, N. and Haberle, S.G. (2006) Mid-Holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond River estuary, New South Wales, Australia. *Geographical Research* 44, 63–76.

Heap, A.D., Bryce, S. and Ryan, D.A. (2004) Facies evolution of Holocene estuaries and deltas: a large-sample statistical study from Australia. *Sedimentary Geology* 168, 1–17.

Hickey, D. and Bruce, E. (2010) Examining tidal inundation and salt marsh vegetation distribution patterns using spatial analysis (Botany Bay, Australia). *Journal of Coastal Research* 26, 94–102.

Hodgkin, E.P. and Hesp, P. (1998) Estuaries to salt lakes: Holocene transformation of the estuarine ecosystems of south-western Australia. *Marine and Freshwater Research* 49, 183–201.

Holmes, G., McGrath, C., Larsen, J. *et al.* (2013) *Coastal ecosystems management. Case study: regional planning*. Great Barrier Reef Marine Park Authority: Townsville.

Howe, A., Rodrigues, J. and MacFarlane, G. (2005) Vegetation-sediment-flow interactions in estuarine wetlands. In *MODSIM05: International Congress on Modelling and Simulation: Advances And Applications for Management and Decision Making, 2005*. Modelling and Simulation Society of Australia and New Zealand: Melbourne.

Hutchings, P. and Saenger, P. (1987) *Ecology of Mangroves*. Queensland University Press: St Lucia.

Kelleway, J. (2005) Ecological impacts of recreational vehicle use on saltmarshes of the Georges River, Sydney. *Wetlands (Australia)* 22, 52–66.

Kelleway, J., Williams, R., Allen, C. *et al.* (2007) *An assessment of the saltmarsh of the Parramatta River and Sydney Harbour*. NSW Department Primary Industries: Cronulla.

Kirkpatrick, J.B. and Glasby, J. (1981) *Saltmarsh in Tasmania: distribution, community, composition and conservation. Occasional paper no. 8*. Department of Geography, University of Tasmania: Hobart.

Kozlowski, T.T. (1997) Responses of woody plants to flooding and salinity. *Tree Physiology Monograph* 17, 490.

Kriwoken, L.K. and Hedge, P. (2000) Exotic species and estuaries: managing Spartina anglica in Tasmania, Australia. Ocean and Coastal Management 43, 573–584.

Laegdsgaard, P. (2006) Ecology, disturbance and restoration of coastal saltmarsh in Australia: a review. *Wetlands Ecology and Management* 14, 379–399.

Lewis, S.E., Sloss, C.R., Murray-Wallace, C.V. *et al.* (2013) Post-glacial sea-level changes around the Australian margin: a review. *Quaternary Science Reviews* 74, 115–138.

Lin, C. and Melville, M. (2010) Mangrove soil: a potential contamination source to estuarine ecosystems of Australia. *Wetlands (Australia)* 11, 68–75.

Lovelock, C., Adame, M., Bennion, V. *et al.* (2014) Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of south east Queensland, Australia. *Estuaries and Coasts* 37, 763–771.

Lovelock, C.E., Ball, M.C., Martin, K.C. and Feller, I.C. (2009) Nutrient enrichment increases mortality of mangroves. *PLoS ONE* 4, e5600.

Lovelock, C., Grinham, A., Adame, M. and Penrose, H. (2010a) Elemental composition and productivity of cyanobacterial mats in an arid zone estuary in north Western Australia. *Wetlands Ecology and Management* 18, 37–47.

Lovelock, C., Sorrell, B., Hancock, N. *et al.* (2010b) Mangrove forest and soil development on a rapidly accreting shore in New Zealand. *Ecosystems* 13, 437–451.

Lovelock, C.E., Feller, I.C., Adame, M.F. *et al.* (2011) Intense storms and the delivery of materials that relieve nutrient limitations in mangroves of an arid zone estuary. *Functional Plant Biology* 38, 514–522.

Lovelock, C.E., Adame, M.F., Bennion, V. *et al.* (2015a) Sea level and turbidity controls on mangrove soil surface elevation change. *Estuarine, Coastal and Shelf Science* 153, 1–9.

Lovelock, C.E., Cahoon, D.R., Friess, D.A. *et al.* (2015b) The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* 526, 559–563.

Lucas, R.M., Milne, A.K., Mitchell, A. *et al.* (2000) Use of stereo aerial photography for assessing changes in the extent and height of mangrove canopies in tropical Australia. *Wetlands Ecology and Management* 10, 159–173.

Macnae, W. (1966) Mangroves in eastern and southern Australia. *Australian Journal of Botany* 14, 67–104.

Mazda, Y., Wolanski, E., King, B. *et al.* (1997) Drag force due to vegetation in mangrove swamps. *Mangroves and Salt Marshes* 1, 193–199.

Mazumder, D., Saintilan, N., Williams, J.R., Szymczak, R. (2011) Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. *Marine and Freshwater Research* 62, 11–19.

McGuinness, K.A. (1996) Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. *Oecologia* 109, 80–87.

McKee, K., Rogers, K. and Saintilan, N. (2012) Response of salt marsh and mangrove wetlands to changes in atmospheric CO2, climate, and sea level. In *Global Change and the Function and Distribution of Wetlands*, ed. B.A. Middleton. Springer: Dordrecht. pp. 63–96.

Mills, M., Leon, J.X., Saunders, M.I. *et al.* (2015) Reconciling development and conservation under coastal squeeze from rising sea-level. *Conservation Letters* doi:10.1111/conl.12213

Mitchell, A.L., Lucas, R.M., Donnelly, B.E. *et al.* (2007) A new map of mangroves for Kakadu National Park, northern Australia, based on stereo aerial photography. *Aquatic Conservation: Marine and Freshwater Ecosystems* 17, 446–467.

Morrisey, D. (1995) Saltmarshes. In *Coastal Marine Ecology of Temperate Australia*, ed. A.J. Underwood and M.G. Chapman. University of New South Wales Press: Sydney, pp. 205–220.

National Biodiversity Strategy Review Task Group (2010) *Australia's Biodiversity Conservation Strategy 2010–2030*. Australian Government: Canberra.

OzCoasts (2009) *National Intertidal/Subtidal Benthic Habitat.* Australian Government: Canberra.

Paling, E.I. and McComb, A.J. (1994) Cyanobacterial mats: a possible nitrogen source for arid-coast mangroves. *International Journal of Ecology and Environmental Sciences* 20, 47–54.
Paul, S., Young, R. (2006) Experimental control of exotic spiny rush, Juncus acutus from Sydney Olympic Park: I. Juncus mortality and re-growth. *Wetlands (Australia)* 23, 1–13.
Pidgeon, I.M. (1940) The ecology of the central coastal area of New South Wales. III. Types of primary succession. *Proceedings of the Linnean Society of New South Wales* 65, 221–249.
Plaziat, J.-C., Cavagnetto, C., Koeniguer, J.-C. and Baltzer, F. (2001) History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. *Wetlands Ecology and Management* 9, 161–180.
Poffenbarger, H., Needelman, B. and Megonigal, J. (2011) Salinity influence on methane emissions from tidal marshes. *Wetlands* 31, 831–842.
Pole, M.S. and Macphail, M.K. (1996) Eocene *Nypa* from Regatta Point, Tasmania. *Review of Palaeobotany and Palynology* 92, 55–67.
Polidoro, B.A., Carpenter, K.E., Collins, L. *et al.* (2010) The loss of species: mangrove extinction risk and geographic areas of global concern. *PLoS ONE* 5, e10095.
Prahalad, V.N., Kirkpatrick, J.B. and Mount, R.E. (2011) Tasmanian coastal saltmarsh community transitions associated with climate change and relative sea level rise 1975-2009. *Australian Journal of Botany* 59, 741–748.
Proske, U. and Haberle, S.G. (2012) Island ecosystem and biodiversity dynamics in north-eastern Australia during the Holocene: unravelling short-term impacts and long-term drivers. *Holocene* 22, 1097–1111.
Reef, R. and Lovelock, C.E. (2014) Historical analysis of mangrove leaf traits throughout the 19th and 20th centuries reveals differential responses to increases in atmospheric CO_2. *Global Ecology and Biogeography* 23, 1209–1214.
Reef, R., Feller, I.C. and Lovelock, C.E. (2010) Nutrition of mangroves. *Tree Physiology* 30, 1148–1160.
Rogers, K. and Saintilan, N. (2009) Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *Journal of Coastal Research* 24, 63–69.
Rogers, K. and Woodroffe, C.D. (2014) Tidal flats and salt marshes. In *Coastal Environments and Global Change*, ed. G. Masselink and R. Gehrels. Wiley and Sons: Oxford, pp. 227–250.
Rogers, K., Saintilan, N. and Heijnis, H. (2005) Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence and sea level rise. *Estuaries* 28, 551–559.
Rogers, K., Wilton, K.M. and Saintilan, N. (2006) Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science* 66, 559–569.
Rogers, K., Saintilan, N. and Copeland, C. (2012) Modelling wetland surface elevation and its application to forecasting the effects of sea-level rise on estuarine wetlands. *Ecological Modelling* 244, 148–157.
Rogers, K., Saintilan, N. and Copeland, C. (2013a) Managed retreat of saline coastal wetlands: challenges and opportunities identified from the Hunter River estuary, Australia. *Estuaries and Coasts* 37, 67–78.
Rogers, K., Saintilan, N., Howe, A.J. and Rodríguez, J.F. (2013b) Sedimentation, elevation and marsh evolution in a south-eastern Australian estuary during changing climatic conditions. *Estuarine, Coastal and Shelf Science* 133, 172–181.
Rogers, K., Saintilan, N. and Woodroffe, C.D. (2014) Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: implications for coastal wetland response to climate change. *Estuarine, Coastal and Shelf Science* 149, 46–56.

Rogers, K., Boon, P.I., Branigan, S. *et al.* (2016) The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. *Marine Policy* 72, 139–155.
Saenger, P. (1982) Morphological, anatomical and reproductive adaptations of Australian mangroves. In *Mangrove Ecosystems in Australia: Structure, Function and Management*, ed. B.F. Clough. Australian National University Press: Canberra, pp. 153–191.
Saenger, P. (1998) Mangrove vegetation: an evolutionary perspective. *Marine and Freshwater Research* 49, 277–286.
Saenger, P. (2002) *Mangrove Ecology, Silviculture and Conservation.* Kluwer Academic Press: Dordrecht.
Saenger, P., Specht, M.M., Specht, R.L. and Chapman, V.J.(1977) Mangal and coastal saltmarsh communities in Australasia. In *Ecosystems of the World I: Wet Coastal Ecosystems*, ed. V.J. Chapman. Elsevier: Amsterdam.
Saintilan, N. (1997a) Above- and below-ground biomass of mangroves in a sub-tropical estuary. *Marine and Freshwater Research* 48, 601–604.
Saintilan, N. (1997b) Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Marine and Freshwater Research* 48, 147–152.
Saintilan, N. (2009) Biogeography of Australian saltmarsh plants. *Austral Ecology* 34, 929–937.
Saintilan, N. and Hashimoto, T.R. (1999) Mangrove-saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia. *Hydrobiologia* 413, 95–102.
Saintilan, N., Rogers, K. (2013) The significance and vulnerability of Australian saltmarshes: implications for management in a changing climate. *Marine and Freshwater Research* 64, 66–79.
Saintilan, N. and Rogers, K. (2015) Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. *New Phytologist* 205, 1062–1070.
Saintilan, N., Rogers, K., Mazumder, D. and Woodroffe, C. (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in south-eastern Australian coastal wetlands. *Estuarine, Coastal and Shelf Science* 128, 84–92.
Saintilan, N., Wilson, N.C., Rogers, K. *et al.* (2014) Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology* 20, 147–157.
Sainty, G., Hosking, J., Carr, G.W. and Adam, P. (2012) *Estuary Plans and What's Happening to Them in South-east Australia*. Sainty and Associates Pty Ltd: China.
Sammut, J., Melville, M.D., Callinan, R.B. and Fraser, G.C. (1995) Estuarine acidification: impacts on aquatic biota of draining acid sulphate soils. *Australian Geographical Studies* 33, 89–100.
Sammut, J., White, I. and Melville, M. (1996) Acidification of an estuarine tributary in eastern Australia due to drainage of acid sulfate soils. *Marine and Freshwater Research* 47, 669–684.
Santini, N.S., Reef, R., Lockington, D.A. and Lovelock, C.E. (2015) The use of fresh and saline water sources by the mangrove *Avicennia marina*. *Hydrobiologia* 745, 59–68.
Scholl, D.W. (1964) Recent sedimentary record in mangrove swamps and rise in sea level over the south-western coast of Florida: part 1. *Marine Geology* 1, 344–366.
Semeniuk, V. (1980) Mangrove zonation along an eroding coastline in King Sound, north-western Australia. *The Journal of Ecology* 68, 789–812.
Semeniuk, V. (1983) Mangrove distribution in north-western Australia in relationship to regional and local freshwater seepage. *Vegetatio* 53, 11–31.
Sinclair, S. and Boon, P.I. (2012) Changes in the area of coastal marsh in Victoria since the mid 19th century. *Cunninghamia* 12, 153–176.
Spencer, J.A., Monamy, V. and Breitfuss, M. (2009) Saltmarsh as habitat for birds and other vertebrates. In *Australian Saltmarsh Ecology*, ed. N. Saintilan. CSIRO Publishing: Collingwood.

Stoddart, D.R. (1980) Mangroves as successional stages, inner reefs of the northern Great Barrier Reef. *Journal of Biogeography* 7, 269–284.
Stuart, S.A., Choat, B., Martin, K.C. *et al.* (2007) The role of freezing in setting the latitudinal limits of mangrove forests. *New Phytologist* 173, 576–583.
Thom, B. (1982) Mangrove ecology: a geomorphological perspective. In *Mangrove Ecosystems in Australia*. Australian National University Press: Canberra, pp. 3–17.
Thom, B.G., Wright, L.D. and Coleman, J.M. (1975) Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf-Ord River, Western Australia. *Journal of Ecology* 63, 203–232.
Traill, L.W., Perhans, K., Lovelock, C.E. *et al.* (2011) Managing for change: wetland transitions under sea-level rise and outcomes for threatened species. *Diversity and Distributions* 17, 1225–1233.
Waisel, Y. (1972) *Biology of Halophytes.* Academic Press: California.
Wei, L., Lockington, D.A., Yu, S. and Lovelock, C.E. (2015) Nitrogen sharing and water source partitioning co-occur in estuarine wetlands. *Functional Plant Biology* 42, 410–417.
Williams, R.J. and Watford, F.A. (1997) *Change in the Distribution of Mangrove and Saltmarsh in Berowra and Marramarra Creeks. 1941–1992*. NSW Fisheries Office of Conservation, Fisheries Research Institute: Cronulla.
Wolanski, E. (2006) The evolution time scale of macro-tidal estuaries: examples from the Pacific Rim. *Estuarine, Coastal and Shelf Science* 66, 544–549.
Woodroffe, C. (1992) Mangrove sediments and geomorphology. In *Tropical Mangrove Ecosystems*, ed. A.I. Robertson and D.M. Alongi. American Geophysical Union: Washington, pp. 7–41.
Woodroffe, C.D. (1987) *Pacific Island Mangroves: Distribution and Environmental Settings.* University of Hawaii Press: Hawaii.
Woodroffe, C.D. (1988) Relict mangrove stand on Last Interglacial terrace, Christmas Island, Indian Ocean. *Journal of Tropical Ecology* 4, 1–17.
Woodroffe, C.D. (2003) *Coasts: Form, Process and Evolution.* Cambridge University Press: New York.
Woodroffe, C.D., Mulrennan, M.E. and Chappell, J. (1993) Estuarine infill and coastal progradation, southern van Diemen Gulf, northern Australia. *Sedimentary Geology* 83, 257–275.
Woodroffe, C.D., Rogers, K., McKee, K.L. *et al.* (2015) Mangrove sedimentation and response to relative sea-level rise. *Annual Review of Marine Science* 8, 243–266.

Austral ECOLOGY A Journal of ecology in the Southern Hemisphere

Austral Ecology (2009) **34**, 929–937

Biogeography of Australian saltmarsh plants

NEIL SAINTILAN

NSW Department of Environment, Climate Change and Water, PO Box A290, Sydney 2001, NSW, Australia (Email: Neil.Saintilan@environment.nsw.gov.au)

Abstract The paper seeks to define patterns in the distribution of Australian saltmarsh plants over a continental scale, and test for associations with environmental variables. The distribution of 93 species of Australian saltmarsh plants was documented from the records of the Australian Virtual Herbarium and published reports. The Interim Bioregionalisation of Australia provided a spatial unit for the analysis of patterns of diversity. Saltmarsh diversity was shown to be strongly correlated with latitude and temperature. Multivariate routines including cluster analysis demonstrated consistent geographic patterns in species assemblages. The primary distinction was found to be a north-south divide dissecting the continent at the latitude of 23° south, separating a species-rich southern flora from a species-poor northern flora. Subsequent dissimilarities were defined between coastlines of contrasting orientation. Mean minimum temperature was found to explain nearly 80% of variability in saltmarsh species diversity between bioregions, with diversity inversely related to temperature.

Key words: bioregion, distribution, flora, saltmarsh, temperature.

INTRODUCTION

Coastal (intertidal) saltmarsh has been defined by Adam (1996) as an intertidal plant community dominated by herbs and low shrubs. However, the plants that comprise coastal saltmarsh are not exclusively intertidal, a characteristic that sets them apart from mangrove. Most saltmarsh species take advantage of inland saline environments, both aquatic and arid, and their intertidal occurrence is sometimes best understood as a continuation of a network of saline aquatic environments. This is particularly true of the South Australian saltmarsh flora.

The characteristics that suit plants to this harsh environment are a tolerance of extreme ranges of salinity and soil water content. Periodic inundation of the intertidal environment by seawater salinizes the soil, and salts will subsequently concentrate by processes of evaporation and transpiration. While this phenomenon occurs the world over, in Australia the range of salinity encountered is enhanced by the extremes of climatic variability and (in the tropics) seasonality (Adam 1996).

Plants occupying the saltmarsh must be able to withstand periodic soil salinity and inundation. There is a range of survival strategies among the 100 or more species in Australian saltmarshes. The adaptations to saline conditions are often at the expense of growth rate, and it is this that explains the narrow penetration of saltmarsh plants into upslope freshwater terrestrial environments (Adam 1990).

Accepted for publication November 2008.

Two-thirds of the 90 Australian saltmarsh plant species listed in Table 1 belong to five families: Chenopodiaceae, Poaceae, Cyperaceae, Aizoaceae and Asteraceae. While there is a high degree of endemism at a species level among Australian saltmarshes, at a generic and family level there are numerous commonalities with the saltmarshes of other continents (Adam 1990). In this sense the saltmarshes of Australia are not as distinctly Australian as the terrestrial vegetation communities, though there are unique ecological features of the Australian saltmarsh.

Most confirmed records of species occurrences in Australia are now represented in the Australian Virtual Herbarium, an interactive Internet-based tool which can be accessed through the websites of participating herbaria. Bridgewater and Cresswell (2003) used a prototype version of this tool, along with published records and personal observations, to define the distribution of saltmarsh species groups throughout the continent. Their work presented the first systematic presentation of saltmarsh species assemblage distribution in Australia.

Bridgewater and Cresswell (2003) used a manual sorting procedure to identify five coastal/inland saltmarsh phytogeographic groups in their analysis of previous publications and the (then) prototype Australian Virtual Herbarium. The data were manually sorted, though the decision rules were not presented. Two of these groups, the *Sclerostegia tenuis* Group and the *Halosarcia pergranulata* subsp. *pergranulata* Group were inland associations, being characteristic of the central arid/semiarid and Murray-Darling basin regions respectively. Some degree of renaming is required

© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia

doi:10.1111/j.1442-9993.2009.02001.x

Table 1. Plant species included in the analysis

Selected Australian saltmarsh plant species		
Aizoaceae	**Caryophyllaceae**	*Tecticornia arbuscula*
Carpobrotus rossii	*Spergularia marina*	*Tecticornia australasica*
C. glaucescens	**Centrolepidaceae**	*T. disarticulata*
Disphyma crassifolium	*Centrolepis polygyna*	*T. indica*
Sesuvium portulacastrum	**Chenopodiaceae**	*T. pergranulata*
Tetragonia tetragonoides	*Atriplex cinerea*	*T. pruinosa*
Amaranthaceae	*A. hypoleuca*	*T. pterygosperma*
Hemichroa pentandra	*A. semibaccata*	*T. auriculata*
Apiaceae	*Chenopodium glaucum*	*T. deleiformis*
Apium prostratum	*Dissocarpus biflorus*	*T. flabelliformis*
Lilaeopsis polyantha	*Dysphania littoralis*	*T. halocnemoides*
Asteraceae	*Enchylaena tomentosa*	*T. laeptoclada*
Angianthus preissianus	*Maireana brevifolia*	*T. leptidosperma*
Aster australasica	*M. oppositifolia*	*T. peltata*
Centaurium spicatum	*Neobassia astrocarpa*	*T. syncarpa*
Cotula coronifolia	*Rhagodia crassifolia*	*T. tenuis*
Reptinella reptans	*R. candolleana*	*Threlkeldia diffusa*
Senecio pinnatifolius	*Salsola tragus*	**Convolvulaceae**
Bataceae	*Sarcocornia*	*Wilsonia backhousei*
Batis argillicola	*quinqueflora*	*W. humilis*
Campanulaceae	*S. blackiana*	*W. rotundifolia*
Lobelia anceps	*Suaeda australis*	
	S. arbusculoides	**Restionaceae**
Cyperaceae	**Juncaginaceae**	*Apodasmia brownii*
Baumea acuta	*Triglochin striata*	**Scrophulariaceae**
B. teretifolia	*T. minutissima*	*Mimulus repens*
B. juncea	*T. mucronatum*	**Theophrastaceae**
Fimbristylis ferruginea	**Malvaceae**	*Samolus repens*.
F. polytrichoides	*Lawrencia spicata*	
Gahnia filum	**Myoporaceae**	
Finicia nodosa	*Myoporum insulare*	
Isolepis cernua	**Plumbaginaceae**	
Schoenus nitens	*Limonium solanderi*	
Cyperaceaae	**Poaceae (Gramineae)**	
Cyperus laevigatus	*Austrostipa stipoides*	
Fabaceae	*Distichlis distichophylla*	
Lotus australis	*Lachnagrostis billardierei*	
Frankeniaceae		
Frankenia pauciflora	*Phragmites australis*	
F. ambita	*Puccinellia stricta*	
F. tetrapetala	*Sporobolus virginicus*	
Goodeniaceae	*Xerochloa imberbis*	
Selliera radicans	*Zoysia macrantha*	
Juncaceae	**Portulacaceae**	
Juncus bufonius	*Portulaca bicolour*	
Juncus kraussii	*P. oleracea*	
	P. pilosa	

after the incorporation of *Halosarcia* and *Sclerostegia* into the genus *Tecticornia* following the review of Shepherd and Wilson (2007). The remaining three groups covered the major coastal saltmarsh associations, summarized as follows:

- The *Sclerostegia (Tecticornia) arbuscula- Juncus krausii* Group, characteristic of the southern Australian coastline and Tasmania. Species distinguishing this group included *Juncus kraussii*, *Selliera radicans*, *Cotula coronopifolia*, *Angianthus preissianus*, *Centrolepis polygyna*, *Samolus repens*, *Suaeda australis*, *Triglochin striatum*, *Sarcocornia quinqueflora* and *Parapholis incurva*.
- A Western Australian central coast/inland group (corresponding to the arid northern though including the western part of the southern). The species distinguishing this group are largely Chenopod shrubs of the genus *Halosarcia* (now *Tecticornia*) including *Tecticornia doleiformis*, *T. leptoclada*, *T. undulata*, *T. halocnemoides*, *T. halocnemoides subsp.*

doi:10.1111/j.1442-9993.2009.02001.x
© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia

14429993, 2009, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2009.02001.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

catenulata, *T. pergranulata pergranulata*, *T. pterygosperma pterygosperma*, *T. lylei*, *T. peltata*, *Maireana oppositifolia* and *Sclerostegia* (now *Tecticornia*) *disarticulata*.

- A group characteristic of the central eastern and northern Australian coastline, termed the *Suaeda arbusculoides – Tecticornia indica julacca* group. Species distinguishing this group are *Suaeda arbusculoides, Tecticornia indica* subsp. *julacea, T. indica* subsp. *leiostachya, T. pergranulata* subsp. *queenslandica* and *Tecticornia australasica*.

There are a number of reasons to revisit the biogeography of Australian saltmarsh plants. First, the Australian Virtual Herbarium has been largely completed and a comprehensive database of saltmarsh plant distribution now exists for the continent. Second, the derived database is amenable to the application of multivariate routines providing *a priori* ordinations of biogeographic patterns. Third, the publication of the Ozestuaries database (http://www.ozcoasts.org.au) has allowed the exploration of relationships between saltmarsh assemblages and a range of environmental variables.

The paper therefore has two primary aims. First, by using the most extensive distribution accounts available, biogeographic provinces will be defined *a priori* from multivariate techniques, and compared with those identified by Bridgewater and Cresswell (2003). Second, relationships will be tested between saltmarsh assemblage and a range of environmental variables including climate (rainfall, temperature and evaporation), aerial extent (saltmarsh, mangrove and intertidal), location (latitude and longitude) and the number of estuaries within each bioregion.

METHODS

The Interim Bioregionalisation of Australia (IBRA) was used to provide the fundamental spatial unit for this analysis (Environment Australia 2000). While a marine and coastal regionalization has also been developed (Commonwealth of Australia 2006), there are a greater number of IBRA coastal bioregions (36) than the Interim Marine and Coastal Regionalisation of Australia coastal bioregions (15), with the Interim Marine and Coastal Regionalisation of Australia regions for the most part aggregations of the IBRA coastal regions. The decision of Bridgewater and Cresswell (2003) to use the IBRA regions is followed in this analysis.

For this paper, the analysis was repeated using the completed records for 93 species of saltmarsh plant now within the Australian Virtual Herbarium, listed in Table 1. This analysis derives saltmarsh biogeographic provinces on the basis of multivariate analyses, using a number of routines in the PRIMER statistical package (Clarke & Warwick 2001). The analysis proceeded through four stages:

1. The Australian Virtual Herbarium was used to determine the known distribution of 93 species listed in Table 1. This list was compiled primarily on the basis of species lists in Adam (1981), Adam *et al.* (1988), Kirkpatrick and Glasby (1981), Bridgewater, Rosser & Corona (1981), Johns (2006), Delta Environmental Consulting (2008) and Bridgewater and Cresswell (2003). Some adjustments were made where published accounts expanded the range of some species including, for example, the detailed biogeographic work of Kirkpatrick and Glasby (1981) for Tasmanian saltmarshes.
   On several occasions species were found to occur in herbarium records under two or more names. Observations of *Stipa stipoides* were collated under *Austrastipa stipoides*, observations of *Scirpus nodosa* and *Isolepsus nodosa* were collated under *Ficinia nodosa*, and observations of *Limonium solanderi* were included under *Limonium australe*. Introduced species were excluded from the analysis.
2. The distribution was categorized on the basis of IBRA bioregions (Fig. 1). The Hampton and Nullabor bioregions in South Australia were excluded given the absence of intertidal area on the Great Australian Bight between Fowlers Bay, SA (33°14′S 124°02′E, and Point Dempster WA (32°11′S 133°28′E).
3. Information was extracted from the Ozestuaries data base (http://www.ozcoasts.org.au) on the number of estuaries within each bioregion and the extent of mangrove, saltmarsh and intertidal area. Average annual rainfall, evaporation, maximum daily temperature and daily minimum temperatures for the nearest meteorological station to the estuaries of each bioregion were accessed from the Bureau of Meteorology.
4. The multivariate techniques in the PRIMER program (Clarke & Warwick 2001) were used to
   - Present a cluster analysis of bioregions on the basis of the presence or absence of saltmarsh species. A Bray-Curtis measure of dissimilarity was used as the basis of this analysis.
   - Determine species contributing most to the clustering of bioregions, using the SIMPER routine.
   - Explore relationships between community composition and environmental variables using BIOENV. This procedure compares patterns in the ordination of bioregions using biotic and environmental variables, identifying the subset of variables producing a similarity matrix that maximizes Spearman Rank Correlations with that produced using species occurrence (Clarke & Ainsworth 1993). The environmental variables included were latitude, longitude, saltmarsh area, mangrove area, intertidal area,

© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia
doi:10.1111/j.1442-9993.2009.02001.x

14429993, 2009, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2009.02001.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

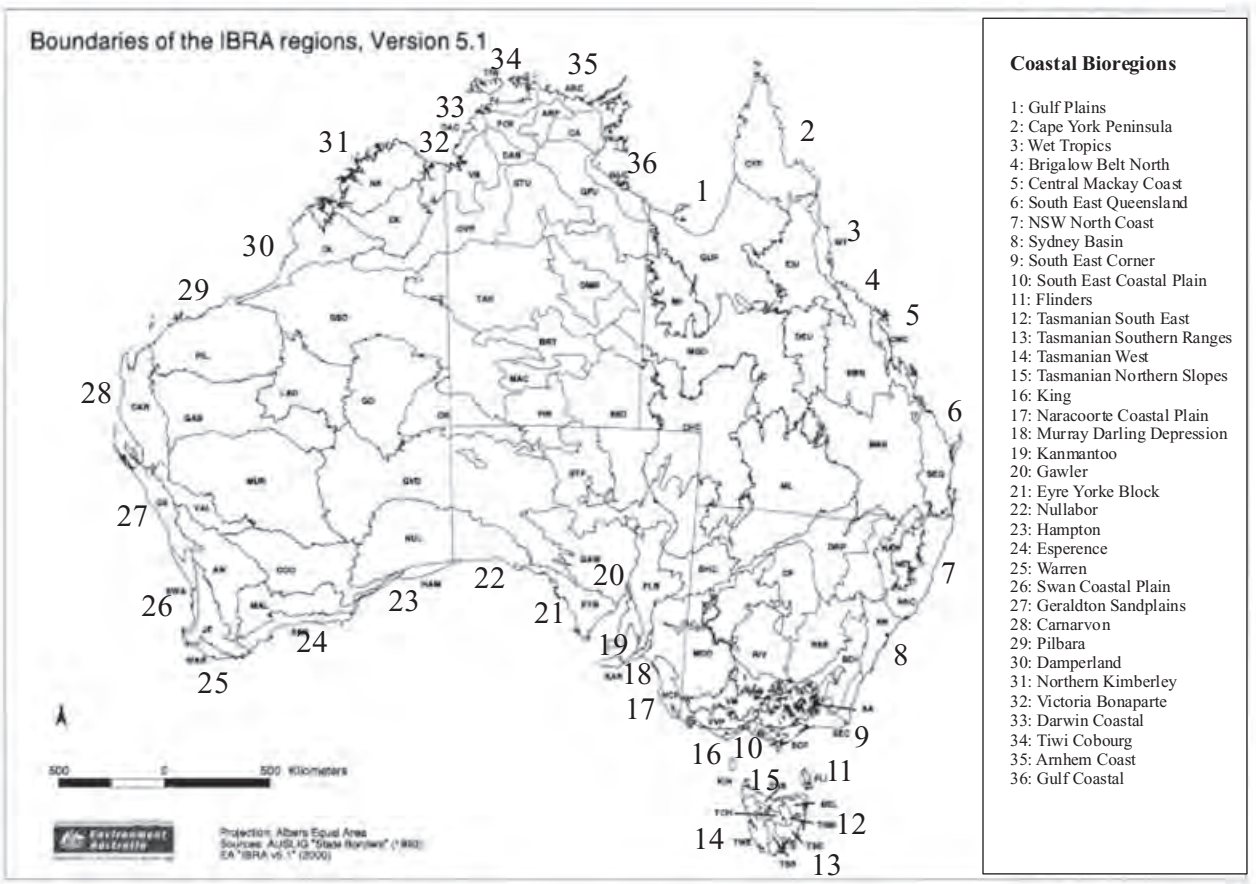


Fig. 1. Coastal bioregions included in the analysis.

mean minimum daily temperature, mean maximum daily temperature, mean annual rainfall and mean annual evaporation. Environmental variables were transformed using Euclidean distance prior to their incorporation into a Bray-Curtis similarity matrix.

Univariate regression was used to test relationships between species diversity and temperature, latitude and saltmarsh area.

RESULTS

Environmental patterns in species assemblage and diversity

Temperature and geographic location (latitude and longitude) proved to be the environmental factor explaining most of the variation in species assemblage, with the BIOENV analysis returning a Spearman Rank Correlation between species assemblage and the three variables of 0.913. Latitude alone returned a correlation coefficient with species assemblage of 0.9. BIOENV was recalculated removing latitude and longitude from the variables. The highest resulting correlation was between species assemblage and mean minimum and mean maximum temperatures, of 0.8. The other climatic variables (evaporation and rainfall) did not provide additional explanatory power, nor did those variables relating to the extent of intertidal area.

Univariate regression analysis showed the relationship between species diversity and latitude to be particularly strong ($r^2 = 0.69$, $P < 0.001$; Fig. 2). Temperature also showed a strong inverse relationship with species diversity, for both mean maximum daily temperature ($r^2 = 0.70$, $P < 0.001$; Fig. 3) and mean minimum daily temperature ($r^2 = 0.78$, $P < 0.001$). The increase in diversity with temperature is non-linear, with diversity declining below a mean minimum temperature of 8°C. Species diversity showed an inverse relationship with saltmarsh area ($r^2 = 0.3$, $P < 0.001$) with saltmarsh area increasing with decreasing latitude. Only a weak, and inverse, association was found between species diversity and the number of estuaries within each bioregion ($r^2 = 0.3$, $P = 0.02$).

doi:10.1111/j.1442-9993.2009.02001.x
© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia

14429993, 2009, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2009.02001.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

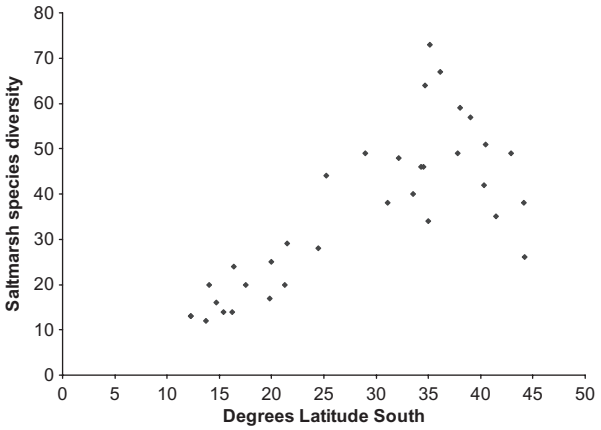


Fig. 2. Relationship between saltmarsh diversity and latitude for 34 Australian coastal bioregions. (Saltmarsh plants listed in Table 1) ($r^2 = 0.69$, $P < 0.001$).

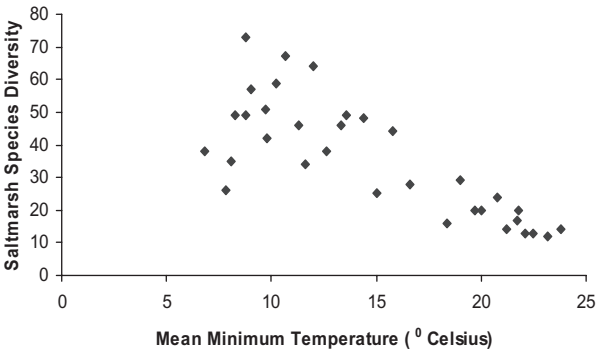


Fig. 3. Relationship between saltmarsh diversity and mean minimum daily temperature for 34 Australian coastal bioregions. (Saltmarsh plants listed in Table 1) ($r^2 = 0.73$, $P < 0.001$).

Clustering of bioregions

The cluster classification dendrogram (Fig. 4) represents the similarity or dissimilarity of bioregions based on presence or absence of saltmarsh species. The Bray-Curtis similarity index ranges from 0 (no species in common) to 100 (all species in common). The broader divisions on the tree are therefore between groups of sites with a lower proportion of species in common (e.g. 23% in the first major division). Higher-order branchlets represent similar bioregions in the overall 'assemblage' of saltmarsh plant species present (up to 90% of species in common in some cases). The abundance of saltmarsh plants in each bioregion was not considered in this analysis.

The northern and southern divisions

The clustering of coastal bioregions in terms of species presence and absence reveals a hierarchy of sites of three layers (Fig. 4). The primary division is between a northern and southern saltmarsh flora, separated at 23° latitude. The two divisions of the continent have less than 25% of species in common.

Species occurring primarily in the northern bioregions include *Tecticornia australasica*, *Fimbristylis polytrichoides*, *Fimbristylis ferruginea*, *Portulaca bicolor*, *Batis agrillicola*, *Xerochloa imberis* and *Sesuvium portulacastrum*. Species occurring primarily in the southern bioregions include are *Samolus repens*, *Atriplex cinerea*, *Apium prostratum*, *Myoporum insulare* and *Cotula coronifolia* (see Fig. 5 for examples).

Some genera do not show strong overlap in the distribution of member species. For example, the two species of *Carpobrotus* show mutually exclusive ranges, with *C. rossii* and *C. glaucescens* occupying the southern and eastern coastlines respectively. Often, though, and particularly among sedges, species show strongly sympatric ranges, as illustrated in Figure 6.

Subgroups based on coastal orientation

The cluster analysis represented in Figure 4 suggests a tertiary level of division based on contiguous stretches of coastline demarcated by orientation. These subgroups characteristically share between 70% and 80% of species. In the southern division these may be described as eastern, southern and western assemblages. Examples of primarily eastern species include *Baumea teretifolia*, *Carpobrotus glaucescens*, *Aster australasica*, *Fimbristylis ferrugubea* and *Sesuvium portulacastrum*. Primarily southern species include *Sarcocornia blackiana*, *Hemichroa pentandra*, *Tecticornia arbuscula* and *Distichlis distichophylla*.

The northern division can be similarly divided geographically. The western coast has been discussed previously, being arid with few estuaries. The tropical northern segment can be divided into a north-facing coast, though including the eastern section of Cape York Peninsula. The saltmarsh flora of the north-facing coastlines is relatively depauperate, though contains a few characteristic species such as *Xerochloa imberbis*. The Queensland tropical east coast supports a higher number of saltmarsh species with *Agristis subulata*, *Baumea juncea* and *Limonium australe* becoming important.

DISCUSSION

The increasing saltmarsh species diversity with latitude in Australia has been mentioned by several authors (Saenger *et al.* 1977; Specht 1981; Adam 1996) and contrasts to the decreasing diversity of mangrove species (Saenger *et al.* 1977). This analysis provides firm quantitative support, with latitude

© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia
doi:10.1111/j.1442-9993.2009.02001.x

14429993, 2009, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2009.02001.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

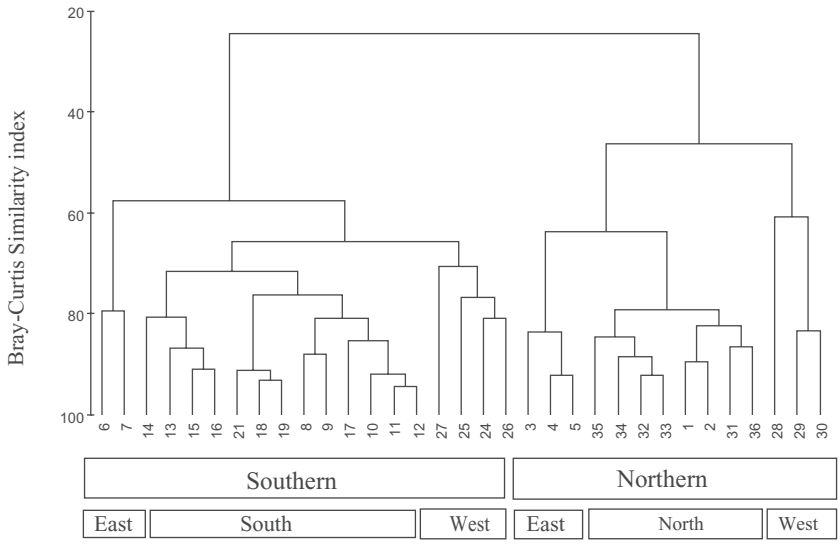


Fig. 4. Clustering dendrogram of Interim Bioregionalisation of Australia bioregions on the basis of saltmarsh floristic composition. At the highest level of dissimilarity, the continent can be divided north-south along 23° latitude.

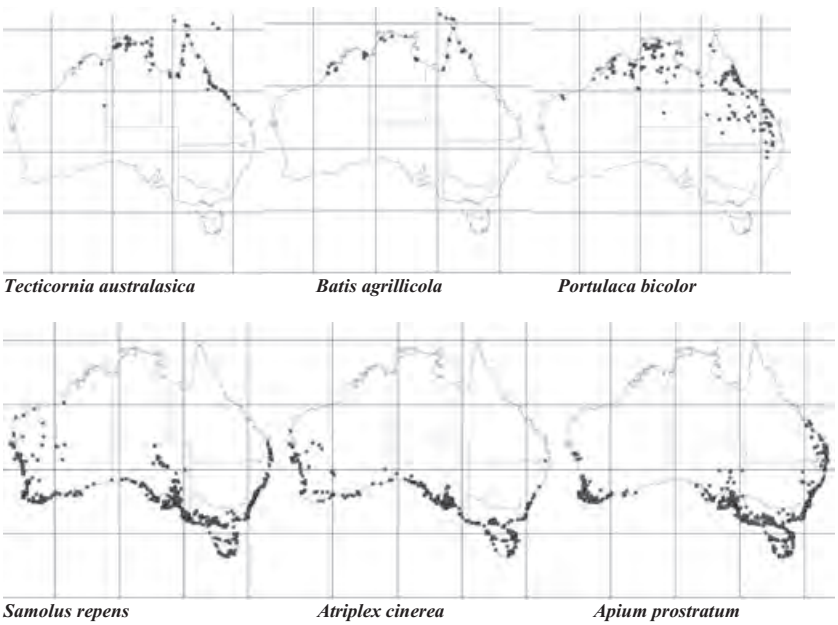


Fig. 5. Species characteristic of northern and southern continental divisions.

explaining more than two-thirds of the variation in saltmarsh species diversity between coastal bioregions. The trend holds even with the significant variation between bioregions in saltmarsh area, (which is inversely related to latitude), and mean annual rainfall.

In general, there is little relationship between the intertidal area available to saltmarsh plants and saltmarsh biodiversity. Northern Australia supports a low diversity of saltmarsh in spite of the large intertidal area available to saltmarsh colonization. To some degree this may be related to climatic constraints, with hypersaline conditions developing during the dry season in many parts of northern Australia. Wide intertidal areas will be devoid of saltmarsh in these situations. Notwithstanding, the four southern states of Tasmania, Victoria, South Australia and New South Wales contain less than 2.5% of the total saltmarsh/saltpan area yet together support 90% of the saltmarsh species of Australia.

The strong inverse relationship between mean minimum daily temperature and species diversity ($r^2 = 0.78$) suggests that the germination and growth

doi:10.1111/j.1442-9993.2009.02001.x
© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia

14429993, 2009, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2009.02001.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

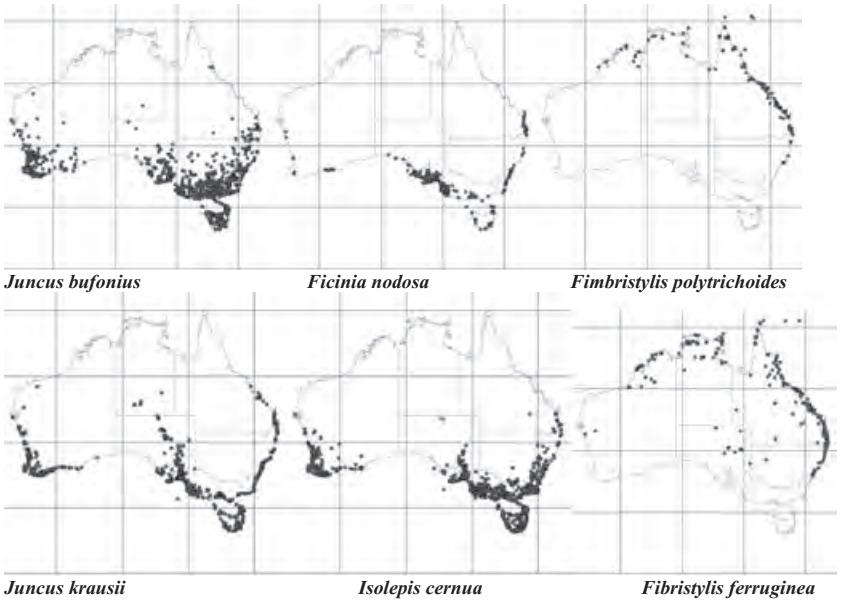


Fig. 6. Confirmed distribution of the common saltmarsh rushes *Juncus bufonius, Juncus kraussii, Ficinia nodosa* and *Isolepis cernua*. The coastal distributions largely sympatric. The tropical sedge *Fimbristylis ferruginea* and *Fimbristylis polytrichoides* are sympatric through the northern division.

Table 2. Percentage of the total Australian saltmarsh flora present in each bioregion

Bioregion	%	Bioregion	%	Bioregion	%
Gulf Plains	19	Tasm. Southrn Ranges	36	Geraldton Sandplains	46
Cape York Peninsula	19	Tasmanian West	24	Carnarvon	26
Wet Tropics	22	Tasm. Northn. Slopes	33	Pilbara	19
Brigalow Belt North	23	King	39	Dampierland	16
Central Mackay Coast	27	Naracoote Coastal Plain	55	Northern Kimberley	15
South East Queensland	41	Murray Darling Depress	63	Victoria Bonaparte	13
NSW North Coast	36	Kanmantoo	68	Darwin Coastal	11
Sydney Basin	43	Gawler	37	Tiwi Cobourg	12
South East Corner	46	Eyre Yorke Block	60	Arnhem Coast	12
SE Coastal Plain	53	Esperance	43	Gulf Coastal	13
Flinders	48	Warren	32		
Tasmanian South East	46	Swan Coastal Plain	45		

of several species may be inhibited by higher temperatures. Physiological research in this regard is limited and equivocal. Khan and Ungar (1984) found the germination of the halophyte *Atriplex triangularis* to be promoted by higher day-time and lower night-time temperatures, while Greenwood and MacFarlane (2006) recently found that the germination of *Phragmites australis* was inhibited by higher temperatures. It is notable that the dominant saltmarsh species in the northern division is the C_4 species *Sporobolus virginicus*. One potential implication of global warming for Australian saltmarsh is the southward migration of climatic zones, possibly leading to a decrease in the diversity of the southern saltmarsh flora.

The development of an IBRA was a useful aid to the systematic conservation of Australia's aquatic resources. The value of this approach is obvious when used as the basis for exploring saltmarsh biogeographic patterns. Table 2 represents the proportion of the total saltmarsh flora species present in each of the 36 coastal bioregions. Clearly, some bioregions are of particular significance in that they contain a high proportion of the nation's saltmarsh species, with the South Australian bioregions of Kanmantoo, Murray-Darling Depression and Eyre Yorke Block being good examples. Three quarters of the 93 listed saltmarsh species grow within 200 km of Adelaide.

The highest level of clustering of bioregions on the basis of saltmarsh flora is between a northern and southern division separated at 23° latitude with less than 25% overlap between species. The relatively depauperate northern division corresponds broadly to the

© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia
doi:10.1111/j.1442-9993.2009.02001.x

14429993, 2009, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2009.02001.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Arid Tropical, Dry Tropical, Wet-Dry Tropical, Gulf and Wet Tropical groups of Bridgewater and Cresswell (1999). The diverse southern division corresponds to Bridgewater and Cresswell's (1999) Warm Temperate, Temperate Tasmania, Mediterranean and Western Transitional groupings.

Lower levels of clustering are more equivocal, though particularly arid bioregions (the Arid Tropical region of Bridgewater & Cresswell 1999), and the arid, rock-dominated south Australian bioregions of the Great Australian Bight, separate out from more humid segments of the major divisions. A final level of classification based on coastal orientation is proposed for both divisions. The proposed scheme has strong affinities with that of Bridgewater and Cresswell (2003) though is not identical.

The herbarium and published record data have not to date been analysed on an estuary-by-estuary basis. Species lists for Australian estuaries would have several advantages. First, such a list would provide a finer scale of resolution in documenting the occurrence of saltmarsh plants. Further, the lists would provide important guidance to regional natural resource management bodies, in identifying threatened or endangered species within estuaries and suggesting species lists for appropriate saltmarsh rehabilitation.

The development of biogeographic theory has been underpinned by two nearly ubiquitous relationships, namely the decreasing diversity of species within increasing latitude, and the increasing diversity of species within increasing area (Pianka 1966; MacArthur 1972; Hillebrand 2004; Qian, Fridley and Palmer 2007). Patterns in the diversity of Australian saltmarsh flora at a continental scale provide an exception to both, with diversity increasing with increasing latitude and decreasing with the intertidal area available. The causes of latitudinal patterns in diversity are unresolved, with considerable debate continuing over hypotheses including the age, size, and mid-domain effects of tropical latitudes (Gorelick 2008), higher rates of endemism, and lower extinction rates (Mittelbach *et al.* 2008). Of relevance to Australian saltmarsh diversity is the distribution of mangrove, the dominant intertidal assemblage of tropical shorelines. The high diversity and endemism of Australian saltmarsh at its southern limits may be related to the rarity or absence of mangroves along southern shorelines during much of the Quaternary, though little is known of the distribution and abundance of either mangrove or saltmarsh in Australia beyond the Holocene.

ACKNOWLEDGEMENTS

Rob Williams, Paul Adam and Robert Whittaker are thanked for helpful comments on an earlier draft of this paper. Leroy Gonzalves assisted with accessing data for this analysis.

REFERENCES

Adam P. (1981) Saltmarsh plants of New South Wales. *Wetlands (Aust)* **1,** 11–9.

Adam P. (1990) *Saltmarsh Ecology*. Cambridge University Press, Cambridge.

Adam P. (1996) Saltmarsh. In: *State of the Marine Environment Report for Australia* (eds L. P. Zann & P. Kailola) pp. 97–105. Technical Annexe 1. Department of Environment, Sport and Territories, Canberra.

Adam P., Wilson N. C. & Huntley B. (1988) The phytosociology of coastal saltmarsh vegetation in New South Wales. *Wetlands (Aust)* **7,** 35–57.

Bridgewater P. & Cresswell I. D. (2003) Identifying biogeographic patterns in Australian saltmarsh and mangal systems: a phytogeographic analysis. *Phytocoenologia* **33,** 231–50.

Bridgewater P. B. & Cresswell I. D. (1999) Biogeography of mangrove and saltmarsh vegetation: implications for conservation and management in Australia. *Mangroves and Salt Marshes* **3,** 117–25.

Bridgewater P. B., Rosser C. & Corona A. (1981) *The Saltmarsh Plants of Southern Australia*. Monash University Botany Department, Melbourne.

Clarke K. R. & Ainsworth M. (1993) A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.* **92,** 205–19.

Clarke K. R. & Warwick R. M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edn. PRIMER-E, Plymouth.

Commonwealth of Australia (2006) A guide to the integrated coastal and marine bioregionalisation of Australia. Version 4. National Oceans Office Branch, Department of Environment and Heritage, Hobart.

Delta Environmental Consulting (2008) Coastal Flora for South Australia. [Cited 10 January 2008.] Available from URL: http://www.deltaenvironmental.com.au/archives/SA_flora/SA_flora.htm

Environment Australia (2000) *Revision of the Interim Biogeographic Regionalisation of Australia (IBRA) and the Development of Version 5.1*. – Summary Report. Department of Environment and Heritage, Canberra.

Gorelick R. (2008) Species richness and the analytic geometry of latitude and altitudinal gradients. *Acta Biotheor.* **56,** 197–203.

Greenwood M. E. & MacFarlane G. R. (2006) Effects of salinity and temperature on the germination of *Phragmites Australis*, *Juncus Kraussii*, and *Juncus Acutus*: implications for estuarine restoration initiatives. *Wetlands* **26,** 854–61.

Hillebrand H. (2004) On the generality of the latitudinal diversity gradient. *Am. Nat.* **163,** 192–211.

Johns L. (2006) *Field guide to Common Saltmarsh Plants of Queensland*. Queensland Department of Primary Industries.

Khan M. A. & Ungar I. A. (1984) The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. *Am. J. Bot.* **71,** 481–9.

Kirkpatrick J. B. & Glasby J. (1981) *Saltmarshes in Tasmania*. Occasional Paper No. 8. Department of Geography, University of Tasmania. p. 62.

MacArthur R. H. (1972) *Geographical Ecology*. Harper and Row, New York.

Mittelbach G. G., Schemske D. W., Cornell H. V. *et al.* (2008) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* **10,** 315–31.

doi:10.1111/j.1442-9993.2009.02001.x

© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia

14429993, 2009, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2009.02001.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Pianka E. R. (1966) Latitudinal gradients in species diversity: a review of concepts. *Am. Nat*. **100,** 33.

Qian H., Fridley J. D. & Palmer M. W. (2007) The latitudinal gradient of species-area relationships for vascular plants of North America. *Am. Nat*. **170,** 690–701.

Saenger P., Specht M. M., Specht R. L. & Chapman V. J. (1977) Mangal and coastal saltmarsh communities in Australasia. In: *Ecosystems of the World I: Wet Coastal Ecosystems* (ed. V. J. Chapman) pp. 293–345. Elsevier, Amsterdam.

Shepherd K. A. & Wilson P. G. (2007) Incorporation of the genera *Halosarcia*, *Pachycornia*, *Sclerostegia*, and *Tegicornia* into *Tecticornia* (Salicornioideae, Chenopodiaceae). *Aust. Syst. Bot.* **20,** 319–31.

Specht R. L. (1981) Biogeography of halophytic angiosperms (salt-marsh, mangrove and sea-grass). In: *Ecological Biography of Australia* (ed. A. Keast) pp. 575–89. Dr. W. Junk Publishers, The Hague.

© 2009 The Author
Journal compilation © 2009 Ecological Society of Australia

doi:10.1111/j.1442-9993.2009.02001.x

14429993, 2009, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2009.02001.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Global Ecology and Biogeography (1999) **8**, 117–124

RESEARCH LETTER

Mangrove transgression into saltmarsh environments in south-east Australia

NEIL SAINTILAN and ROBERT J. WILLIAMS *Australian Catholic University, PO Box 968, North Sydney, NSW 2059, Australia, and Fisheries Research Institute, 202 Nicholson Pde, Cronulla, NSW 2230, Australia*
email: N.Saintilan@mackillop.acu.edu.au

ABSTRACT

The landward transgression of mangroves into saltmarsh environments in the estuaries of south-east Australia over the last five decades is established as a widespread trend through a review of a number of independent studies. This process is occurring in a range of geomorphic settings, and in some cases reversing the direction of longer-term vegetation change. Several hypotheses are advanced to explain this occurrence, including increases in rainfall, revegetation of areas cleared for agriculture, altered tidal regimes or estuary water levels, and increases in nutrient levels and sedimentation.

Key words. Succession, intertidal vegetation, sea-level, mangrove, saltmarsh, estuary, Australia.

INTRODUCTION

The coastal estuaries of south-eastern Australia originated with a postglacial marine transgression that stabilized 6500 years ago (Roy, 1984). Throughout the Holocene, infilling has occurred with the deposition of both fluvial and marine sediments, creating a range of intertidal environments from the tidal deltas and back-barrier depressions at the mouths of estuaries to bayhead deltas and fluvial point-bars in upstream reaches. All these intertidal environments are suitable for colonization by mangroves and saltmarshes, and they are important habitats for fish, crabs, prawns and migratory birds (Hutchings & Saenger, 1987).

The diversity of mangrove species declines on the Australian east coast with increasing latitude. While twenty-seven species have been identified in the Hinchinbrook Channel (Duke, 1995), the number declines to seven within Moreton Bay and five at the New South Wales-Queensland border. *Avicennia marina* (Forssk.) Veirh. is the dominant species in the estuaries of NSW, occurring in association with *Aegiceras corniculatum* (L.) Blanco, *Rhizophora stylosa* Griff., *Bruguiera gymnorhiza* L. lamk. and *Excocaria agallocha* L. in the northern estuaries, and with *A. corniculatum* alone in the estuaries of the central and southern coastline (West *et al*., 1985). Within the southern states of Victoria and South Australia, *A. marina* is the sole species of mangrove.

By comparison, saltmarsh communities are more diverse, with Adam *et al*. (1988) recording over 250 species of saltmarsh and fringe vegetation in NSW. Important species include *Sporobolus virginicus* var. *minor* F. Bailey, *Samolus repens* (J.R. & G. Forst.) Pers., *Juncus krausii* Hochst., *Sarcocornia quinqueflora* (Bunge ex Ung.-Sternb.) A.J.Scott and *Suaeda australis* (R.Br.) Moq. (Adam, 1994). Saltmarsh characteristically occurs at higher elevations than mangroves, and is, as a consequence, inundated by fewer tides (Chapman, 1974). Soil conditions of the two community types differ in response to inundation frequency, with saltmarsh soils being in general drier and subject to a greater range of salinities (Clarke & Hannon, 1967).

Owing to the fact that mangrove and saltmarsh communities are often delimited by elevation, and because mangroves have the capacity to contribute to vertical accretion, the mangrove-saltmarsh zonation has been presented by some authors as an illustration of seral succession. For example, Pidgeon (1940)

© 1999 Blackwell Science Ltd. http://www.blackwell-science.com/geb

and Chapman (1974) have argued that mangroves accelerate rates of accretion as adventitious roots slow tidal flows and encourage deposition. Furthermore, mangroves translate significant volumes of atmospheric carbon to their root systems (Saintilan, 1997a) thereby contributing to organic accretion, and, particularly upon senescence, contributing litter to strandline environments. It is not unreasonable to suppose that mangroves could promote the accretion of intertidal environments to supratidal elevations where saltmarsh is better suited, thereby contributing to a seral succession in the classical model of Pidgeon (1940).

With these assumptions in mind, it is interesting to note the degree to which mangroves are expanding their range into saltmarsh environments in south-east Australian estuaries. In this paper, we seek to demonstrate that the combined weight of over twenty independent photogrammetric surveys conveys a regional pattern of landward mangrove incursion. A review of these papers allows for the identification of a number of potential contributing factors, each of which is discussed with reference to the broader biogeographic and geomorphic context of these observations.

OBSERVATIONS OF MANGROVE TRANSGRESSION

Analysis of historic air photographs of the past five decades by a number of investigators has demonstrated losses of saltmarsh in Queensland, New South Wales, Victoria and South Australia. The northernmost observation is that of Ebert (1995, cited in Duke, 1995), documenting the loss of saltpan in the Hinchinbrook Channel (146°10, 18°20 Fig. 1). The area of saltpan decreased by 78% in the period 1943–91. Saltpan was replaced by tall mangrove, the change being attributed to an increase in annual rainfall.

Further south, McTainsh *et al*. (1988) noted the landward incursion of mangroves at Oyster Point from 1944 to 1983, and Morton (1994) established the trend occurring over the wider Moreton Bay region (Fig. 1), noting that while mangroves in many places are recolonizing areas previously used for agriculture, at least 65 hectares of landward mangrove expansion in the 50 years following 1944 has occurred in areas not so used.

Within the northern rivers of NSW, landward incursions of mangroves have been observed in a number of locations. On the Tweed River, the most significant landward incursions of mangroves in the period 1941–94 have occurred in areas affected by agricultural practices, in the form of recolonization of previously cleared land, or the occupation of areas drained for sugar cane farming, which could have lead to local subsidence (Saintilan, 1998). Within the Brunswick and Clarence Rivers, landward mangrove incursions appear isolated to tidal channels – possibly to those affected by dredging works (Saintilan, 1997b).

A number of studies on the NSW central coast have revealed significant losses of saltmarsh to mangrove. Within the Hawkesbury River estuary, these changes have occurred in a number of geomorphic settings. Mangroves proliferating on the sand deltas in Pittwater near the mouth of the Hawkesbury have replaced 50% of the saltmarsh since 1941 (Wilton, 1997). Sites along Berowra and Marramarra Creeks within the lower estuary have lost saltmarsh to mangrove over the same period (Williams & Watford, 1997), and on the wide intertidal bars of the main fluvial delta mangroves are encroaching on saltmarsh within Mangrove Creek (Saintilan, 1997c).

Other central coast estuaries in which saltmarsh has been lost to mangrove include Port Stephens (Pipeclay Creek, B.G. Thom, personal communication), Lake Macquarie (25% of saltmarsh lost; Winning, 1990), the Hunter River from 1954 to 1994 (67% of saltmarsh lost; Buckney, 1987; Williams *et al*., 1999), Homebush Bay within the Paramatta River (more than 80% lost, Clarke & Bensen 1988), the Lane Cove River (McLoughlin, 1987), and the Kurnell Peninsula in Botany Bay, where over 30% of the saltmarsh has been lost from the Ramsar-listed Towra Point wetland since the 1930s (Mitchell & Adam 1989b).

The barrier estuaries of the NSW south coast have been similarly affected. Mangroves have replaced saltmarsh in Currembene Creek, Jervis Bay (Fig. 2), particularly in the period 1944–84 (Clarke, 1995), although in some creeks within Jervis Bay saltmarshes have expanded their range (P.J. Clarke, personal communication). A survey of wetland distributions within the Minnamurra estuary (Chafer, 1998) revealed a 49% reduction in the saltmarsh area between 1938 and 1997, as mangroves expanded their range landward and swamp oak forests encroached seaward. Landward incursions of mangroves have been noted in Cullendulla Creek (A.D. Short, personal communication) and have been described as 'extensive' in Corner Inlet, Victoria for the period 1941–85 (Vanderzee, 1988). Landward incursions of mangroves have also been observed in South Australia. On the eastern shore of the Gulf St.

14668238, 1999, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1046/j.1365-2699.1999.00133.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

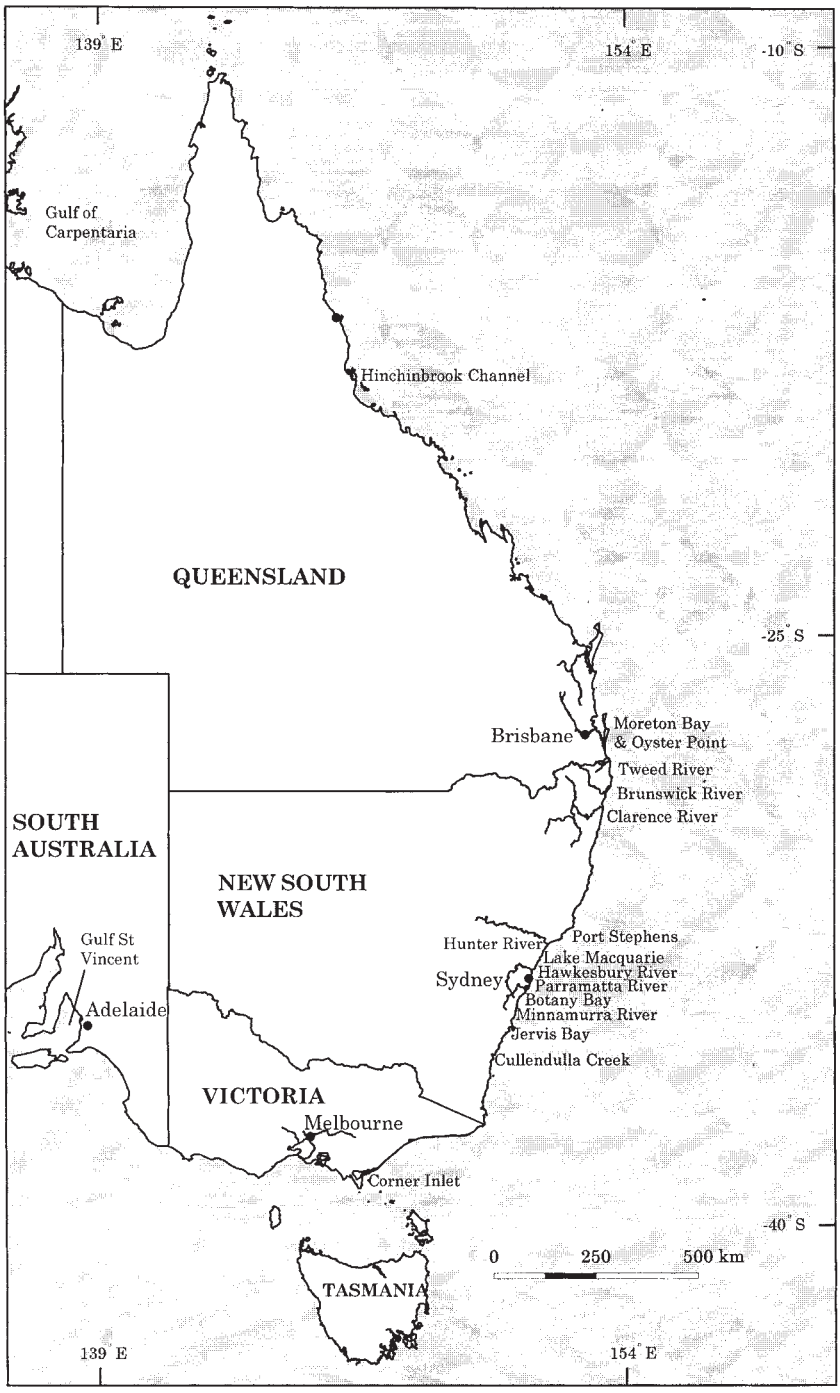


Fig. 1. Location of environments on the Australian east coast in which the landward transgression of mangroves has been observed.

14668238, 1999, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1046/j.1365-2699.1999.00133.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Fig. 2. Juveniles of the mangrove *Avicennia marina* established in the *Sporobolus virginicus* saltmarsh, Currembene Creek, New South Wales. *Juncus krausii* and *Casuarina glauca* form the landward saltmarsh units. Photograph: N. Saintilan.

Vincent, mangroves extended their landward edge at a rate of 17 m per year in the period 1949–79 (Burton, 1982; Fotheringham, 1994).

SUGGESTED MECHANISMS FOR MANGROVE INCURSIONS

While studies of the mangrove–saltmarsh boundary have revealed a consistent trend in a range of estuaries, little unanimity exists as to the causes of the landward incursion of mangroves. Several suggestions have been made, falling into the broad categories of changing patterns of precipitation, change in or cessation of agricultural practices, altered tidal regime or sea-level, catchment modifications leading to altered sedimentation and nutrient levels, and land subsidence. Each of these mechanisms is reviewed in turn.

Precipitation

Average annual precipitation has increased in the period following 1945 along the east Australian coast (Pittock, 1988), a feature which could have diluted salts within saltmarsh soils to the extent that mangrove colonization might have been enhanced. The ephemeral nature of mangroves in the saltpan fringe has been noted by Duke *et al*. (1997). Egbert (1995, cit. Duke, 1995) suggested that the replacement of saltpan by mangrove in the Hinchinbrook channel is primarily due to increases in annual rainfall, and Duke (1995) notes in this context that Fosberg (1961) drew an association between the proportion of saltpan to mangrove and the annual precipitation. McTainsh *et al*. (1988) traced the landward expansion of mangroves along drainage lines, and suggested that higher rainfall might explain the movement of mangroves into higher intertidal environments. Extremes of salinities encountered in these less frequently inundated sites would be lessened if rainfall were more consistent between inundations.

Buckney (1987) related the expansion of mangroves in the Hunter estuary to an increase in rainfall, and noted a loss of vigour in the same mangroves during the *El Niño* drought of 1982. The observation by Chafer (1998) that oak forests in Minnamurra estuary have encroached upon saltmarsh from the landward edge would also suggest a freshening of the saltmarsh plain.

Agricultural practices

In many instances, mangroves have been observed occupying areas previously used for agriculture; this

14668238, 1999, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1046/j.1365-2699.1999.00133.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

may represent a recolonization of cleared areas. Morton (1994) notes the regrowth of 65 hectares of mangroves cleared from islands in Moreton Bay following the cessation of agricultural practices, and Mitchell & Adam (1989b) suggest that much of the landward spread of mangroves at Towra Point may be regrowth following a long history of agricultural and industrial disturbance. Photographs of Currembene Creek, Jervis Bay, between 1944 and 1971, show signs of grazing, including cattle trails, and the removal of cattle from these sites might have promoted the growth of *Avicennia marina* seedlings on these flats (P.J. Clarke, personal communication).

In parts of the Sydney district, the clearance of mangroves took place from the early 1800s (Mitchell & Adam, 1989a). Initially, mangrove wood was burnt to generate alkali ash for soap. As the colony expanded, the harvesting of timber for this purpose may have moved to other regional centres, in turn contributing to additional losses. In the mid 1800s grazing areas were expanded and in the latter part of the 19th century, an oyster industry began in NSW with mangrove sticks being cut for the settlement of oyster spat. It is difficult to identify unequivocally sites that have been affected by these activities in urbanized catchments.

Altered tidal regime

Morton (1994) attributes the landward expansion of mangroves in areas unaffected by agriculture to alterations in the tidal regime of Morton Bay, due to the modification of entrance conditions, and the construction of a tidal barrage. Dredging in the northern rivers of NSW has also been noted to have altered tidal range significantly (Druery & Curedale, 1979), which may have promoted the landward colonization of mangroves in the Tweed and Brunswick Rivers (Saintilan, 1997b). Dredging of the mouths of barrier estuaries in southern NSW in the 1970s could also have influenced tidal hydrodynamics, leading to the rapid upslope colonization of mangroves. However, larger drowned river valleys, such as the Hawkesbury, are less affected by dredging, and the hypothesis cannot be applied to all situations.

A small eustatic sea-level rise has been observed for the Australian east coast since the beginning of the 20th century (Gordon, 1988). This rise has averaged $0.5\,mm\,y^{-1}$, and appears to follow a pattern of increasing temperature and rainfall in the latter half of the century. The low gradients of the upper intertidal zone translate small increments in sea-level into substantial alterations in the frequency of inundation over wide areas, and this may be one factor contributing to mangrove incursion upon saltmarsh.

Sedimentation and nutrients

The landward incursion of mangroves has often occurred in association with progradation at the seaward edge (Botany Bay – Mitchell & Adam, 1989b; Morton Bay – McTainsh *et al*., 1988; Hawkesbury River – Williams & Watford, 1997; Wilton, 1997; Tweed River – Saintilan 1997c). While this might be an outcome of an increased tidal amplitude, the trend is more commonly interpreted as evidence of high rates of vertical accretion. Clearing of land in the catchments of tidal rivers has increased the delivery of sediment and nutrients to these environments (McLoughlin, 1985).

While vertical accretion would lower inundation frequencies, experimental evidence suggests that fresh sediment promotes the establishment of mangrove propagules in upper intertidal environments (Clarke & Allaway, 1993). In an environment where the oxidation of sediments leads to losses of nitrogen (Boto & Wellington, 1983) and potassium (Ward & Larcombe, 1996), the introduction of a veneer of nutrient-laden sediment, coupled with elevated concentrations of nutrients in the tidal waters of developed coastal estuaries, may allow mangroves to colonize environments from which they have been previously excluded by nutrient deficient soils. Duke (1995) notes the possibility of changes in the sediment and nutrient supply of the Herbert River influencing the performance of intertidal vegetation in the Hinchinbrook Channel.

Subsidence

Subsidence of an intertidal surface influences the distribution of mangroves and saltmarsh and can be the outcome of a number of factors. Regional subsidence may play a role, due to tectonic crustal movement or underground mine collapse, a factor which has led to the dieback of mangroves in Lake Macquarie (P. Adam, personal communication). Alternatively, acid soils are present along the major portion of the eastern Australian coast and agricultural drainage practices in these areas has caused irreversible soil shrinkage leading to subsidence of estuarine floodplains (White *et al*., 1997). Furthermore, unconsolidated sediments compress under the influence of gravity, leading to the lowering of the marsh surface,

14668238, 1999, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1046/j.1365-2699.1999.00133.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

unless offset by vertical accretion (Reed & Cahoon, 1993). The diversion of sediment away from intertidal marshes has led, for this reason, to the drowning of saltmarsh in the Gulf of Mexico (Guilcher, 1981).

Vanderzee (1988) draws parallels between marsh loss in the Gulf states and the drowning of low-lying coastal land in Corner Inlet, Victoria. Both environments show microcliffing at the seaward edge of the saltmarsh, a profile suggested on theoretical grounds by Orsen *et al*. (1985) to be the result of erosion following an increase in relative sea-level. Similar microcliffing at the mangrove–saltmarsh boundary has been observed in Mangrove Creek on the Hawkesbury River, and Currembene Creek in Jervis Bay.

DISCUSSION

It would be tempting to describe mangrove transgression into saltmarsh as a ubiquitous trend relating to a common causal factor, such as greenhouse-related sea-level rise. Closer examination of the observations to date suggests a more complicated picture. The trend is not ubiquitous, and mangrove-saltmarsh boundaries in many estuaries have remained stable over the time period spanned by the historic photo record. For example, within the Jervis Bay system, mangrove transgression into saltmarsh has occurred in Currembene Creek, but not in Carama Creek (CSIRO, 1994). Within Port Stephens, mangrove transgression has occurred at Pipeclay Creek, but not Tilligherry Creek (Wilton, 1997).

Where incursions have occurred, a number of causal mechanisms can be invoked, including climatic change, altered tidal regime, sedimentation and subsidence. No single explanation suits all locations, given the diversity of geomorphic settings in which the changes are and are not occurring. Further research is clearly necessary in order to elucidate the relative importance of the contributing factors on an estuary-by-estuary basis.

Whatever the principal causes, saltmarsh appears to be a vulnerable and diminishing resource on the temperate Australian east coast. It is disturbing to note that many estuaries have lost over one quarter of their saltmarsh in the last five decades, and in some cases the figure is as high as 80%. If this trend is part of a natural oscillation of mangroves into and out of saltmarsh environments, perhaps linked to drought- and flood-dominated regimes documented for the temperate east coast (Erskine & Warner, 1988), then the issue is less of concern. However, stratigraphic examination of saltmarsh plains on the Hawkesbury River and at Curremebene Creek, Jervis Bay, has demonstrated the existence of mangrove root systems well beneath an overlying unit of saltmarsh soils, suggesting that the longer-term history of seral succession has been the replacement of mangroves by saltmarsh as vertical accretion has occurred (Saintilan, 1997).

It is unlikely that the rate of vertical accretion has recently slowed, given the degree of siltation occurring in many of these estuaries, and the concurrent expansion of mangroves at their seaward edge. That mangroves are also moving landward in many locations is more plausibly attributed to either increased nutrient levels resulting from anthropogenic inputs, or to the combined effect of increased precipitation and estuarine water levels, freshening the saltmarsh environment, renewing interstitial potassium (Keene, personal communication), and increasing the delivery of propagules to the upper intertidal zone.

Given predictions of renewed sea-level rise globally, and little prospect of a reduction in nutrient levels in south-east Australian estuaries, it would appear that coastal wetlands will continue to be dramatically impacted, with a spread in the areal extent of mangroves and a corresponding decline in the distribution of saltmarsh. In many situations, further landward progression of saltmarsh is impossible, given urban and agricultural constraints. These considerations may have important implications for the extent and biodiversity of south-east Australian wetlands.

ACKNOWLEDGMENTS

The authors would like to thank the many co-workers who drew relevant survey reports to their attention, including Ron West, Paul Adam, Norman Duke, and Karen Edyvane. Fiana Watford produced the figure.

REFERENCES

Adam, P. (1994) Saltmarsh and mangrove. *Australian vegetation* (ed. by R.H. Groves), 2nd edn, pp. 395–435. Cambridge University Press, Cambridge.

Adam, P., Wilson, N.C. & Huntley, B. (1988) The phytosociology of coastal saltmarsh vegetation in New South Wales. *Wetlands (Aust.)*, **7,** 35–85.

Boto, K.G. & Wellington, J.T. (1983) Phosphorus and nitrogen nutritional status in a northern Australian mangrove forest. *Mar. Ecol. Prog. Ser.* **11,** 63–69.

14668238, 1999, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1046/j.1365-2699.1999.00133.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Buckney, R.T. (1987) Three decades of habitat change: Kooragang Island, New South Wales. *Nature conservation, the role of remnants of native vegetation* (ed. by D.A. Saunders, G.W. Arnold, A.A. Burrbidge and A.J.M. Hopkins), pp. 227–232. Surrey, Beatty and Sons, Sydney.

Burton, T. (1982) Mangrove changes recorded north of Adelaide. *Safic,* **6,** 8–12.

Chafer, C.J. (1998) *Draft: A spatio-temporal analysis of estuarine vegetation change in the Minnamurra River* 1938–97, p. 47. Minnamurra Estuary Management Committee.

Chapman, V.J. (1974) *Salt marshes and salt deserts of the World*, 2nd edn, p. 342. Cramer, Lehre [Ger.].

Clarke, P.J. (1995) The population dynamics of the mangrove shrub *Aegiceras corniculatum* (Myrsinaceae): fecundity, dispersal, establishment and population structure. *Proc. Linn. Soc. N.S.W.* **115,** 35–44.

Clarke, P.J. & Allaway, W.G. (1993) The regeneration niche of the grey mangrove (*Avicennia marina*): effects of salinity, light and sediment factors on establishment, growth and survival in the field. *Oecologia,* **93,** 548–556.

Clarke, P.J. & Bensen, D. (1988) The natural vegetation of Homebush Bay- two hundred years of changes. *Wetlands (Aust.),* **8,** 2–15.

Clarke, L.D. & Hannon, N.J. (1967) The mangrove swamp and saltmarsh communities of the Sydney district. I. Vegetation, soils and climate. *J. Ecol.* **55,** 754–771.

CSIRO Division of Fisheries (1994) *Jervis Bay Baseline Studies. Final Report, May 1994*, p. 1282. Marmion Marine Laboratories, North Beach, Western Australia.

Druery, B.E. & Curedale, J.W. (1979) *Tweed River dynamics study. Report No. 78009,* p. 135. Public Works Department of NSW.

Duke, N.C. (1995) Mangroves in the Great Barrier Reef World Heritage Area: current status, long-term trends, management implications and research. *State of the Great Barrier Reef World Heritage Area Workshop. Proceedings of a Technical Workshop held in Townsville, Queensland, Australia 27–29 November 1995* (ed. by D. Wachenfeld, J. Oliver & K. Davis), pp. 288–299. Great Barrier Reef Marine Park Authority.

Duke, N.C., Ball, M.C. & Ellison, J.C. (1997) Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecol. Biogeogr. Letts,* **7,** 27–47.

Erskine, W.D. & Warner, R.F. (1988) Geomorphic effects of alternating flood and drought dominated regimes in New South Wales coastal rivers. *Fluvial geomorphology in Australia* (ed. by R.F. Warner), pp. 223–244. Academic Press, Sydney.

Fosberg, F.R. (1961) Vegetation-free zone on dry mangrove coastline. *U.S. Geol. Soc. Prof. Pap*. **424 (D),** 216–218.

Fotheringham, C.M. (1994) *A vegetation survey of Barker Inlet, Gulf St. Vincent, South Australia*. Management Issues and Recommendations. Coastal Management Branch, Technical Report 94/1, Department of Environment and Natural Resources.

Gordon, A.D. (1988) A tentative but tantalising link between sea-level rise and coastal recession in New South Wales, Australia. *Greenhouse: planning for climatic change* (ed. by G.I. Pearman), pp. 121–134. CSIRO, Melbourne.

Guilcher, A. (1981) Shoreline changes in salt marshes and mangrove swamps (mangals) within the past century. *Coastal dynamics and scientific sites* (ed. by E.C.F. Bird and K. Koike), pp. 31–53. Department of Geography, Komazama University, Tokyo.

Hutchings, P. & Saenger, P. (1987) *Ecology of mangroves,* p. 388. University of Queensland Press, Brisbane.

McLoughlin, L. (1985) *The middle Lane Cover River: a history and a future*. CEUS Monograph no. 1. Centre for Environmental and Urban Studies, Macquarie University.

McLoughlin, L. (1987) Mangroves and grass swamps: Changes in the shoreline vegetation of the Middle Lane Cove River, 1780s to 1880s. *Wetlands (Aust.)* **7,** 13–24.

McTainsh, G., Iles, B. & Saffigna, P. (1988) Spatial and temporal patterns of mangroves at Oyster Point Bay, south east Queensland. 1944–83. *Proc. R. Soc. Qld.* **99,** 83–91.

Mitchell, M.L. & Adam, P. (1989a) The relationship between mangrove and saltmarsh communities in the Sydney Region. *Wetlands (Aust.)* **8,** 37–46.

Mitchell, M.L. & Adam, P. (1989b) The decline of saltmarsh in Botany Bay. *Wetlands (Aust.)* **8,** 55–60.

Morton, R.M. (1994) Fluctuations in wetland extent in southern Moreton Bay. *Future marine science in Moreton Bay* (ed. by J.G. Greenwood and N.J. Hall), pp. 145–150. School of Marine Science, University of Queensland.

Orsen, R., Panageotou, W. & Leatherman, S.P. (1985) Response of tidal salt marshes of the U.S. Atlantic and Gulf Coasts to rising sea levels. *J. Coastal Res.* **1,** 29–37.

Pidgeon, I.M. (1940) The ecology of the central coast of New South Wales III. Types of primary succession. *Proc. Linn. Soc. N.S.W.* **65,** 221–249.

Pittock, A.B. (1988) Actual and anticipated changes in Australia's climate. *Greenhouse: planning for climatic change* (ed. by G.I. Pearman), pp. 35–51. CSIRO, Melbourne.

Reed, D.J. & Cahoon, D.R. (1993) Marsh subsidence vs. marsh accretion: interpreting accretion deficit data in Coastal Lousisiana. *Coastal Zone 93. Proceedings, 8th Symposium on Coastal and Ocean Management, New Orleans, Louisiana*, pp. 243–257. American Society of Civil Engineers, New York.

Roy, P.S. (1984) Holocene sedimentation histories of estuaries in southeastern Australia. *W.A. Dept. Conserv. Environ. Bull.* **161,** 23–59.

Saintilan, N. (1997a) Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Mar. Freshw. Res.* **48,** 147–152.

Saintilan, N. (1997b) *Tweed River estuary; photo-grammetric survey of wetland distribution*. 1930–94. Report to the Department of Land and Water Conservation.

Saintilan, N. (1997c) Mangroves as successional stages in the Hawkesbury River estuary, New South Wales. *Wetlands (Aust.)* **16,** 99–107.

14668238, 1999, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1046/j.1365-2699.1999.00133.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Saintilan, N. (1998) Photogrametric survey of the Tweed River wetlands. *Wetlands (Aust.)* **17,** 74–82.

Vanderzee, M.P. (1988) Changes in saltmarsh vegetation as an early indication of sea-level rise. *Greenhouse: Planning for Climatic Change* (ed. by G.I. Pearman), pp. 147–160. CSIRO, Melbourne.

Ward, I.A.K. & Larcombe, P. (1996) A geochemical comparison of modern and holocene mangrove sediments, Townsville region, North Queensland. *Wetlands (Aust.)* **15,** 10–21.

West, R.J., Thorogood, C.A., Walford, T.R. & Williams, R.J. (1985) *An estuarine inventory for New South Wales, Australia,* p. 141. Fisheries Bulletin 2, Department of Agriculture, New South Wales.

White, I., Melville, M.D., Wilson, B.P. & Sammut, J. (1997) Reducing acidic discharges from coastal wetlands in eastern Australia. *Wetlands Ecol. Mgmnt,* **5,** 55–72.

Williams, R.J. & Watford, F.A. (1997) Change in the distribution of mangrove and saltmarsh in Berowra and Marramarra Creeks. 1941–92. *Report to Hornsby Shire Council.*

Williams, R.J., Watford, F.A. & Balashov, V. (1999) *Kooragang Wetland Rehabilitation Project: Changes in wetland fish habitats of the lower Hunter River.* NSW Fisheries Office of Conservation, Fisheries Research Institute, Cronulla, NSW.

Wilton, K. (1997) Changes in mangrove and saltmarsh areas in the Sydney Region, with specific reference to Careel Bay, Pittwater. *Published, abstracts, Conference on the Ecology of Estuaries and Soft Sediment Habitats, January 1997, Deakin University.*

Winning, G. (1990) *Lake Macquarie littoral habitats study.* Report Prepared for Lake Macquarie City Council by Shortlands Wetlands Centre.

14668238, 1999, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1046/j.1365-2699.1999.00133.x by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

SHORT NOTE: THE DECLINE OF SALTMARSH IN SOUTHEAST AUSTRALIA: RESULTS OF RECENT SURVEYS.

N. Saintilan
Australian Catholic University, PO Box 968, North Sydney 2059
Fax: (02) 9739 2805, Phone: (02) 9739 2874
Email: N.Saintilan@mackillop.acu.edu.au

Author to whom correspondence should be addressed
R.J. Williams
NSW Fisheries Office of Conservation
Cronulla Fisheries Centre
202 Nicholson Pde, Cronulla NSW 2230.

Abstract

The results of twenty-eight photogrammetric surveys published since 1982 are presented to establish that the decline of saltmarsh is a widespread trend in southeast Australian estuaries. The decline of saltmarsh is usually associated with invasion by the mangrove *Avicennia marina* (Forssk.) Vierh., though development pressures have also contributed to local losses.
Key Words: saltmarsh, mangrove, estuary, conservation, diversity, development.

Introduction

We present here in summarised form the results of twenty-eight photogrammetric surveys which document substantial losses of saltmarsh in a number of southeastern Australian estuaries (Table I). The purpose of this review is to establish that the trend is widespread, and raise important questions about the long-term viability of saltmarsh along a major portion of the Australian coast.

Discussion

Aerial photographs were first taken of portions of the southeast Australian coastline nearly 70 years ago and contain a valuable source of data about coastal habitats. Starting in the mid 1980s a number of investigators used these photographs to assess changes in estuarine vegetation. Table I lists a series of photographic surveys which document substantial decreases in the area of saltmarsh. The primary cause of this decline has been the landward encroachment of mangroves, principally the grey mangrove, *Avicennia marina* (Forssk.) Vierh. These studies also show that losses to urban development have been an important, though secondary, cause. While many mechanisms have been advanced explaining the landward encroachment of mangroves (Saintilan and Williams 1999), the cause or causes of this phenomenon have yet to be conclusively determined.

Only two surveys revealed an increase in saltmarsh area. Sedimentation on the Tweed River created considerable new intertidal habitat colonised by saltmarshes as well as mangroves, but overall saltmarsh has declined in area in this river since 1971 (West 1993, Saintilan 1998). The increase in the area of saltmarsh on Comerong Island took place in the absence of mangroves, but following the reopening of an adjacent channel in 1989, local losses have occurred

to encroachment by mangrove (Chafer 1998b).

The saltmarsh area of NSW at the time of European colonisation has never been quantified, and it is probably impossible to do so. Nevertheless, the losses expressed in Table I should be placed in context: in 1982, the east and southeast coastal bioregions contained only 354 square kilometres of saltmarsh of a national total of 23,322 square kilometres, and yet contained the highest species richness and incidence of species endemic to Australia (State of the Environment Advisory Council, 1996).

There can be little doubt that the area of mangrove has increased in a number of estuaries. The occupation of the upper intertidal environment by mangroves may be ephemeral, and we cannot discount the possibility of a natural cyclicity in mangrove transgression, perhaps corresponding to patterns of rainfall and sea-level in eastern Australia. However, it is also the case than the most significant of human modifications of the estuary, increased siltation and elevated nutrient levels, appear to promote the expansion and productivity of mangroves more obviously than that of saltmarshes, and competition between these communities along the intertidal gradient may be shifted in favour of mangroves in developed estuaries. Until the mechanisms of mangrove encroachment are properly understood, it will be difficult to determine what, if any, management intervention is warranted.

Social perceptions may operate alongside physical impacts to decrease the competitiveness of saltmarshes in east Australian estuaries. Mangroves have long been recognised as fish habitats (Hutchings and Saenger 1988) which has afforded them greater legislative protection than saltmarshes, even though the contribution of saltmarshes to estuarine fisheries has not been adequately quantified in Australia. For example in NSW unlike mangroves, saltmarshes are not protected under the Fisheries Management Act (1994), and the State Environmental Planning Policy for Wetlands (SEPP 14) does not cover metropolitan areas where development pressures in the upper intertidal zone are greatest.

While examples of saltmarsh rehabilitation have apparently been successful in New South Wales (Burchett *et al.* 1998 a & b), mangroves are more easily and commonly planted in community and government-based rehabilitation programs. It may be timely to review the desirability of mangrove transplanting and rehabilitation in estuaries where mangroves are proliferating naturally, at the expense of other saline wetland communities. A more holistic approach could be taken to intertidal wetland management in these situations, which considered longer-term trends in the relative proportions of mangroves, saltmarshes and seagrasses.

The saltmarsh flora is considerably more diverse than the mangrove flora in temperate southeast Australia (e.g., Adam 1994). If community and species diversity is to be preserved in southeast Australian estuaries, along with the unique faunal habitats they represent, saltmarsh ecology and conservation will need to be addressed as a matter of priority.

Acknowledgements

The authors would like to thank Paul Adam, Norm Duke, Ron West, and Karen Edyvane

for bringing to their attention relevent survey data.

Table I: Changes in the extent of saltmarsh in eastern Australian estuaries.

LOCATION	Saltmarsh lost (% unless specified)	Period	Source
Queensland			
Hinchinbrook Channel	78 (saltpan)	1943-1991	Ebert 1995 cit. Duke 1995
Oyster Point	75 (saltpan)	1944-1983	MacTainsh *et al.* 1988
Moreton Bay	65 hectares	1944-1988	Morton 1994
Coolangatta-Caloundra	11	1974-1987	Hyland & Butler 1988
NSW			
Tweed River	72	1947-1986	West 1993
	local increase	1930-1994	Saintilan 1998
Clarence River	15	1942-1986	West 1993
Macleay River	reduced	1956-1980	Middleton *et al.* 1985
	35	1942-1986	West 1993
Hunter River (excluding Hexham),	67	1954-1994	Williams *et al.* In prep.
Lake Macquarie	25	1954-1986	Winning 1990
Berowra-Marramarra Creek	25	1941-1994	Williams & Watford 1997
Careel Bay	92	1938-1994	Wilton 1997
Couranga Pt., Hawkesbury River	30	1954-1994	Saintilan & Hashimoto 1998
Lane Cove River	not specified	1930-1986	McLoughlin 1987
Homebush Bay Parramatta River	>80	1930-1983	Clarke & Benson 1988
Quibray Bay, Botany Bay	70	1950-1997	Evans 1997
Weeney Bay, Botany Bay	100	1950-1994	Fenech 1994
Woolaware Bay, Botany Bay	63	1950-1994	Fenech 1994, Hughes 1998
Towra Point, Botany Bay	30	1942-1997	Mitchell & Adam 1989
Minnamurra River	49	1938-1997	Chafer 1998a
Comerong Island, Shoalhaven River	increase	1949-1996	Chafer 1998b
Currembene Creek	14 hectares	1944-1989	CSIRO 1994
Merimbula Lake	30	1948-1994	Meehan 1997
Pambula Lake	40	1948-1994	Meehan 1997
Victoria			
Corner Inlet	"extensive"	1941-1985	Vanderzee 1988
South Australia			
Gulf St Vincent	865 hectares	1935-1979	Burton 1982, Fotheringham 1994

References

Adam, P. (1994) Saltmarsh and mangrove. Chapter 14 in R.H. Groves (ed.) *Australian Vegetation* 2nd ed. Cambridge University Press, pp. 395-435.

Burchett, M.D., A. Pulkownik, C. Grant and G. Macfarlane (1998a) Rehabilitation of saline wetlands, Olympic 2000 site, Sydney (Australia) - I: Management strategies based on ecological needs assessment. *Marine Pollution Bulletin* **37**:526-534.

Burchett, M.D., C. Allen, A. Pulkownik, and G Macfarlane (1998b) Rehabilitation of saline wetlands, Olympic 2000 site, Sydney (Australia) - II: Saltmarsh transplantation trials and application. *Marine Pollution Bulletin* **37**: 526-534.

Burton, T. (1982) Mangrove changes recorded north of Adelaide. *Safic* **6**: 8-12.

Chafer, C.J. (1998a) *A spatio-temporal analysis of estuarine vegetation change in the Minnamurra River 1938-1997*. Minnamurra Estuary Management Committee.

Chafer, C.J. (1998b) *The effect of temporal geomorphological processes on shorebird populations at Shoalhaven Heads, NSW*. Master of Science Thesis, Faculty of Science, University of Wollongong.

Clarke P. and Benson D. (1988) The natural vegetation of Homebush Bay-two hundred years of changes, *Wetlands (Australia)* **8**: 3-15.

CSIRO Division of Fisheries (1994) *Jervis Bay Baseline Studies*. Final Report, May 1994. Marmion Marine Laboratories, North Beach, Western Australia. 1282 pp.

Duke, N.C. (1995) Mangroves in the Great Barrier Reef World Heritage Area: current status, long-term trends, management implications and research. In *State of the Great Barrier Reef World Heritage Area Workshop* (ed. D. Wachenfeld, J. Oliver and K. Davis). Proceedings of a technical workshop held in Townsville, Queensland, Australia 27-29 November 1995. Great Barrier Reef Marine Park Authority.

Ebert, S.P. (1995) *The geomorphological response to sediment discharge from the Herbert River, north Queensland, 1943-1991*. B.Sc. Honours Thesis. Department of Geology, James Cook University. 78 pp. plus appendices.

Evans, M. (1997) *Historical distribution of estuarine wetlands at Kurnell Peninsula, Botany Bay- the need and potential for rehabilitation*. B.Sc. Honours Thesis, Faculty of Science, University of Wollongong.

Fenech H. (1994) *An assessment of the estuarine wetland status within the Sutherland Shire*. Unpublished B.Env.Sc. Thesis, Faculty of Science, University of Wollongong.

Fotheringham, C.M. (1994) *A vegetation survey of Barker Inlet, Gulf St. Vincent, South Australia*. Management Issues and Recommendations. Coastal Management Branch, Technical

Report 94/1, Department of Environment and Natural Resources.

Hughes, N. (1998) *The changing mangrove-saltmarsh boundary: studies in the Sydney district*. B.Sc. Honours Thesis, School of Geosciences, University of Sydney.

Hutchings P. and Saenger P. (1987) *Ecology of mangroves*. University of Queensland Press, St Lucia. 388 pp.

Hyland, S.J. and Butler, C.T. (1988) *The distribution and modification of mangroves and saltmarsh-claypans in southern Queensland*. Queensland Department of Primary Industries, Information Series QI89004. 74 pp.

McLoughlin, L. (1987) Mangroves and grass swamps: Changes in the shoreline vegetation of the Middle Lane Cove River, 1780's to 1880's. *Wetlands (Australia)* **7**: 13-24.

McTainsh, G., Iles, B. and Saffigna, P. (1986) Spatial and temporal patterns of mangroves at Oyster Point Bay, south east Queensland, 1944-1983. *Proeedings of the Royal. Society of Queensland*. **99**: 83-91.

Meehan, A. (1997) *Historical changes in seagrass, mangrove and saltmarsh communities in Meribula Lake and Pambula Lake*. B.Sc. Honours Thesis, Faculty of Science, University of Wollongong.

Middleton, M.J., Rimmer, M.A. and Williams, R.J. (1985) Structural flood mitigation works and estuarine management in New South Wales-Case Study of the Macleay River. *Coastal Zone Management Journal* **13**: 1-23.

Mitchell, M.L. and Adam, P. (1989) The decline of saltmarsh in Botany Bay. *Wetlands (Australia)* **8**: 55-60.

Morton, R.M. (1993) Fluctuations in wetland extent in southern Moreton Bay. *Future Marine Science in Moreton Bay*. Greenwood, J.G. and Hall, N.J. School of Marine Science, University of Queensland.

Saintilan N. (1998) Photogrammetric survey of the Tweed River wetlands. *Wetlands (Australia)* **17**: 74-82.

Saintilan, N. and Hashimoto, R. (1998) Mangrove-saltmarsh dynamics on a prograding bayhead delta on the Hawkesbury River estuary, New South Wales, Australia. *Symposium: Recent Advances in Mangove Research: Biodiversity, Genetics, Evolutionary Biology and Restoration*. 8-10th July, Toulouse, France.

Saintilan, N. and Williams, R.J. (2000) Mangrove transgression into saltmarsh environments in southeast Australia. *Global Ecology and Biogeography Letters*. **8**: 117-124.

State of the Environment Advisory Council (1996) State of the Environment, Australia. CSIRO Publishing. Collingwood, Australia. 540 pp.

Vanderzee, M.P. (1988) Changes in saltmarsh vegetation as an early indication of sea-level rise. Pp. 147-160 in Pearman G.I. (ed.) *Greenhouse: planning for climatic change*. CSIRO Australia, Melbourne.

West R.J. (1993) *Estuarine fisheries resources of two south eastern Australian rivers.* Ph.D. Thesis, School of Biological Science, University of New South Wales.

Wilton, K. (1997) Changes in mangrove and saltmarsh areas in the Sydney region, with specific reference to Careel Bay, Pittwater. *Published abstracts, Conference on the Ecology of Estuaries and Soft Sediment Habitats*, January 1997, Deakin University.

Williams, R.J. and Watford, F.A. (1997) *Change in the distribution of mangrove and saltmarsh in Berowra and Marramarra Creeks, 1941-1992.* Report prepared by NSW Fisheries Office of Conservation to Hornsby Shire Council.

Williams, R.J., Watford, F.A. and Balashov, V. (In prep.) *Kooragang Wetland Rehabilitation Project: History of changes to estuarine wetlands of the lower Hunter River.* NSW Fisheries Final Report Series.

Winning, G. (1990) *Lake Macquarie littoral habitats study.* Report prepared for Lake Macquarie City Council by Shortlands Wetlands Centre. Unpublished.

Hydrobiologia **413:** 95–102, 1999.
R.S. Dodd (ed.), Diversity and Function in Mangrove Ecosystems.
© 1999 *Kluwer Academic Publishers. Printed in the Netherlands.*

Mangrove-saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia

N. Saintilan[1] & T. R. Hashimoto
[1]*School of Arts and Sciences, Australian Catholic University, P.O. Box 968, North Sydney 2059, Australia*
[2]*Division of Geography, School of Geosciences, University of Sydney, 2006, Australia*

Key words: mangrove, saltmarsh, delta, estuary sea-level, accretion, coastal wetlands, Holocene, succession

Abstract

Mangroves of the species *Avicennia marina* and *Aegiceras corniculatum* occupy a range of intertidal environments in the Hawkesbury River estuary, New South Wales, Australia. Over the previous four decades, these species have, in a number of locations, encroached upon upper-intertidal saltmarsh environments. The authors have investigated the upper stratigraphy of saltmarsh plains to determine whether evidence can be found of prior occupation of these sites by mangroves. On the prograding bayhead deltas, mangrove root systems were found preserved at approximately 0.3 m beneath the current saltmarsh surface indicating that vegetation progression has occurred from mangrove to saltmarsh with the accretion of the flat. The mangrove roots dated from 500 to 1700 years before present, indicating that the current landward transgression of mangroves is contrary to the longer-term successional trend in these environments.

Introduction

One of the predicted outcomes of sea-level rise is the landward translation of the mangrove zone (Woodroffe, 1990). Studies from Florida (Alexander, 1974; Alexander & Crook, 1974) and Australia (Vanderzee, 1988; Saintilan & Williams, 1999) have described the extension of mangroves into terrestrial vegetation in this context, with the suggestion that mangrove transgression may be an indicator of relative sea-level rise.

A growing body of evidence has suggested that a landward incursion of mangrove into saltmarsh is a consistent trend across temperate Southeast Australia and is a potential threat to the extent and biodiversity of saltmarsh (Saintilan & Williams, 1999). This trend has been identified in 22 separate estuaries, including the Ramsar-listed wetlands of Moreton Bay, Queensland (Morton, 1994), Towra Point, New South Wales (Mitchell & Adam, 1989a) and Corner Inlet, Victoria (Vanderzee, 1988). In some situations, saltmarsh loss has exceeded 70% in the previous three decades (Evans, 1997).

Determining the principal causes of this change is difficult, given the number of factors which could be involved. Suggestions have been varied, including the recolonization by mangroves of areas from which they have been cleared (Mitchell & Adam, 1989a), the response of mangroves to eustatic increases in sea-level (Saintilan & Williams, 1999) and the improved conditions for colonization of mangroves in higher intertidal environments in the presence of additional nutrients and sediment following the development of catchments (Wilton, 1998).

It has further been suggested that saltmarsh is a pioneer community and is replaced by mangrove in temporal succession (Mitchell & Adam, 1989b; Morrisey, 1995). This theory of successional change contradicts the more traditional view that in the absence of changes in relative sea-level, mangroves are progressively replaced over time by saltmarsh, as the flat is vertically accreted by tidally-borne sediments (Pidgeon, 1930). Mitchell & Adam (1989b) suggested this theory after stratigraphic studies in the Georges and Hacking Rivers failed to identify the presence of mangrove roots beneath contemporary saltmarsh.

However, the recent discovery of mangrove roots preserved beneath the saltmarsh plains of the Hawkesbury River supports the traditional model of

depositionally-driven succession (Saintilan, 1997), at least on prograding fluvial deltas. The present paper presents the stratigraphic position and age of these mangrove root systems and places contemporary changes in the context of longer-term mangrove-saltmarsh dynamics on the Hawkesbury River.

Description of sites studied

The Hawkesbury River occupies a deeply-incised valley of Triassic quartz sandstone (Conaghan, 1980; Herbert, 1983). The estuary formed as the result of the postglacial marine transgression which initially converted the fluvial valley into an estuarine central basin. Infilling of the central basin with fluvial muds was rapid, essentially keeping pace with sea-level rise (Roy, 1984). The present day sea-level was attained at approximately 6400 years B.P. and has since been relatively stable (Thom & Roy, 1983). The progradation of the sandy bay-head delta in the upper estuary over these fluvial muds commenced less than 500 years after the start of this stillstand (Nichol et al., 1995). However, evidence from the lower estuary suggests that some fluvial sand was already being transported into the central basin during the transgression (Roy, 1984). Today, the lower bay-head delta is dominated by subtidal and intertidal point bars, levees and distributary mouth bars, while the upper delta comprises a subaerial alluvial plain traversed by a leveed channel. The channel is tidal to Richmond, 106 km from the coast.

Materials and methods

Survey techniques

The lower bay-head delta is the principal habitat of mangroves and saltmarshes in the Hawkesbury system (Saintilan, 1997), with the most extensive area at the confluence of the Hawkesbury River and Mangrove Creek, 27 km from the Hawkesbury mouth. The saltmarsh flora consists principally of *Juncus krausii*, *Sarcocornia quinquiflora, Sporobolus virginicus, Somolus repens* and a landward fringe of *Casuarina glauca*.

Mangroves of the species *Avicennia marina* and *Aegiceras corniculatum* form a sympatric association. Contemporary distributions of mangrove and saltmarsh were mapped using the 1994 Sydney air photograph series and ground truthed in January 1997. Comparisons of distributions were then made at a 1: 25000 scale using the 1954 Gosford series (Run 11).

Initial reconnaissance consisted of seven bank-normal transects of four to eight cores to 1.8 m depth at the mouth of the Glenworth Valley, Mangrove Creek and Couranga Point and Gentlemans Halt in the Hawkesbury Valley. The survey revealed decaying mangrove root material beneath saltmarsh within Mangrove Creek and Allens Creek and these sites became the location of more detailed stratigraphic analysis.

Four locations were selected for the dating of preserved mangrove root material. Within Mangrove Creek, two locations were chosen within 100 m of the contemporary mangrove-saltmarsh boundary (Figure 1 Samples 1, 2), with an additional sample collected closer to the landward edge of the saltmarsh (Figure 1 Sample 2A). One sample was collected from Allens Creek (Figure 1, Sample 3) close to the landward edge of the saltmarsh plain. Shell material was extracted for dating from estuarine / deltaic sediment beneath Sample 2 (Mangrove Creek) and Sample 3 (Allens Creek).

Cores were extracted from the sites of samples 1, 2 and 3 (cores H1, H2 and H3, respectively) for more detailed analysis as described below. At these three locations, transects surveys of vegetation and elevation were undertaken from the landward saltmarsh boundary to the seaward mangrove edge, in order to determine the contemporary elevational characteristics of mangrove and saltmarsh within the tributaries. Elevation with respect to the spring tidal level was determined using poles marked with soluble die, a method described by English et al. (1997).

Dating of shells and roots

Shells were washed and submitted to acid etch before standard radiometric dating. Muds containing roots were excavated and roots retrieved individually from the mud matrix. Roots were then given an acid/alkali/acid pretreatment before undergoing standard radiometric dating. The measured age of shell and root material was converted into the conventional C14 age after applying $^{13}C/^{12}C$ corrections.

Core-logging and subsampling

After collection, the cores were split into halves, then visually logged for sediment colour, field texture,

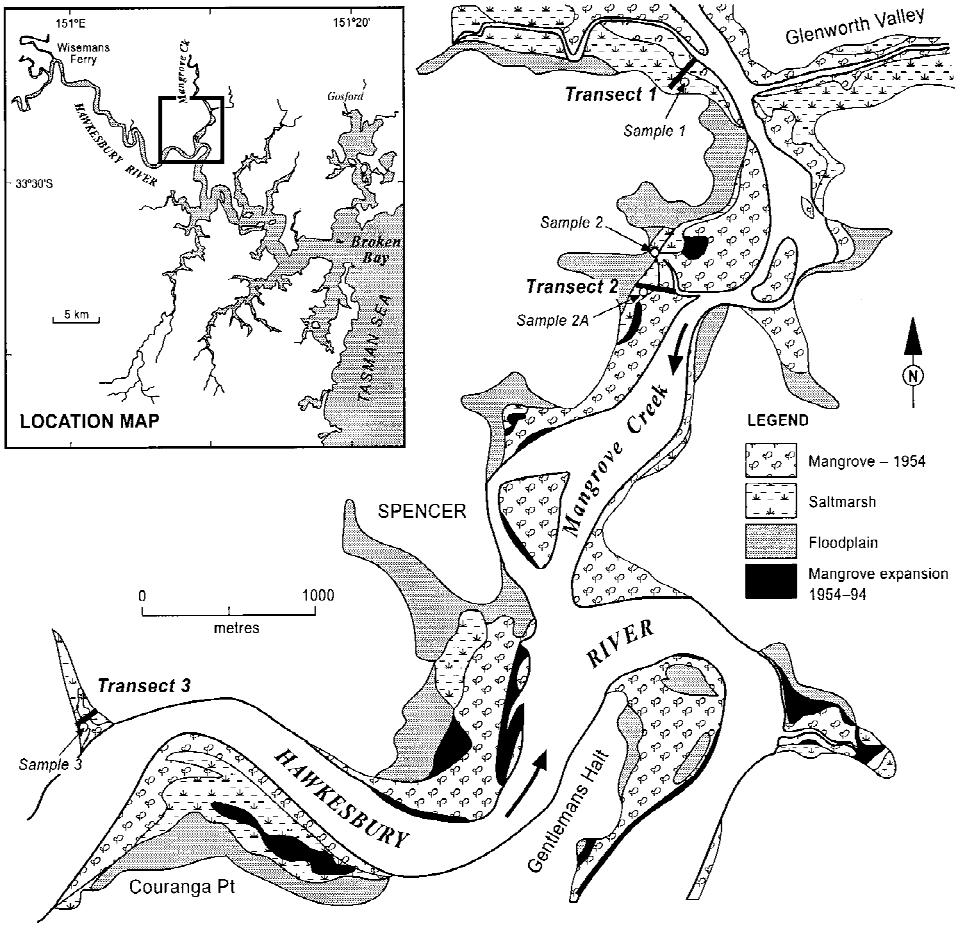


Figure 1. The location of the intertidal bayhead vegetation on the Hawkesbury River estuary. The extent of mangrove transgression in the period 1954–1994 appears in black. Profile and core locations are also shown.

presence of organic matter (particularly *Juncus* and *Avicennia* roots) and shells, and stratigraphic changes. After logging, subsamples were taken from each major stratigraphic unit recognized within the cores for the determination of sediment bulk density, moisture content, organic matter content and gravel / sand / silt / clay ratio.

The bulk density of each subsample was determined by weighing a known volume (20 cm^3) of sediment and applying the formula:

$$\text{Bulk density (g / cm}^3\text{)} = \frac{\text{mass (g)}}{\text{volume (cm}^3\text{)}}$$

Then, 20 cm^3 sediment samples were oven-dried at 70 °C for 48 h and reweighed, to determine their moisture content, expressed as percentage loss of mass upon drying relative to the wet mass.

To determine the organic content of each subsample, 10 – 16 g of oven-dried sediment was placed in a ceramic crucible and heated to 430 °C for 24 h in an electric furnace. The crucibles were then allowed to cool in a desiccator jar and reweighed. The organic matter content was expressed as percentage loss of mass upon combustion relative to the original dry sediment mass.

The gravel / sand / silt / clay ratio for each subsample was determined through sieving and hydrometer measurements. Wet sieving was carried out on 40 – 60 g of wet sediment disaggregated initially with a dispersant solution (tetra - potassium pyrophosphate) in an ultrasonic bath (30 min). The sediment – dispersant mixture was then passed through a 63 μm mesh stainless steel sieve, whereby the <63 μm fraction and the solution were retained and transferred into a 1000 ml measuring cylinder. The mixture was agitated vig-

orously for 30 s, then the concentration of suspended solids within the mixture was measured with a hydrometer ($R1$). Another hydrometer measurement ($R2$) was taken 2 h after the first measurement. The relative proportion of clay and silt in the total mud fraction (i.e. clay and silt) was calculated as:

$$\text{Clay (\%)} = \frac{R2}{R1} \times 100$$

$$\text{Silt (\%)} = \frac{R1 - R2}{R1} \times 100$$

The >63 μm fraction (i.e. sand and gravel) retained in the sieve was oven-dried at 70 °C overnight, then its organic component was removed by hand and combustion at 430 °C for 24 h. Then it was separated into gravel- and sand-fractions with a 2 mm mesh sieve, then reweighed. The ratio of gravel -, sand -, silt - and clay - sized particles was recalculated as a mass percentage of the sediment free of >63 μm organic matter. The organic matter in the <63 μm fraction was not excluded from calculations, due to the likelihood that a significant proportion of this would be allochthonous and, therefore, indicative of the depositional conditions.

Results

Changes in the distribution of mangrove and saltmarsh

A comparison of 1994 and 1954 air photography revealed high rates of incursion of *Avicennia marina* upon saltmarsh (principally communities of *Sarcocornia quinquiflora* and *Sporobolus virginicus)* on intertidal flats adjacent to the Hawkesbury channel near Spencer, Marlows Gully and Couranga Point where 17.5 ha of saltmarsh has been replaced by mangrove (Figure 1). Within Mangrove Creek, the *S. quinquiflora* groundcover of an *Avicennia marina* community has been replaced by *Aegiceras corniculatum* south of transect 2. The extensive plains of *Juncus krausii* in the Glenworth Valley and the upper reaches of the Mangrove Creek estuary do not seem to have been affected, though microcliffing at the mangrove-saltmarsh boundary indicates a slow rate of lateral erosion of the saltmarsh plain.

Location of preserved mangrove roots

Decaying mangrove root systems were found in particularly high concentrations at Allens Creek and the saltmarsh plains on the western bank of Mangrove Creek. While mangrove roots were found beneath saltmarsh further upstream in Mangrove Creek and at the mouth of the Glenworth Valley, they were highly decayed and heavily interpenetrated with the root system of *Juncus krausii*. Older mangrove roots were less commonly found on the point bars of the main Hawkesbury Channel, being absent from Gentlemans Halt and occurring at Couranga Point only in locations currently receiving fresh incursions of juvenile *A.marina*.

Elevation characteristics of mangrove and saltmarsh

Within Mangrove and Allens Creeks, the change from mangrove to saltmarsh occurs at approximately 30 cm below the level of the highest spring tide (Figure 2). Mangroves then occupy the intertidal flat to 60 cm below the level of the highest spring tide.

Sediment characteristics and stratigraphy

At Mangrove Creek (cores H1 and H2) oxidized dark grey-brown mud containing a large amount of *Juncus* rootlets and rhizomes (some live) occurs from the saltmarsh surface to a depth of 25 – 30 cm. At Allens Creek (core H3), oxidized sandy mud and muddy sand extend to 45 cm below the surface. The upper limit of *Avicennia* cable roots occurs at approximately 20 cm below the surface at all locations, within this oxidized zone (Figure 3).

The oxidized sediments are underlain by reduced dark grey mud containing abundant *Avicennia* roots in their upper parts. These roots have been dated at 1700 +/- 90 years BP (Beta 105369) at Allens Creek, 490 +/- 70 years BP (Beta 105370) in core H2 at Mangrove Creek, 1220 +/- 80 years BP (Beta 106995) at a more landward location within the same saltmarsh and 520 +/- 70 years BP (Beta 106994) in core H1, Mangrove Creek. At Allens Creek, the upper part of the reduced zone remains sandy (coarse in places) to 70 cm and becomes more muddy below this level. In all cases, the abundance of *Avicennia* cable roots and fibrous rootlets declines with depth and becomes absent below approximately 170 – 180 cm below the surface. Shell fragments were observed in the lower parts of the range of *Avicennia* roots, below 172 cm in core H2, Mangrove Creek (2660 +/- 70 C14 years BP; Beta 105368) and below 110 cm at Allens Creek (5420 +/- 120 C14 years BP; Beta 105367). At all locations, the mud grades into fine micaceous sandy mud toward the

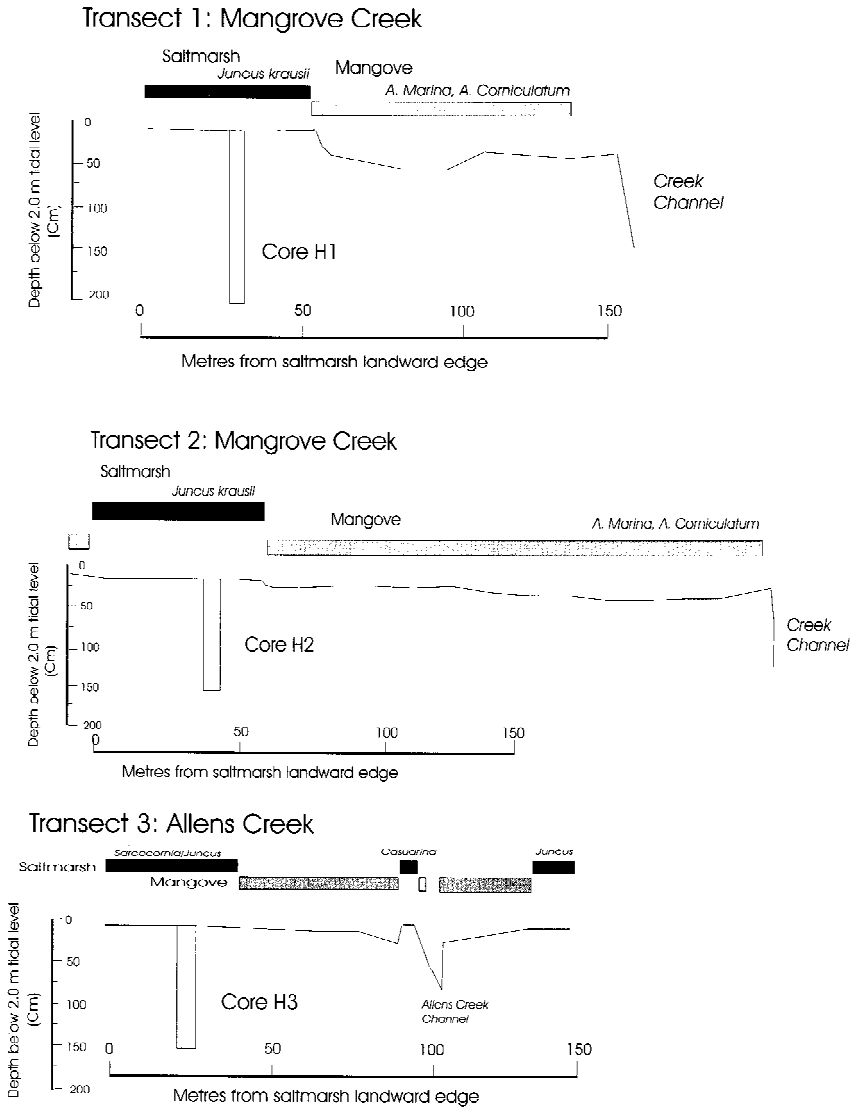


Figure 2. Elevation profiles, vegetation transects and core locations. Refer to Figure 1 for the location of transects.

bottom of the core (below 200 cm at Mangrove Creek, below 150 cm at Allens Creek, Figure 3).

At Mangrove Creek, the highest values of organic matter (10 – 20%) and moisture content (55 – 70%) and the lowest bulk density values (1.2 – 1.4 g / cm^3) occur within the oxidized zone and the upper parts of the reduced *Avicennia*-rich mud. Below this, organic matter / moisture contents decrease, and the bulk density increases downward through the reduced mud into the sandy mud unit at the base of the cores. At Allens Creek, the sandy sediments of the oxidized and the *Avicennia*-rich zones record the highest bulk density (1.83–1.87 g / cm^3) and the lowest moisture content (21 – 33%) values. However, as at Mangrove Creek, the highest organic matter content (12%) is recorded within the *Avicennia*-rich zone.

Discussion

The formation of the intertidal flats in the study area appears to be a consequence of the growth of subaqueous point bars. These point bars were initiated after the expansion of the bay-head delta front through the estuary. As they grew through lateral accretion of sandy fluvial sediments delivered from upstream

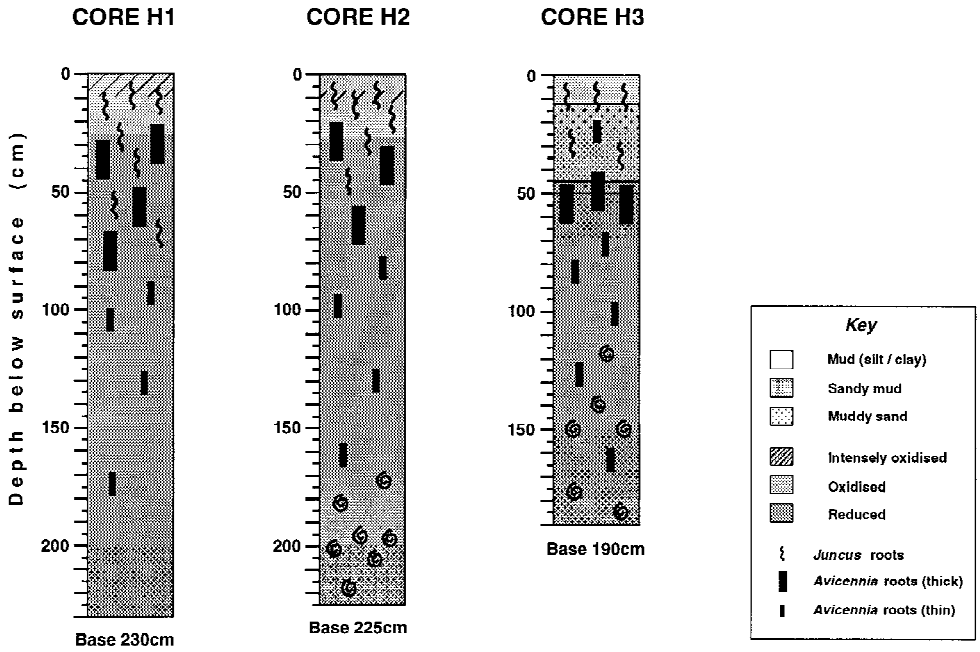


Figure 3. Stratigraphic Sections of cores. Refer to Figure 2 for the location of cores.

during floods, vertical accretion of mud through tidal action began to raise the older (landward) parts of the bar to intertidal elevations, allowing colonization by mangrove initially, and by saltmarsh with continued accretion to upper intertidal levels. Within Mangrove Creek, the age of the preserved mangrove root systems varies from approximately 500 years BP near the seaward edge of the saltmarsh to 1200 years BP near the landward edge, suggesting a gradual replacement of mangrove by saltmarsh landward to seaward in parallel with the growth of the point bar.

The preserved mangrove roots are within the elevation range of contemporary mangrove root systems and are overlain by 20–30 cm of sediment, both clastic and organic. The frequency of tidal inundation of the saltmarsh would decrease rapidly as its surface elevation approaches the upper limit of the intertidal zone. The considerable difference in the age of preserved mangrove roots at Mangrove Creek and Allens Creek, despite the compatible elevations of their current saltmarsh surface, suggests that the rate of vertical accretion slows to a negligible quantity with the decline in frequency of inundation (as proposed by French et al., 1995).

The incursion of mangrove upon saltmarsh was evident throughout the study area, though the rate of encroachment varied between geomorphic settings. Within Mangrove Creek, saltmarsh communities of *Juncus krausii* were subject to slow rates of mangrove encroachment as the seaward edge of the saltmarsh was eroded (Figure 4a).The mechanism is similar to that described for receding saltmarsh in the subsiding coastlines of southeast England and the United States Gulf coast (Guilcher, 1981; Salinas et al., 1986; Phillips, 1986) and has been observed in Corner Inlet, Victoria (Vanderzee, 1988). While the erosion fronts are active and unvegetated, changes were not of a scale detectable from air photo reconnaissance.

Where saltmarsh communities were dominated by *Sarcocornia quinquiflora* and *Sporobolus virginicus*, rates of mangrove encroachment were more rapid. No microcliffing was evident at the mangrove-saltmarsh boundary, and within Mangrove Creek the loss of saltmarsh was primarily due to the replacement of *S. quinquiflora* by the mangrove *Aegiceras corniculatum* (Figure 4c). On the intertidal banks of the main Hawkesbury River channel, the replacement of *S. quinquiflora* is primarily by the grey mangrove *Avicennia marina*. This incursion has been particularly rapid at Couranga Point where mangroves have spread behind a levee bank at the seaward edge of the saltmarsh plain (Figure 4b).

There is little stratigraphic evidence to suggest that post-depositional compaction and subsidence has been

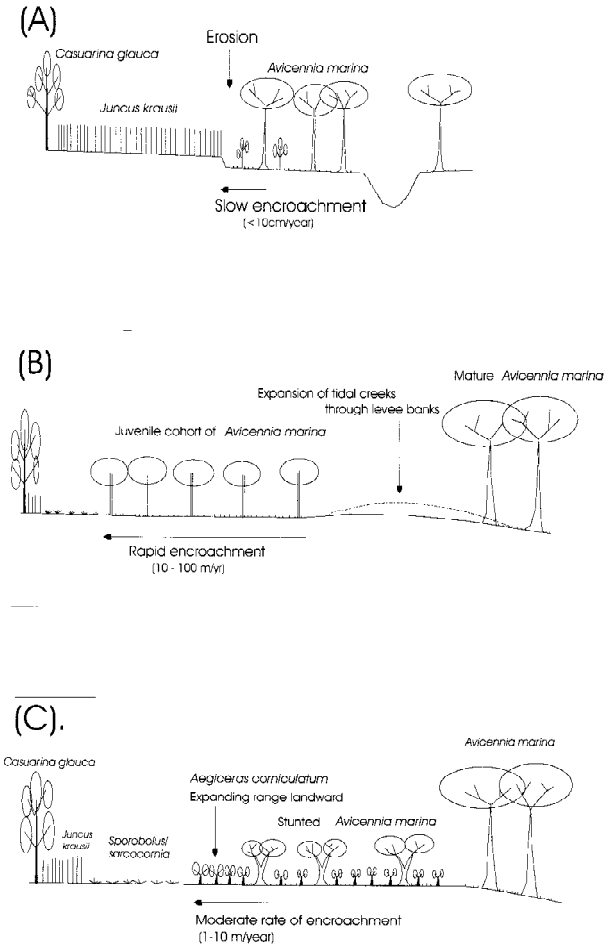


Figure 4. Modes of mangrove encroachment upon saltmarsh in the study area. (a) Recession of saltmarsh along an erosion front. (b) Expansion of the tidal creek network through a frontal levee leading to the rapid colonization of the saltmarsh plain. (c) Expansion of *A. corniculatum* on a gently inclining intertidal slope.

responsible for mangrove transgression. Although the downward increase in sediment bulk density, and a corresponding decrease in the moisture content at Mangrove Creek, and a deeper lower limit of oxidation at Allens Creek seem to suggest sediment compaction over time, the comparable depth of mangrove root occurrence in both areas and the higher upper limit of shell occurrence at Allens Creek, despite the difference in the time of deposition, indicate that compactional subsidence has been minor. In fact, the parallelism in trends suggests that the variations in bulk density and moisture content are controlled by the content of organic matter and sand in the sediment, rather than by any post-depositional changes.

That mangroves are now observed encroaching upon saltmarsh suggests a change in the relationship between sea-level and the rate of sedimentation in the Hawkesbury. It is unlikely that rates of sedimentation and accretion have declined in recent decades. The lateral expansion of mangroves at their seaward edge and a significant narrowing of the channel width (Gardiner, 1995), suggests an increased rate of sediment accumulation over the air photo period. Sea level has risen on the Sydney coastline over the same period, with a particularly high rate of increase in the period 1940–1986 (1.5 mm/yr; Gordon, 1988). Mangroves show their maximal rate of incursion between the air photograph series of 1954 and 1982, which corresponds to the period of maximum sea-level rise allowing for the lag between propagule establishment and growth of a juveniles large enough to be identified in the photographs.

These observations highlight the importance of temporal scale in the prediction of coastal wetland reponses to sea-level change. The average rate of sea-level rise and the average rate of accretion over the previous four decades would not suggest the likelihood of mangrove incursion into saltmarsh, given longer-term trends. However, we propose that a brief period of rapid sea-level rise was sufficient to offset increases in accretion and allow the expansion of mangroves in some, though not all of the geomorphic settings studied.

Acknowledgements

This research was made possible through funding from the Australian Research Council. Peter Johnson is thanked for assistance in the preparation of figures.

References

Alexander, T. R., 1974. Evidence of recent sea level rise derived from ecological studies on Key Largo, Florida. In Gleason, P. J. (ed.), Environments of South Florida: Present and Past. Memoir 2. Miami Geol. Soc. 219–21.

Alexander, T. R. & A. G. Crook, 1974. Recent vegetation change in southern Florida. In Gleason, P. J. (ed.), Environments of South Florida: Present and Past. Memoir 2. Miami Geol. Soc. 61–72.

Conaghan, P. J., 1980. The Hawkesbury sandstone: Gross characteristics and depositional environment. In Herbert, C. & R. Helby (eds), A Guide to the Sydney Basin. Geological Survey of New South Wales, Department of Mineral Resources, Bull. 26: 188–254.

English, S., C. Wilkinson & V. Baker, 1997. Survey manual for tropical marine resources (2nd edn) Australian Institute of Marine Science, Townsville, Queensland.

Evans, M., 1997. Historical distribution of estuarine wetlands at Kurnell Peninsula, Botany Bay – The need and potential for rehabilitation. B.Sc. Honours thesis, University of Wollongong.

French, J., T. Spencer & D. J. Reed, 1995. Geomorphic Responses to sea-level rise: existing evidence and future impacts. Earth Surface Processes and Landforms 20: 1–6.

Gardiner, B., 1993. Hawkesbury-Nepean River Sediment Dynamics Study. Sediment accumulation and sediment cycling in two estuarine depositional environments in the Foul Weather Reach and Spencer areas. Report No. 93/133. Australian Water Technologies, Science and Environment Division. West Ryde, NSW.

Gordon, A. D., 1988. A tentative but tantalizing link between sea-level rise and coastal recession in New South Wales. In Pearman, G. I. (ed.), Greenhouse, Planning for Climatic Change. CSIRO Division of Atmospheric Research, Melbourne.

Guilcher, A., 1981. Shoreline changes in salt marshes and mangrove swamps (mangals) within the past century. In Bird, E. C. F. & K. Koike (eds), Coastal Dynamics and Scientific Sites. 31–53.

Herbert, C., 1983. Geology of the Sydney 1:100 000 sheet 9130, Geological Survey of New South Wales, Department of Mineral Resources: 121–127.

Mitchell, M. L. & P. Adam, 1989a. The decline of saltmarsh in Botany Bay. Wetlands (Aust.) 8: 55–60.

Mitchell, M. L. & P. Adam, 1989b. The relationship between mangrove and saltmarsh communities in the Sydney Region. Wetlands (Aust.) 8: 37–46.

Morrisey, D., 1995. Saltmarshes. Chapter 13. In Underwood, A. J. & M. G. Chapman (eds), Coast. Mar. Ecol. Temperate Australia. UNSW Press, Sydney.

Morton, R. M., 1993. Fluctuations in wetland extent in southern Moreton Bay. In Greenwood, J. G. & N. J. Hall (eds), Future Marine Science in Moreton Bay. School of Marine Science, University of Queensland.

Nichol, S. L., B. A. Zaitlin & B. G. Thom, 1997. The upper Hawkesbury River, New South Wales, Australia: a Holocene example of an estuarine bayhead delta complex. Sedimentology 44: 263–266.

Phillips, J. D., 1986. Coastal submergence and marsh fringe erosion. J. Coast. Res. 2: 427–436.

Pidgeon, I. M., 1940. The ecology of the central coast of New South Wales. III. Types of primary succession. Proc. linn. Soc. N.S.W. 65: 221–249.

Roy, P. S., 1984. Holocene sedimentation histories of estuaries in southeastern Australia. In Hodgkin, E. P. (ed.), Estuarine Environments of the Southern Hemisphere. Department of Conservation and Environment, Western Australia, Bulletin No. 161: 23–59.

Salinas, L. M., R. D. DeLaune & W. H. Patrick, 1986. Changes occurring along rapidly submerging coastal area: Louisiana, USA. J. Coast. Res. 2: 269–284.

Saintilan, N., 1997 Mangroves as successional stages on the Hawkesbury River. Wetlands (Aust.) 16: 99–107.

Saintilan, N., & R. Williams, 1999. Mangrove transgression into saltmarsh environments in New South Wales, Australia. Global Biogeogr. Ecol. Letters. 8: 117–124.

Thom, B. G. & P. S. Roy, 1983. Sea-level change in New South Wales over the past 15 000 years. In Hopley D. (ed.), Australian Sea Levels in the Last 15 000 Years: A Review. Townsville, James Cook University, Monograph Series Occasional Paper No. 3: 64–85.

Vanderzee, M. P., 1988. Changes in saltmarsh vegetation as an early indication of sea-level rise. In Pearman, G. I. (ed.), Greenhouse: Planning for Climatic Change. CSIRO Publications, Melbourne: 147–160.

Wilton, K., 1998. Changes in Mangrove and Saltmarsh Areas in the Sydney Region, with Specific Reference to Careel Bay, Pittwater. M.Sc. Thesis, Macquarie University, Australia.

Woodroffe, C. D., 1990. The impact of sea-level rise on mangrove shorelines. Progr. Physic. Geogr. 14: 483–520.

Wetlands Ecology and Management **9:** 409–420, 2001.
© 2001 *Kluwer Academic Publishers. Printed in the Netherlands.*

Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia

N. Saintilan & K. Wilton
Australian Catholic University, PO Box 968, North Sydney 2059, Australia

Received 5 July 1999; accepted in revised form 22 June 2000

Key words: elevation, incursion, mangroves, nutrients, saltmarsh, sea-level

Abstract

The decline of saltmarsh in Currambene Creek and Cararma Inlet, in Jervis Bay, eastern Australia, in the period 1944–1999 has been documented through photogrammetric analysis. The area of saltmarsh has declined in Currambene Creek by approximately 52.5% and in Cararma Inlet by approximately 35%. In Currambene Creek the decline of saltmarsh is primarily due to the landward encroachment of mangroves, while in Cararma Creek the seaward encroachment of *Melaleuca* and *Casuarina* have more significantly contributed to losses of saltmarsh. Regional sea-level rise is excluded as a primary cause of this transgression. A more plausible hypothesis involves an increase in the delivery of freshwater and nutrients to the intertidal environments in response to higher rainfall and catchment modifications.

Introduction

A landward incursion of mangroves into saltmarsh environments in the estuaries of southeastern Australia over the last five decades has been established as a widespread trend in a review of photogrammetric surveys (Saintilan and Williams, 1999, 2000). In many places the invasion of saltmarshes by mangroves has led to a serious decline in the areal extent of saltmarsh (McTainsh et al., 1988; Mitchell and Adam, 1989a; Williams et al., 1999). Many estuaries on the south coast of New South Wales have been affected, including Currambene Creek, Jervis Bay (CSIRO, 1994).

In a review of this phenomenon, Saintilan and Williams (1999) identified seven key hypotheses which might explain mangrove transgression into saltmarsh in southeast Australia. Briefly, these hypotheses were:

i) sea-level rise has allowed the colonisation of the saltmarsh by mangroves,
ii) an increase in rainfall has freshened the upper intertidal environment,
iii) increases in nutrient loads in estuaries and the subsequent fertilisation of the saltmarsh plain has facilitated landward colonisation by mangroves,
iv) mangroves are recolonising areas from which they have been cleared,
v) modifications to the estuarine channel or entrance have altered tidal patterns in the estuary,
vi) the intertidal flat has subsided,
vii) saltmarsh is a pioneer species and is subsequently replaced by mangrove.

Many of these hypotheses can be tested by examining historical records and present-day environmental conditions. Hypothesis (i) can be tested by comparing the vertical extent of change with the extent of sea-level rise in the period. Hypothesis (ii) can be examined by comparing rainfall trends with the timing of change and the response of glycophytes in the upper saltmarsh fringe. Hypothesis (iii) can be tested by comparing the nutrient content of soils from affected and unaffected areas. If hypothesis (iv) were true, mangrove stumps should be observable. The remaining hypotheses are more difficult to test *post hoc*, though a combination of elevational modelling and stratigraphic analysis can provide some insights, particularly in relation to hypothesis (vii).

This paper quantifies the rate of change in the intertidal communities of the two principal creeks of Jervis Bay over the period of air photographic records and,

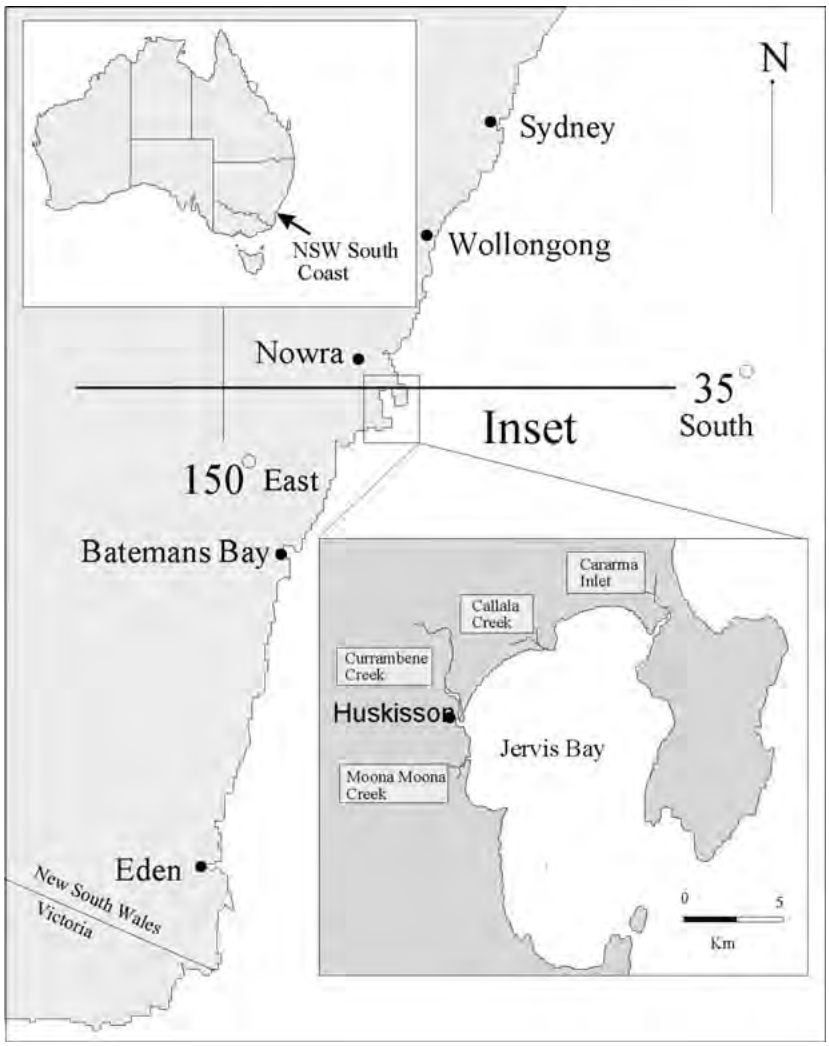


Figure 1. Location of Currambene Creek and Cararma Inlet, Jervis Bay.

in some instances, over a longer time period with the use of mangrove palaeosols. The change in position of these communities is assessed in relation to the extent of mean annual rainfall and sea-level change.

Methods

Study sites

Currambene Creek and Cararma Inlet, Jervis Bay (Figure 1), were chosen for detailed analysis of mangrove-saltmarsh dynamics in the context of these hypotheses. The south coast of NSW is tectonically stable, and the intertidal zones consist primarily of reworked marine sands of Holocene and Pleistocene origin, suggesting a minimum of deep or shallow subsidence. Both creeks have been the site of detailed vegetation surveys (Adam and Hutchings, 1987; Clarke, 1993; Clarke and Jacoby, 1994), and the creeks provide an interesting contrast in geomorphic setting and degree of modification.

A high stationary barrier blocks the northern half of Jervis Bay, and includes buried Pleistocene humate impregnated sand outcropping at both the northern and southern end (Thom, 1987). The backbarrier flat is cut by Cararma Inlet, a tidal creek which drains into the low-energy Hare Bay. Here there has been some wave and aeolian reworking of backbarrier sands enclosing the swamps. Cararma has little fluvial input and little development in the relatively small catch-

ment area. However, the saltmarsh plain is extensive, and relatively undisturbed.

By contrast, Currambene Creek has a relatively large catchment draining agricultural and urban land, and the saltmarsh environments have been grazed in the past. The town of Huskisson is situated at the mouth of the creek, and the creek is a popular site for boating. There is evidence of Pleistocene inner barrier sands occurring in a small area 0.5 km west of the mouth of Currambene Creek (Paterson, 1975; Thom, 1987). The mangrove and saltmarsh environments of Currambene occur on both flooded Pleistocene and prograded Holocene material.

Stratigraphic analysis

Longer-term changes in the extent of mangroves can be gauged through stratigraphic analysis of upper-intertidal soils (Mitchell and Adam, 1989b; Saintilan and Hashimoto, 1999). The occurrence of fossil mangrove root systems beneath the saltmarsh plain is an indication of a vegetation succession from mangrove to saltmarsh with fluvial and/or marine accretion of the intertidal flat. Such data can place historic observations of mangrove-saltmarsh dynamics in the context of changes over centuries and millennia (Saintilan and Hashimoto, 1999).

A hand auger was used to retrieve cores from the saltmarsh plain along two transects extending from the mangrove-saltmarsh boundary to the saltmarsh-*Casuarina* boundary in Cararma Inlet and Currambene Creek (Figures 2, 3).

In both transects preserved root material of the grey mangrove, *Avicennia marina* was retrieved from 0.2–0.5 metres below the contemporary saltmarsh surface. At Cararma Inlet, a dense layer of estuarine shells was found at approximately 0.7 metres beneath the upper intertidal saltmarsh plain.

Shells were washed and submitted to acid etch before standard radiometric dating. Sands containing preserved mangrove roots were excavated, and roots retrieved individually from the mud matrix. Roots were then given an acid/alkali/acid pre-treatment before undergoing standard radiometric dating. The measured age of shell and root material was converted into the conventional C14 age after applying $^{13}C/^{12}C$ corrections.

Photogrammetry

Photogrammetric analysis in this survey was undertaken using the Wild Aviolyt AC3 stereo plotter. This instrument produces high resolution digital spatial data from stereo pairs of aerial photograph diapositives (Hanslow et al., 1997). The stereo plotter has the advantage of rectifying distortion in photo scale and differences in scale between photographs, as well as allowing high resolution magnification of images, assisting in interpretation. Ground control was based on Integrated Survey Grid (ISG) control points provided by the NSW Lands Department. Data output was downloaded to a CADD system for analysis and presentation.

Photographic runs of Currambene Creek used in the photogrammetry were Jervis Bay Run 1, 1949; Jervis Bay Run 1, 1961; Jervis Bay Run 1, 1975; 1986 Huskisson/Callala Beaches 1993 and NSW4126 for 1997. Photographic runs of Cararma Inlet were Jervis Bay-Nowra Run C 1948; Jervis Bay Run 1, 1961; NSW Coastal Wetlands Run 60 1981; and NSW4474 Cabbage Tree Swamp for 1999.

Pure mangrove habitat was defined as mangrove with less than 10 m canopy gaps. A mixed or ecotone category was identified as areas of mangrove and saltmarsh where the gap between mangrove canopy was between 10 and 20 metres. Saltmarsh was defined as vegetated intertidal areas with a greater than 20 m canopy gap between mangroves, though *Casuarina* and *Melaleuca* were identified as separate categories. Only mangrove and saltmarsh areas common to all photographs were included in the analysis.

Topographic analysis

The method for measuring inundation frequency in intertidal environments is a modification of that described in English et al. (1997). Rods marked with water-soluble dye were inserted along transects placed at equal intervals across the intertidal plain before a night Spring tide. A total of 120 rods were used in each of Cararma Inlet and Currambene Creek for this purpose. The tide acts as a level, the depth of inundation at each pole was recorded. The species composition of the surrounding vegetation was recorded for each rod position, providing a basis for the description of the elevation at which each species was observed.

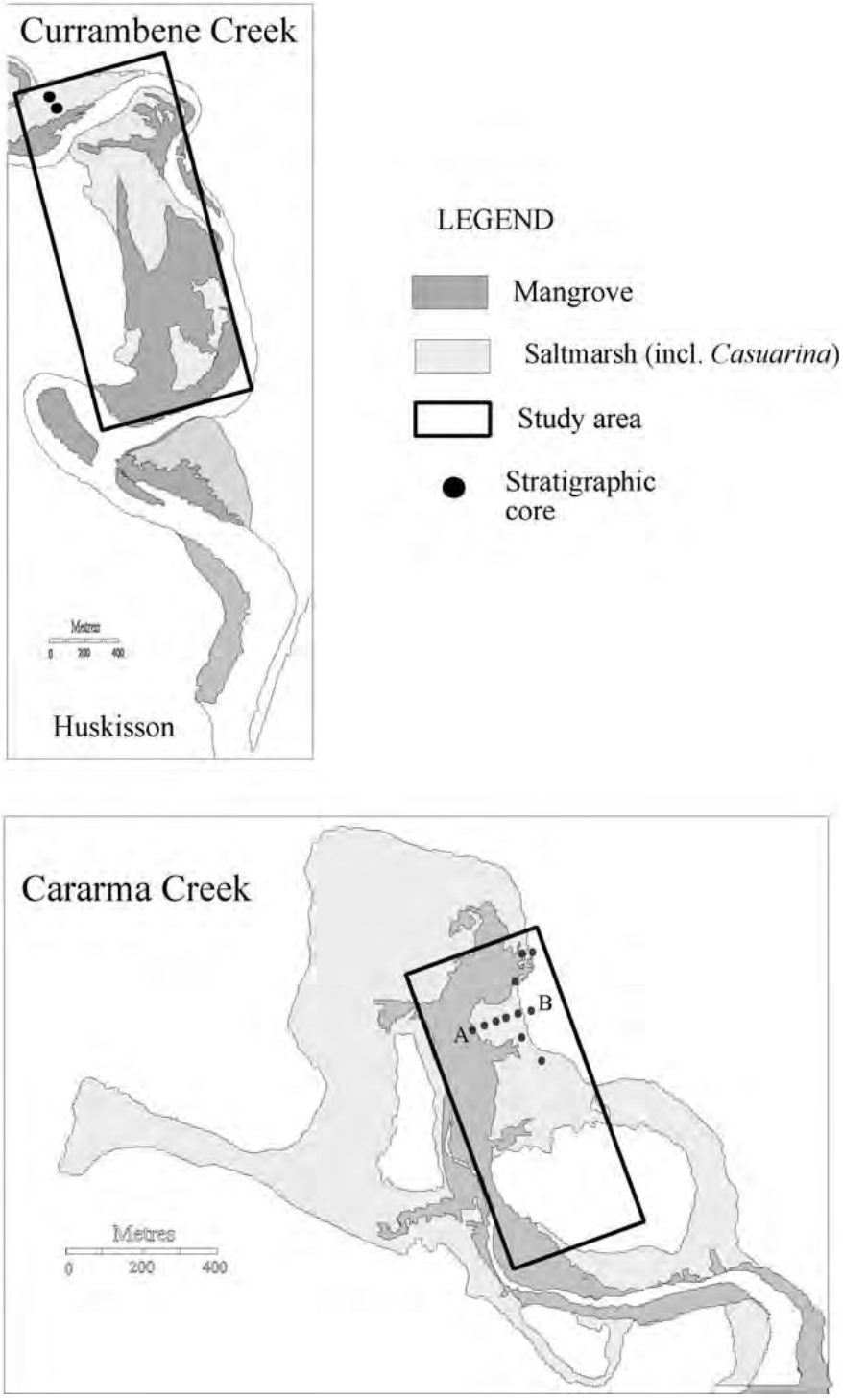


Figure 2. Location of study areas and stratigraphic cores.

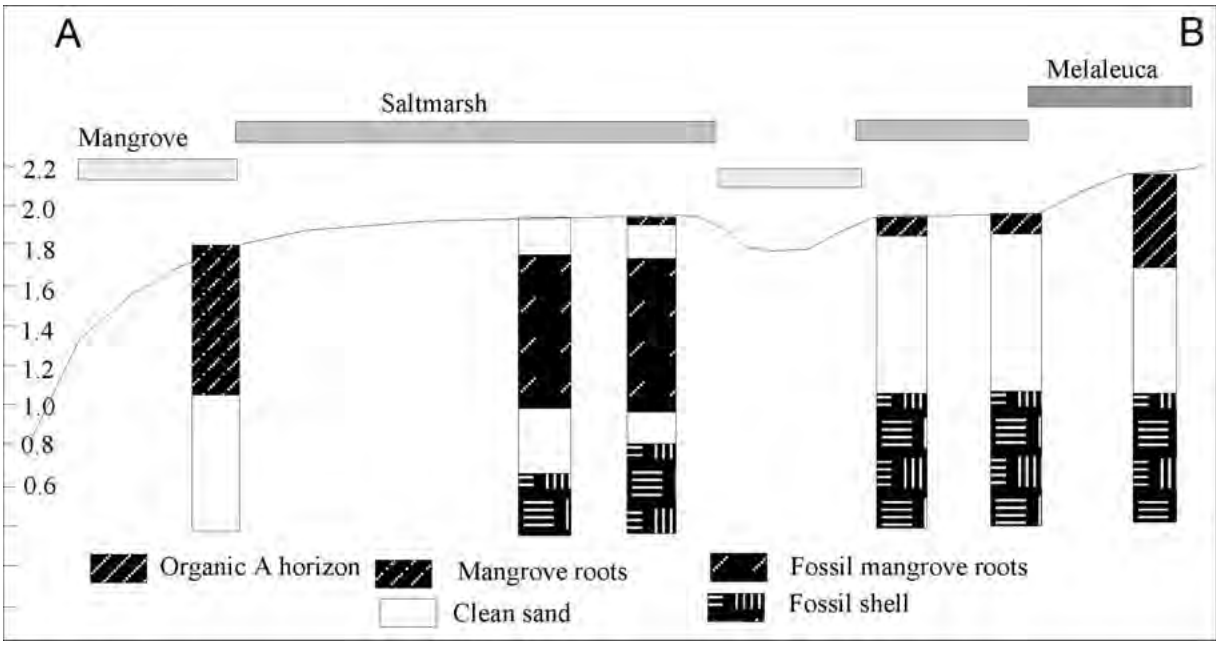


Figure 3. Stratigraphic profile within Cararma Creek, Jervis Bay, from the creek edge 'A' to the landward edge of the saltmarsh 'B' as in Figure 2.

Results

Stratigraphic analysis and C14 dating

Mangrove roots found beneath *Juncus* saltmarsh in the Currambene saltmarsh core dated to 1320 ± 70 C14 yrs BP. Shell deposited at the base of the intertidal unit in Cararma Inlet dated to 3200 ± 60 C14 yrs BP, and the mangrove roots within the same Cararma Inlet core dated to 1920 ± 90 C14 yrs BP.

Changes in the area of mangroves and saltmarshes

The areal extent of 'pure' saltmarsh in the Currambene Creek study area declined from 48 hectares in 1949 to 27.2 hectares in 1993 (Figure 4). Further, the area of mixed mangrove and saltmarsh habitat declined from 26.7 hectares in 1949 to 12 hectares in 1993. Overall the habitat of saltmarsh declined by 52.5% from 74.7 hectares in 1949 to 39.2 hectares in 1993.

Areas of pure mangrove habitat increased from 34.1 hectares to 44.9 hectares in 1993. Since 1975 in particular, the area of pure mangrove habitat has expanded substantially at the expense of the mixed mangrove and saltmarsh habitat.

The area of saltmarsh in Cararma Inlet has declined by 35% from 176.5 hectares in 1949 to 114.2 hectares in 1999. The trend is that of a steady decline with little sign of attenuation (Figures 5 and 6). In contrast to Currambene Creek, the mangrove-saltmarsh boundary in Cararma Inlet has been relatively stable, with little overall increase in the area of mangrove. Most saltmarsh loss has been due to the expansion of terrestrial species at the landward edge of the saltmarsh (*Casuarina*, *Melaleuca, Eucalyptus* and miscellaneous) which increased in area from a combined 80 hectares in 1961 to 128 hectares in 1999.

Tidal inundation

The longest period of sea-level data for the region is Fort Denison, Sydney Harbour, 150 km to the north. Five-year running means of sea-level for this data set (Figure 7) indicate sea-levels approximately 4 cm higher for the period 1950–2000 compared to the first half of the century. This provides a benchmark against which changes in the vertical position of mangroves in the intertidal zone may be gauged. Topographic maps were generated on the basis of flooding depths measured using marker poles (Figure 8).

Single factor analysis of variance was performed with a *post hoc* Student-Newman-Kuels test to determine the elevational associations of species encountered in the elevation survey. At Cararma Inlet, where the saltmarsh plain was widest, *Avicennia marina* was consistently found in the lowest elevation, forming

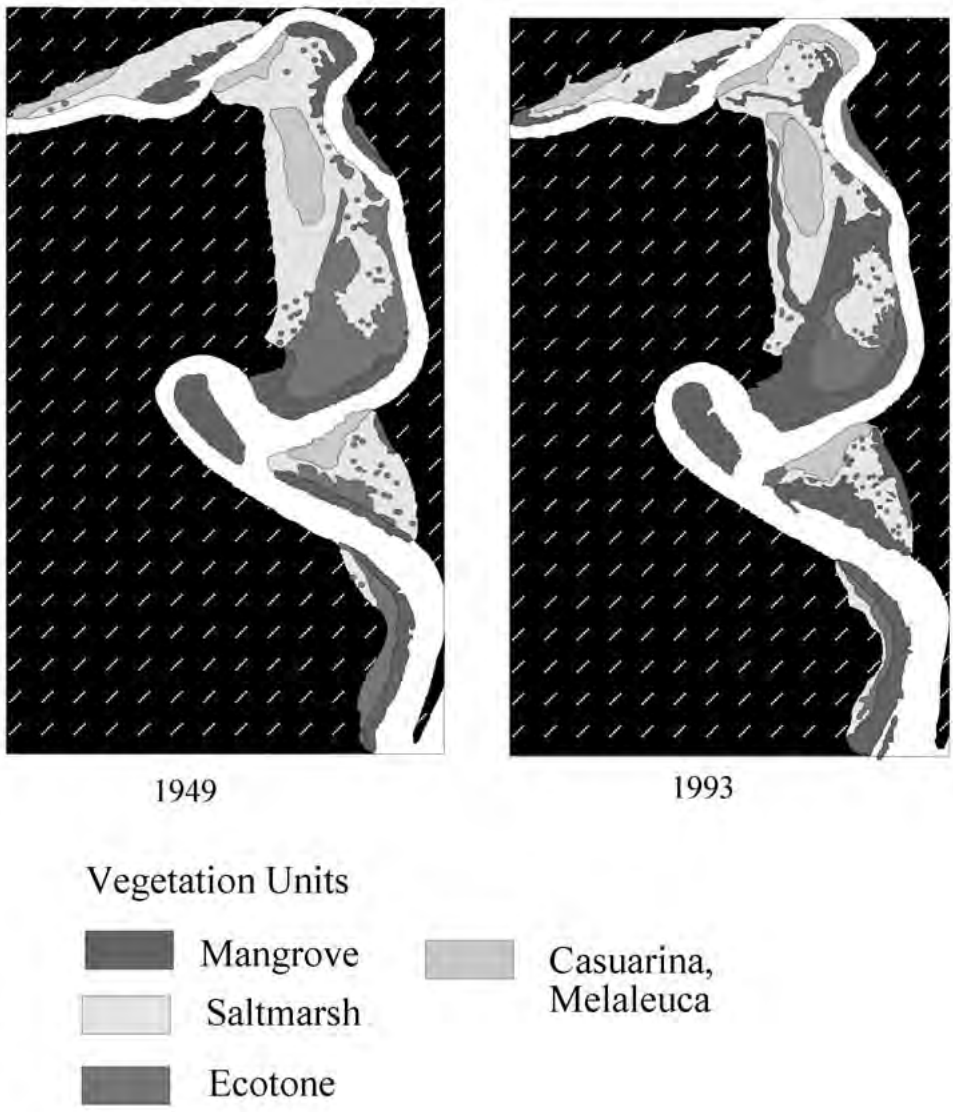


Figure 4. The distribution of intertidal wetland communities, Currambene Creek, 1949 and 1993.

an association with *Samolus repens* at its landward edge. *Sporobolus virginicus* forms a group at intermediate elevation. *Halosarcia pergranulata, Sarcocornia quinqueflora* and *Gahnia filum* form an upper saltmarsh association, with *Juncus kraussii* and *Casuarina glauca* occurring at a level rarely inundated by Spring tides.

Within Currambene Creek the elevation of the species was less distinct. *Avicennia marina*, *Samolus repens*, *Sporobolus virginicus* and *Sarcocornia quinqueflora* could not be statistically differentiated on the basis of elevation. Only *Juncus kraussii* and *Casuarina glauca* occurred at significantly higher elevations.

The elevation at which *Juncus kraussii* and *Sarcocornia quinqueflora* were found growing in Currambene Creek with respect to tidal inundation was lower than that at Cararma Inlet. *Samolus repens, Sporobolus virginicus* and *Avicennia marina* grew at comparable elevations within the two creeks with respect to tidal inundation.

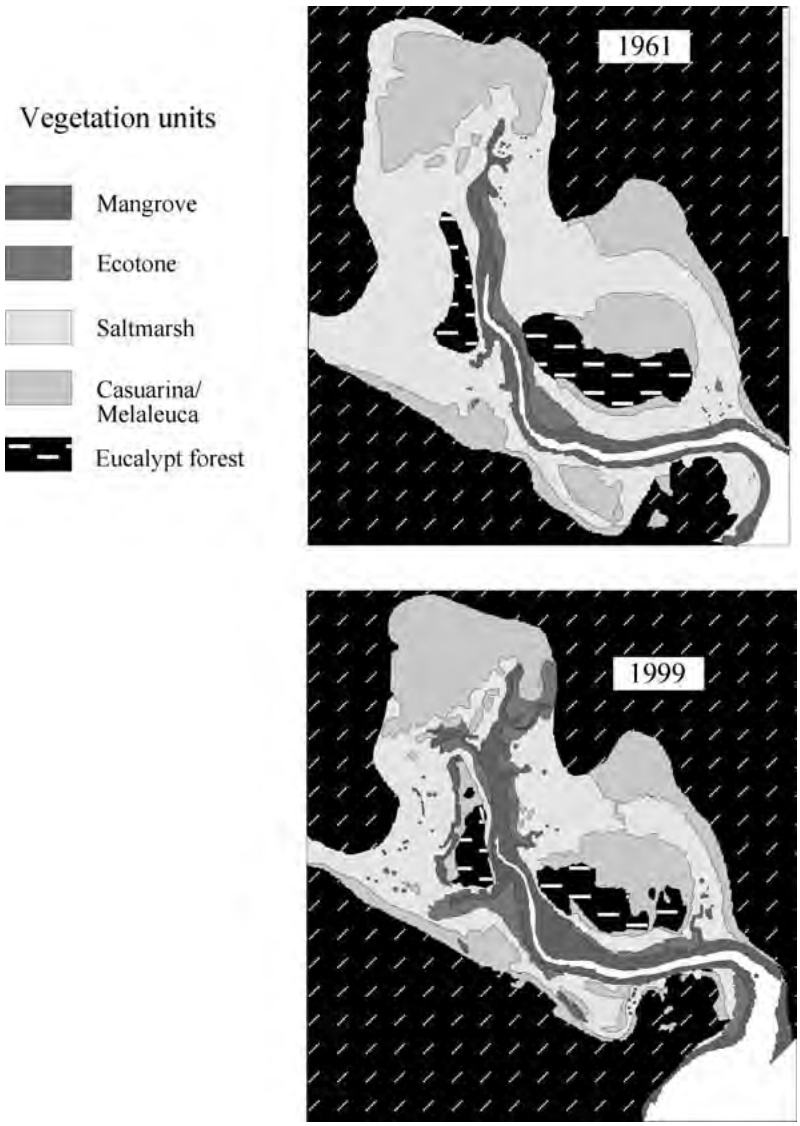


Figure 5. The distribution of intertidal wetland communities, Cararma Inlet. 1949 and 1993.

Discussion

Reconstruction of vegetation history in Cararma Inlet and Currambene Creek

At circa 3000 BP Cararma Inlet appears to have been a shallow estuarine lake sheltered behind a complex Pleistocene-Holocene barrier. The lake must have been highly productive source of shellfish, gauging from the thick, dense deposits of intact estuarine bivalves which have been located at 0.7 m below at least ten hectares of the upper saltmarsh surface.

Tidal reworking of aeolian and wash-over deposits has gradually infilled the lake, creating an intertidal wetland, dominated circa 2000 BP by mangroves. Continued accretion has seen the gradual replacement of mangroves with saltmarsh, so that mangroves now form a fringe to the tidal creek, and the inlet is dominated by one of the most extensive saltmarsh plains on the south coast of New South Wales. Rates of vertical accretion over the previous 2000 years have averaged approximately 0.5–0.8 mm per year.

Currambene Creek has a more complex history, given the greater extent of probable Pleistocene material and the involvement of both fluvial and tidal sedi-

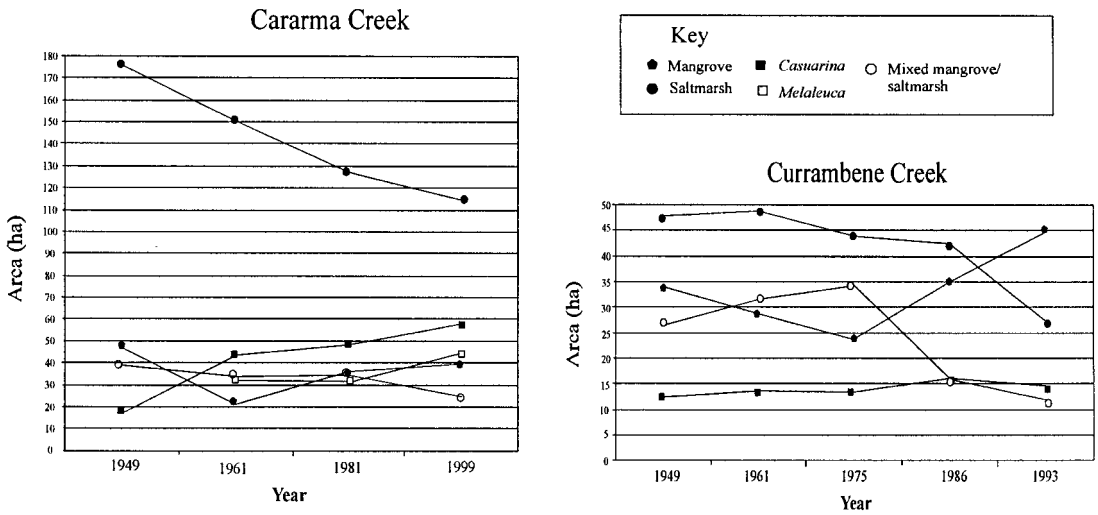


Figure 6. Changes in the area of intertidal wetland communities, Currambene Creek and Cararma Inlet between 1949 and 1999.

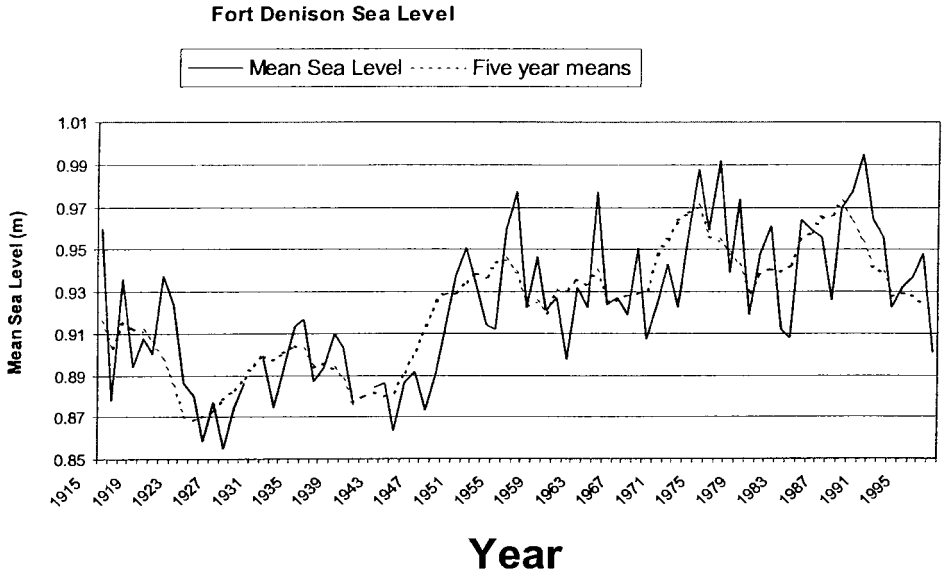


Figure 7. Sea-level trends at Fort Denison, 1915–1998.

mentation through the latter Holocene. On the main intertidal flat immediately upstream of Huskisson, there is no stratigraphic evidence of prior occupation of the upper intertidal flat by mangroves, nor is there evidence of the marine bivalves so prominent in the profile at Cararma Inlet. However, mangrove roots were found beneath the *Juncus* plain 2 kilometres upstream, suggesting that some, though not all, of the current point bars have accreted in the previous two thousand years, and a succession from mangrove to saltmarsh has occurred. The C14 age of this mangrove material suggests a rate of accretion slightly more rapid than that found at Cararma Inlet, of approximately 1 mm per year. These results are comparable to rates of accretion established using the same technique in the Hawkesbury River estuary (Saintilan and Hashimoto, 1999).

The more sporadic occurrence of mangrove palaeo-material in the intertidal plains of Currambene Creek may reflect the more important contribution of channel meandering and horizontal accretion in the creation of point bars. Cut-off meanders are obvious

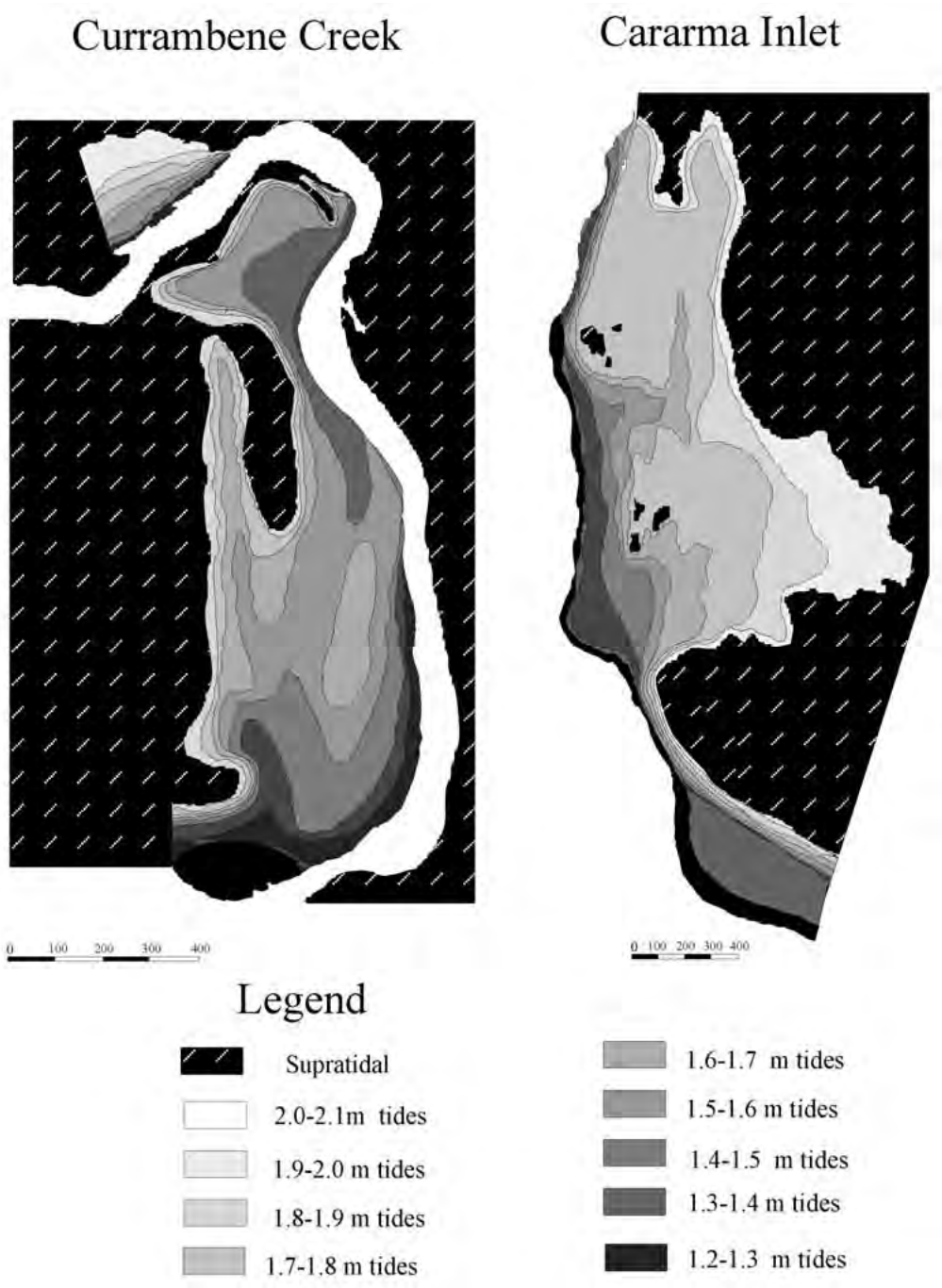


Figure 8. Elevation of selected intertidal environments in Currambene Creek and Cararma Inlet.

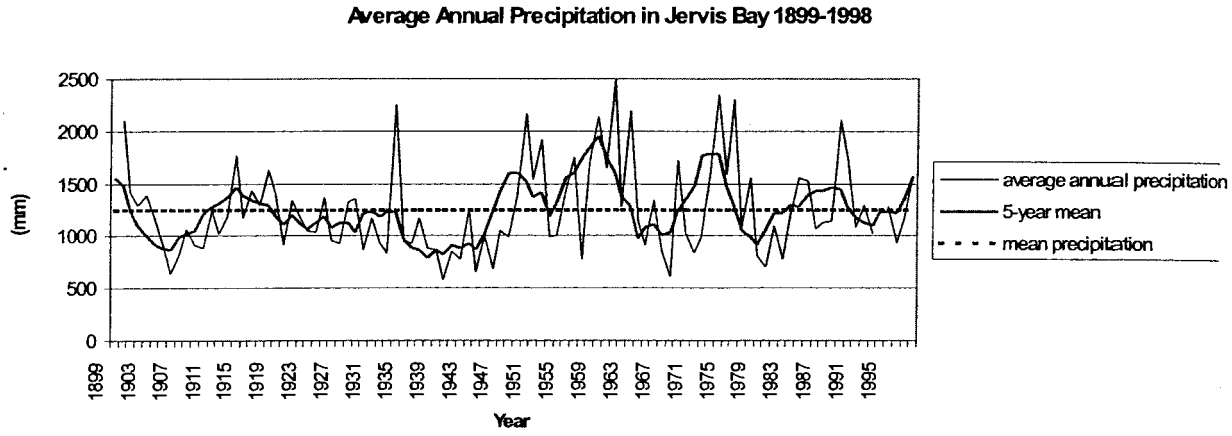


Figure 9. Rainfall for Point Perpendicular, Jervis Bay; 1889–1998. Data from the Bureau of Meteorology.

in the upper tidal reaches, and some are currently occupied by relict mangroves. With continued accretion these will presumably be replaced by saltmarsh.

Recent changes in the distribution of mangroves and saltmarsh

Mangrove has increased in area in Currambene Creek at the expense of saltmarsh. The distance over which mangrove transgression has occurred on the largest intertidal flat in Currambene Creek in some places exceeds 700 metres. The loss of saltmarsh to mangrove incursion in Currambene Creek is of similar magnitude to that described in many NSW estuaries (Saintilan and Williams, 1999).

The mangrove-saltmarsh boundary in Cararma Inlet has been more stable. Within this system a considerable proportion of saltmarsh loss has been due to the encroachment of *Casuarina* and *Melaleuca* onto the saltmarsh plain. The seaward encroachment of *Casuarina* onto the saltmarsh plain has also been described for the nearby Minamurra estuary by Chafer (1998), and suggests an alteration in the hydrology of the upper intertidal plain unrelated to fluctuations in the tidal prism.

Inferences regarding sea-level rise and mangrove transgression

Within Currambene Creek, the vertical range transgressed by mangroves in the photographic period (1949–1993) far exceeds the degree of regional sea-level rise. Judging by the position of the mangrove-saltmarsh boundary in Currambene Creek in 1949, the position of the boundary in 1993, and the difference in inundation depth between poles at both locations, mangroves have extended their vertical range in some places within Currambene Creek by up to 30 cm. This is likely to be a conservative estimate in that inundation frequency, and hence vertical accretion, is higher in lower elevation environments (Stoddart et al., 1989).

At both Currambene Creek and Cararma Inlet the elevation at which saltmarsh replaces mangrove is approximately the position of the mean highest diurnal tide. The implication is that mangroves in Currambene Creek have moved to the position with respect to tidal inundation that they have been consistently occupying in Cararma Inlet. The result is consistent with the supposition that biotic and/or physio-chemical factors had excluded mangroves from sections of the Currambene intertidal flat in the first half of the century.

A further factor telling against a simple translation of vegetation communities in response to sea-level rise is the stability of the saltmarsh-terrestrial boundary. The only instances of *Casuarina* dieback in Currambene Creek are clearly fire-related, and in Cararma Inlet the terrestrial species are advancing onto the saltmarsh plain.

Inferences regarding rainfall, nutrients and mangrove encroachment

Higher rainfall in the second half of the century has been a regional trend for southeastern Australia (Hennesey et al., 1999), and rainfall patterns at Point Perpendicular, Jervis Bay, follow this trend (Figure 9). Mean annual rainfall for the period 1899–1949 was 1150 mm/yr., compared to 1360 mm/yr for the period

1950–1998. A landward encroachment of mangroves with increased rainfall is consistent with the observation of Saenger (1995) that the relative proportion of mangroves and saltmarsh within Australian estuaries is significantly related to average annual precipitation.

The encroachment of both mangrove and terrestrial glycophytes onto the saltmarsh plain would be consistent with the freshening of the intertidal environment which would result from increased precipitation. However, rainfall is also an important source of nitrogen. Nitrogen has been found to be limiting to mangrove growth (Boto and Wellington, 1983). Decreased salt marsh may be due to increased rainfall both freshening the intestinal environment and contributing nitrogen.

Increases in nutrient levels within estuaries following urbanisation is well established for the region (Zann, 1995), as is the proportion of rainfall reaching the estuary from urbanised catchments. This study has shown a contrast between the high degree of mangrove incursion in Currambene Creek, with a highly modified catchment, and the stable mangrove/saltmarsh boundary in Cararma Inlet, with an unmodified catchment. This trend is consistent with that emerging from a review of twenty-eight photogrammetric surveys (Saintilan and Williams, 2000), which showed the highest level of mangrove incursion to be in modified, and in particular urbanised catchments. The suggestion by Wilton (2000) that the degree of mangrove incursion may be related to the degree of urbanisation warrants an examination of the potential role of nutrient and sediment inputs in urbanised catchments in altering the balance between mangrove and saltmarsh.

Acknowledgements

This research was jointly funded by the Lower Shoalhaven Catchment Management Committee, the NSW Department of Land and Water Conservation, and Australian Catholic University through the Internal Research Grants Scheme. The Macintosh Centre for Quaternary Dating (University of Sydney) conducted the radiocarbon analysis. The photogrammetric survey was conducted with the assistance of Christine Gray (Department of Land and Water Conservation). Peter Clarke is thanked for helpful clarification of the aims and insights of the CSIRO monitoring program.

References

Adam, P. and Hutchings, P. 1987. The saltmarshes and mangroves of Jervis Bay. Wetlands (Australia) 6(2): 58–64.

Boto, K.G. and Wellington J.T. 1983. Phosphorus and nitrogen nutritional status of a northorn Australian mangrove forest. Marine Ecology Progress Series 11: 63–69.

Chafer C.J. 1998. A spatio-temporal analysis of estuarine vegetation change in the Minnamurra River 1938–1997. Minnamurra Estuary Management Committee.

Clarke, P.J. 1993. Mangroves, saltmarsh and peripheral vegetation of Jervis Bay. Cunninghamia 3(1): 231–254.

Clarke, P.J. and Jacoby, C.A. 1994. Baseline studies of saltmarsh plants in south-eastern Australia: biomass and productivity. Australian Journal of Freshwater and Marine Research 45: 1521–28.

CSIRO, 1994. Jervis Bay Baseline Studies, Final Report, May 1994. CSIRO Division of Fisheries, Marmion Research Laboratories.

English, S., Wilkinson, C. and Baker, V. 1997. Survey Manual for Tropical Marine Resources. (2nd edition) Australian Institute of Marine Science, Townsville.

Hanslow, D.J., Clout, B., Evans, P. and Coates, B. 1997. Monitoring Coastal Change Using Photogrammetry. *In:* Bliss E. (ed.) Islands: Economy, Society and Environment. Conference Proceedings, Second Joint Conference, Institute of Australian Geographers and New Zealand Geographical Society, University of Tasmania.

Hennessy, K.J., Suppiah, R. and Page, C.M. 1999. Australian Rainfall Changes 1910–1995. Australian Meteorological Magazine 48: 1–13.

McTainsh G., Iles B. and Saffigna P. 1988. Spatial and temporal patterns of mangroves at Oyster Point Bay, south east Queensland, 1944–83. Proc. R. Soc. Qld. 99: 83–91.

Mitchell, M.L. and Adam, P. 1989a. The decline of saltmarsh in Botany Bay. Wetlands (Australia) 8: 55–60.

Mitchell, M.L. and Adam, P. 1989b. The relationship between mangrove and saltmarsh communities in the Sydney Region. Wetlands (Australia) 8: 37–46.

Paterson I.B.L. 1975. The Geology and low-cost extractive resources of the Nowra-Jervis Bay area. Geological Survey of NSW Report GS 1974/208.

Saenger P. 1995. The status of Australian estuaries and enclosed marine waters. *In:* Zann, L. and Kailola P. (eds.), State of the Marine Environment Report for Australia: Technical Annex 1, The Marine Environment. GBRMPA/Ocean Rescue 2000, pp. 53–73.

Saintilan, N. and Hashimoto, T.K. 1999. Mangrove-saltmarsh dynamics on a prograding bayhead delta, Hawkesbury River, New South Wales, Australia. Hydrobiologia 413: 95–102.

Saintilan, N. and Williams, R.J. 1999. Mangrove transgression into saltmarsh environments in southeast Australia. Global Ecology and Biogeography 8: 117–124.

Saintilan N. and Williams R.J., 2000. Short note: the decline of saltmarsh in southeastern Australia: results of recent surveys. Wetlands (Australia) 18(2): 49–54.

Stoddart D.R., Reed D.J. and French J.R. 1989. Understanding saltmarsh accretion, Scolt Head Island, Norfolk, England. Estuaries: 228–236.

Thom, B.G. 1987. Geomorphology of the Jervis Bay area. Wetlands (Australia) 6(2): 19–21.

Williams R.J., Watford F.A. and Balashov V. 1999. Kooragang Wetland Rehabilitation Project: Changes in wetland fish habitats of the lower Hunter River. NSW Fisheries Office of Conservation, Fisheries Research Institute, Cronulla, NSW.

Wilton K. 2000. Changes in the distribution of mangroves and saltmarshes in Careel Bay, Pitwater. Wetlands (Australia) in press.

Zann L.P. 1997. Our Sea, Our Future. Major findings of the State of the Marine Evironment Report for Australia. Ocean Rescue 2000, Department of Environment, Sport and Territories, Canberra.

Aquatic Botany 151 (2018) 30–37

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Reproduction of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit

Nicholas C. Wilson[a,*,1], Neil Saintilan[b]

[a] School of Arts and Sciences (NSW), Australian Catholic University, PO Box 968, North Sydney NSW 2059, Australia
[b] Department of Environmental Sciences, Macquarie University, Sydney, NSW, 2109, Australia

ARTICLE INFO

Keywords:
Rhizophora stylosa
Mangrove
Latitudinal limit
Reproduction
Phenology
Climate change
Australia

ABSTRACT

A study of reproductive phenology and reproductive performance of the mangrove species *Rhizophora stylosa* was conducted in three estuaries spanning the southernmost 265 km of its known range on the east Australian coast. The timing of reproductive primordia, buds, flowers, fruit and propagule fall did not differ significantly over the latitudinal range of the study. Peak propagule fall occurred in April after a mean 19–20 months of development, only slightly longer than accounts for tropical latitudes. On average, 2.1% of buds matured to form viable propagules, with an average of 17.2% of buds becoming advanced fruit and 11.9% of advanced fruit becoming mature propagules, which compares well with the ranges published accounts for Australian tropical *R. stylosa* trees. However, there were relatively few buds per inflorescence on recorded shoots in this study, although formal studies on this in the tropics are absent. Within-site variation in bud and propagule production per shoot was greater than variability between sites in many cases, though our sample size was necessarily low due to the rarity of the trees at the southern limit and the detailed recording method. The species reproduces successfully at its known southern limit, with notable comparability to the eastern Australian Tropics. This suggests there is little thermal limitation on reproduction at the southern limit, where there is evidence of slow spread. "Precocious" reproduction as observed for young *R. mangle* at range limits in North America was not detected.

1. Introduction

Climate has long been implicated inthe latitudinal range of mangrove species, principally through the "climate sifting" of species on cold tolerance (Hutchings and Saenger, 1987; Duke et al., 1998). Recent poleward expansion of mangrove limits has been attributed in part to recent global warming (e.g. Saintilan et al., 2014; Alongi, 2015). However, the response may not be as simple as a step-wise extension of latitudinal range (Alongi, 2015). For example, temperature thresholds did not consistently predict mangrove species limits in the global studies of Quisthoudt et al. (2012) and Osland et al. (2017).

There is no *a priori* reason why the responses of phylogenetically disparate mangrove taxa should be the same, or be independent of the climatic, hydrographic and geomorphic features of different coasts. Since the last major freeze event in 1989, the limits of *Rhizophora mangle* L. have rapidly extended poleward on the US Atlantic coast (Cavanaugh et al., 2014) and the species is reaching sexual maturity early there ("precocious" reproduction) (Dangremond and Feller, 2016). Congeneric case studies can shed light on how typical not only range extensions are, but also identify any other such "anomalous" responses.

Rhizophora stylosa Griff. is a widespread Indo-Pacific mangrove species, ranging from Okinawa Island in the north, to Fiji and the Marshall Islands in the east and to Odisha State, India in the west (Duke, 2006; Kamruzzaman et al., 2013; Ragavan et al., 2016). Its known southern limit is the estuary of South West Rocks Creek (SWR Creek; -30.88°, 153.03°) on the east Australian state of New South Wales (NSW) (Wilson, 2009; Table 1). It occurs in relatively large numbers on the northernmost NSW estuary of the Tweed River (-28.18°, 153.53°), albeit in far smaller numbers than in the Australian tropics (Duke, 2006). South of the Tweed River, it was recorded in lower numbers in 15 of 26 estuaries searched south to the Hastings River (−31.43°, 152.92°) by Wilson (2009). No new estuary records have since been confirmed, although survey effort has only been slight.

Rhizophora stylosa shows evidence of recent expansion on intra- and extra-estuary scales in NSW, but clearly long-established stands are present in about nine estuaries (Wilson, 2009). NSW has a high-energy coast and mangroves are effectively restricted to estuaries.

* Corresponding author.
E-mail addresses: rstylosa@gmail.com (N.C. Wilson), neil.saintilan@mq.edu.au (N. Saintilan).
[1] Present address: 50A Sunrise Road, Palm Beach, NSW, Australia.

https://doi.org/10.1016/j.aquabot.2018.07.009
Received 6 April 2018; Received in revised form 11 July 2018; Accepted 21 July 2018
Available online 25 July 2018
0304-3770/ © 2018 Elsevier B.V. All rights reserved.

Table 1
Details and notes on the estuaries and trees sampled. Estuary details: L = Location; W = Water area; C = Catchment area; M = Mapped area of mangrove (Creese et al., 2009); RS: Known number of *R. stylosa* plants producing buds / producing propagules for the whole estuary in 2004 (Wilson, 2009). Water and catchment areas from http://www.environment.nsw.gov.au/estuaries/list.htm.

Estuary	Estuary details	Number and name code of sampled trees and notes
Brunswick River	L: -28.54°; 153.56° W: 3.6 km^2 C: 226.3 km^2 M: 123.3 ha RS: 120 / circa 35	The Brunswick River system includes 3 arms, including a northern arm known as Marshalls Creek. 7 trees were sampled in the two loose main stands on Marshalls Creek, plus 1 isolated tree on the main Brunswick River arm. Site analyses are restricted to the 7 Marshalls Creek trees.
Richmond River	L: -28.88°; 153.59° W: 38.4 km^2 C: 6861.8 km^2 M: 602.6 ha RS: 84 / circa 44	4 trees: 3 trees were sampled from the only stand at Mobbs Bay, and a single isolated tree on the South Ballina shoreline. The Mobbs Bay stand is longer established than those on Marshalls Creek, as it is denser and with bigger trees.
South West Rocks Creek	L: -30.88°; 153.04° W: 0.9 km^2 C: 3.7 km^2 M: 64.8 ha RS: 3 / 2	2 propagule-producing trees were present only. One more produced buds only during the study, but propagules were recorded in January 2016.

Rhizophora has an unusual anatomy and physiology (Tomlinson, 1994). Reproductive buds arise within the meristematic apical bud of each shoot and paired reproductive bud primordia (hereafter: primordia) sit in the axils of the two new leaves after bud expansion (Tomlinson et al., 1979; Tomlinson, 1994). Shedding of the stipules on bud expansion leaves annular stipular scars ("nodes") that can be used as reliable reference points for the tracking of vegetative and reproductive dynamics on the shoot. As a shoot extends with new leaf emergences above a given locus, new overlapping reproductive generations may develop (Supplementary Fig. S1).

The primordia develop into dichotomised inflorescences, with a variable number of divisions determining the number of buds within and between *Rhizophora* species (Duke and Bunt, 1979). Fertilised flowers develop slowly into acorn-sized fruit, which germinate and develop on the tree into viviparous seedlings ("propagules") (Supplementary Fig. S2). The involved vivipary (Juncosa, 1982) means a lengthy reproductive cycle in *Rhizophora*, with a reported range of 8–13 months in *R. mangle* (Gill and Tomlinson, 1971) to "nearly 3 years" in *Rhizophora apiculata* BL. (Christensen and Wium-Andersen, 1977). A low rate of conversion of buds and/or flowers to propagules has been found to be typical of *Rhizophora* (e.g. Saenger, 2002; Tyagi, 2004; Coupland et al., 2006).

Seasonal peaks in reproductive phenophases are consistently observed for *R. stylosa* (Duke et al., 1984; Leach and Burgin, 1985; Duke, 2002; Coupland et al., 2005; Kamruzzaman et al., 2013) and other *Rhizophora* spp. (e.g. Steinke, 1988; Duke, 2002; Mehlig, 2006; de Lima Nadia et al., 2012). Seasonal timing of reproductive phenophases is not always strictly in accordance. For example, the short flowering stage of *Rhizophora* spp. has been observed during drier seasons (e.g. Duke et al., 1984) and during wetter seasons (e.g. Fernandes, 1999; Mehlig, 2006). Although methodologies and assumptions can differ between studies, often qualified comparisons can be made.

Inter-annual variation in propagule production has been widely observed in *Rhizophora* (Gill and Tomlinson, 1971; Duke et al., 1984; Duke, 2002; Coupland et al., 2005; Mehlig, 2006; Kamruzzaman et al., 2013). Tyagi (2003, 2004) found more flowers and a greater number and size of propagules in *R. stylosa* in "wet" versus "dry" sites in Fiji, suggesting local conditions may be significant.

This study examines the reproduction of *R. stylosa* at its southern limits, partly in the context of warming over recent decades. The data are from the same shoots at the same time as the vegetative study of Wilson and Saintilan (2012) and the two studies are best considered together. Wilson and Saintilan (2012) found no latitudinal clines in vegetative phenology or leaf initiation over the study area and no evidence for a thermal growth limit at SWR Creek. The results were generally comparable to tropical studies.

Effectively all reproduction in *R. stylosa* is sexual and the metabolic costs of reproduction can be considerable (Bazzaz et al., 2000), which might be hypothesised to be more significant at poleward limits. Recent "precocious" reproduction in *R. mangle* (Dangremond and Feller, 2016) suggests potential for anomalous reproductive efforts at the poleward limit as conditions change.

Specific aims of this study were firstly to characterise *R. stylosa*'s reproductive phenology at its southern limits, including propagule maturation time. Secondly, to determine quantitative reproductive success in propagules produced, and the rate of conversion of buds and fruit to propagules.

Null hypotheses are no differences in maturation times and rates of conversion between latitudes in NSW, or between the pooled NSW data and published tropical Australian studies as far as comparisons allow.

2. Methods

2.1. Background and sample selection

Much background in Wilson and Saintilan (2012) applies and so is not repeated in detail here. The study area has a sub-tropical climate, with warmer than average conditions during the study, including over winter. All monthly maxima were higher at SWR Rocks (Smoky Cape Lighthouse station; data from 1939) than the long-term mean by 0.8 to 1.5 °C (+ 1.3 °C overall). Monthly minima were at or above the long term mean, including in the coldest month of July (+ 0.2 °C overall; Wilson, 2009). Rainfall was lower than the long-term means for most months, with major annual deficits of 14% in 2003 and 21% in 2004 against the long-term mean (data: BOM, 2018a).

Selected shoots on 14 mature trees in three estuaries over 265 km of latitude (Table 1) were intensively and repeatedly sampled from October 2002 until October 2004. The sampled trees are the "mature" trees of Wilson and Saintilan (2012) except one isolated slow-growing tree in the Brunswick River estuary only just starting to produce buds. Site analyses for the Brunswick River system only include trees sampled on the Marshalls Creek arm (Table 1).

A range of shoot sizes around the circumference of each tree were selected. The commonplace litterfall trapping is unsuitable for frequently isolated trees of differing (usually small) canopy size, and shoot tracking is well-suited to *Rhizophora* anatomy and information rich, albeit labour intensive. The inter-sampling period averaged 73 days on the Richmond River and SWR Creek and 72 days on the Brunswick River system. Two mature trees only at SWR Creek is not ideal, but the next comparable estuary is 95 km north at Corindi Creek (− 30.02; 153.13), pre-judged as too distant from the southern limit. Austral seasons are referred to unless noted.

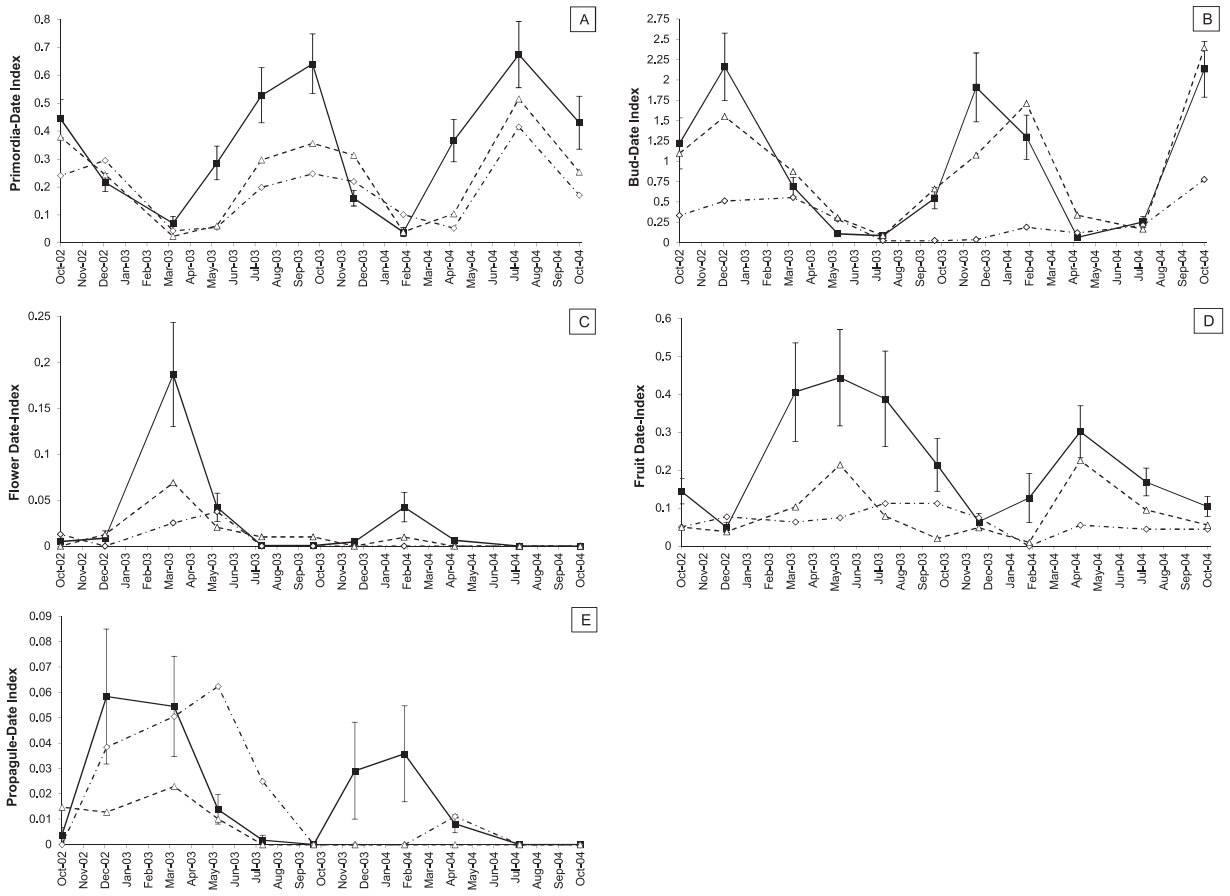


Fig. 1. Plots of the [Organ]-Date Indices for: (A) flower primordia; (B) flower buds; (C) open flowers; (D) advanced fruit; and (E) propagules for 14 sampled trees (closed square), plus data from two trees at South West Rocks, SWR1 (open diamond) and SWR5 (open triangle). The [Organ]-Date Indices are the tree means of each tracked organ stage on each date, divided by the number of sampled shoots on that date (see text). Error bars are the standard error of the mean.

2.2. Sampling and data recording techniques

Basic data were repeated counts of defined reproductive organs on tracked shoots, including initially marked shoots and any side shoots formed by the branching on existing tracked shoots during the study. The new shoots may produce reproductive organs (after a period) and are important in the "modular" vegetatively expansion of relatively small tree crowns as was common in this study. A mean of 12.85 (± 6.62) shoots were initially sampled per tree, with higher numbers of shoots sampled on larger trees and on the two trees at SWR Creek.

Six categories of reproductive organs were recorded (Supplementary Figs. S1 and S2):

- Flower bud primordia: Formed in pairs with new leaf pairs.
- Buds: Recorded from the time the number of buds in an inflorescence could be determined from a developing primordium, even if they are not fully developed.
- Open flowers: A short stage where petals and stamens are still present before falling.
- Fruit: Fruit were counted if organs were being retained after petal fall, even before swelling of the ovary wall. Well-developed fruit with a diameter > 8 mm were distinguished as "advanced fruit". All "fruit" are used to illustrate phenology, but "advanced fruit" are used in the statistical analysis.
- Propagules: Recorded from the time the hypocotyl first erupted from the base of the fruit, even though considerable development was still needed.

Tree height and diameter ($D_{1.3}$, or just above any prop roots at 1.3 m) were recorded at the end of sampling.

2.3. Data compilation and analysis

The sampling period was not fixed for all shoots, as new sampled shoots were added at different times and rates during the study. This precludes many simple measures; hence, two indices were devised and applied in turn to the sampled stages.

Firstly, four indices per tree of the means of the number of Primordia, Buds, Fruit and Propagules on all sampled shoots on each sampling date, divided by the total number of shoots sampled per tree on that sampling date, called [Organ]-Date Indices, e.g. Bud-Date Index. There are indices for each sampling date and they are used to illustrate reproductive phenology and to compare relative organ production temporally during the study between trees and sites. The divisor includes all tracked shoots even if not reproductive on the sampling date.

Secondly, four indices of the tree sums over the whole study period of, in turn, Primordia, Buds, Fruit and Propagules divided by the number of originally marked shoots on each tree, called "[Organ]-Original Shoot Indices', e.g. Bud-Original Shoot Index (Bud-OSI), plus one index using the sums of all four stages (Total-OSI). One of each OSI per tree is generated allowing comparison of tree-scale relative reproductive organ production. Dividing by the number of original shoots gives a common reference, accounting for differing numbers of shoots originally marked on a tree and any organs produced on branched shoots during the study.

Other shoot level data, such as the proportion of reproductive shoots and the number of buds per inflorescence, along with "reproductive

Table 2
Site totals for bud, fruit and propagule numbers for the 2002-04 reproductive generation and propagule totals for the 2001–2003 generation (recorded once off in late 2003), plus site mean % conversion of buds and advanced (adv.) fruit to propagules on tracked shoots. Mean count of flower buds per inflorescence on three dates near peak bud occurrence in three years (n = 1405 inflorescences) is also shown. All trees are included in the data. Individual tree data in Supplementary Table S1.

	2003	2002-2004 generation						
Estuary	**Propagules**	**Buds**	**Advanced Fruit**	**% Buds to adv. fruit**	**% Buds to Propagules**	**% Adv. Fruit to Propagules**	**Propagules**	**Mean no. buds per inflorescence**
Marshalls Creek	27	1053	208	19.75	2.56	12.98	27	2.87 ± 0.18SE
Richmond River	5	313	63	20.13	1.60	7.94	5	2.71 ± 0.19SE
SWR Creek	7	258	14	5.43	0.78	14.29	2	2.52 ± 0.17SE
Total	**43**	**1652**	**285**	**17.25**	**2.06**	**11.93**	**34**	**2.72 ± 0.14SE**

success" measures of the percentage conversion of buds and fruit to propagules, were recorded or derived from the data.

The raw bud data are normally distributed, but the raw fruit and raw propagule data are not as determined by Anderson-Darling tests, so for consistency non-parametric tests were undertaken using R 2.14.0 software (R Core Team, 2014). Correlations used the Kendall's τ-b statistic (McLeod, 2015) using data from the originally marked shoots only and other parameters recorded during this study. Kruskal-Wallis analysis with post-hoc pair-wise comparison by Wilcoxon rank sum tests with Holm's sequential Bonferroni correction (Yatani, 2014) was used to test many differences, including in the Organ-Date and Original Shoot indices. Significance is taken to be < 0.05.

3. Results

3.1. Reproductive phenology

All trees exhibited peak seasonality in reproductive phenophases, although some primordia and buds formed all year (Fig. 1A-E; data for the two mature trees at SWR Rocks are included for comparison to the whole data set). The usual process was: primordia appear in winter/spring with the single cool season leaf initiation (peak circa July-September; Fig. 1A), followed by the progressive development of buds (Fig. 1B); flowers open briefly the following autumn (peak circa March; Fig. 1C); fruit mature until early summer (peak circa late November-December; Fig. 1D) when the radicle erupts from the fruit and the propagules mature before dropping in autumn (peak in April; Fig. 1E).

Flower buds peaked in mid-summer (Fig. 1B). The steep bud loss from the peak commenced first through abortion, which was common but unquantified, then subsequently by flower opening. Bud number was lowest in April-May (Fig. 1B). Flowering was strongly congruent, although small numbers of flowers opened slightly outside the main period of February-March (Fig. 1C).

Broad peaks in fruit number reflect the length of this phase (Fig. 1D). The relatively steep fall from circa July-August to circa early December was due to widespread fruit failure, which tended to accelerate later in the stage. The propagule phase from the eruption of the radicle from the fruit in early summer to propagule fall was typically about five months, and the broad peaks reflect this maturation time (Fig. 1E). The sharp drop in March/April represents peak propagule fall, although the earliest fall was observed at the end of February and the latest in July. Loss after the radicle had emerged, but before maturity, was very rare.

The typical length of the *R. stylosa* reproductive cycle in NSW was estimated from the phenological data as 19–20 months, as primordia emergence peaked in August/September and propagule fall peaked in April of the second year. The happenstance of the field study commencement (October) and the long cycle meant full tracking of a complete cycle over all shoots was impossible. However, maturation times shorter than the norm were fully tracked; while 76% of primordia resulting in propagules in 2004 were present in October 2002, 9% emerged as late as May 2003.

3.2. Quantitative comparisons and reproductive success

3.2.1. Reproductive production

The mean percentage of reproductive shoots to all shoots on all trees over the sampling dates was 44.5% ± 1.71SE (range: 20.3%–77.9%). The mean number of all post-primordium reproductive organs per reproductive shoot per sampling date was 2.40 ± 0.13SE (range: 1.50–3.89). There was no correlation between the production of all reproductive organs on reproductive shoots and the rate of leaf initiation on those shoots (τ-b = -0.13; P = 0.54), nor with tree height (τ-b = -0.02, P = 0.96) or $D_{1.3}$ at the end of the study on single stemmed trees (τ-b = -0.16, P = 0.59).

Intact inflorescences most commonly contained 2 buds (range: 1–8). Based on counts on three dates in three years near the peak of bud presence on all trees, the mean number of buds per inflorescence was 2.72 (range: 1.82–3.92) (Table 2). There was significant variation between trees as a group (H = 25.54; DF = 13; P = 0.02), but between-site variation was not significant (H = 2.79; DF = 2; P = 0.24), despite an apparent fall with increasing latitude (Table 2). Only one tree at SWR Creek was particularly low. Usually one pair of inflorescences was present on a shoot, but two pairs were present on circa 25% of these sampled shoots and three pairs in < 0.5% of samples.

3.2.2. [Organ]-date indices

There was significant variability in the Primordia-Date Index within all trees as a group (Table 3), although there were no significant pair-wise differences between individual trees. SWR Creek was significantly

Table 3
Ranges and Kruskal-Wallis analysis of variance (H value) for Original Shoot Indices (OSI) and [Organ]-Date Indices for reproductive phases. OSI values are between sites (estuaries) (df = 2). The Tree [Organ]-Date Indices include all trees as a group (df = 13) and the Site [Organ]-Date Index includes three sites as a group (df = 2).

	Site OSI			Tree [Organ]-Date Index			Site [Organ]-Date Index	
Organ	**Mean ± SE**	**Range**	**H (P value)**	**Mean ± SE**	**Range**	**H (P value)**	**Range**	**H (P value)**
Primordia	4.76 ± 0.68	1.56 - 9.63	3.45 (0.18)	0.34 ± 0.03	0 - 1.75	37.29 (**< 0.01**)	0.19 - 0.45	7.85 (**0.02**)
Buds	12.67 ± 2.00	3.26 - 25.79	1.16 (0.56)	0.95 ± 0.32	0 - 6.10	24.39 (**0.03**)	0.99 - 1.22	1.61 (0.45)
Fruit	2.97 ± 0.68	0.45 - 8.60	2.51 (0.28)	0.22 ± 0.08	0 - 1.71	45.13 (**< 0.01**)	0.08 - 0.27	7.04 (**0.03**)
Propagules	0.25 ± 0.09	0 - 0.47	0.55 (0.76)	0.19 ± 0.18	0 - 0.35	31.78 (**< 0.01**)	0.01 - 0.03	1.93 (0.38)
Total	16.24 ± 2.64	3.95 - 33.19	0.79 (0.67)	–	–	–	–	–

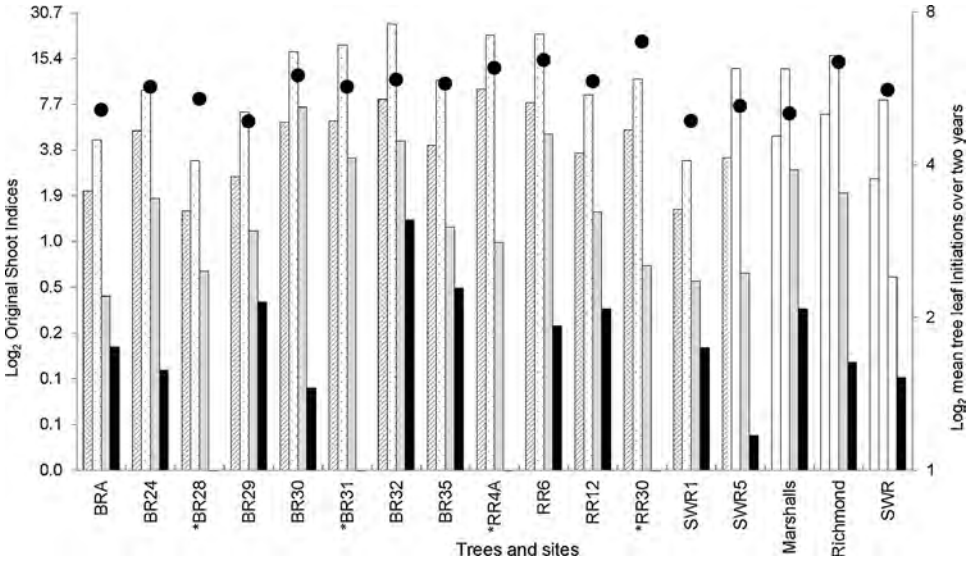


Fig. 2. Log_2 plot of values of Original Shoot Indices for (left to right): flower primordia (cross hatch); flower buds (dots); advanced fruit (solid grey); and propagules (solid black) for sampled trees and three sites. Original Shoot Indices are the sums over all sampling dates of each reproductive organ stage on sampled shoots per tree, divided by the number of originally marked branches on the tree (see text). Four trees marked with asterisks did not produce propagules on tracked branches. Filled circles are Log_2 tree mean leaf initiations on sampled shoots for the trees and sites over two years (Wilson and Saintilan, 2012). For more detail, see Section 3.2.

lower as a site than Richmond River (P = 0.02), but not quite from Marshalls Creek (P = 0.09). Richmond River and Marshalls Creek did not vary significantly (P = 0.17). The Bud-Date Index varied significantly within all trees as a group, but between-site variation was not statistically significant (Table 3). SWR Creek was the lowest ranked site, although some individual trees elsewhere were indistinguishable.

The Fruit-Date Index varied significantly within all trees as a group and between sites (Table 3). SWR Creek is significantly lower than the other sites, but the Richmond River and Marshalls Creek did not differ significantly (Table 3). The only significant pair-wise differences were one tree at SWR Creek with two trees at Marshalls Creek and one at the Richmond River. The Propagule-Date Index varied significantly within all trees as a group, but not between sites (Table 3). Unexpectedly, one tree on Marshalls Creek strongly dominated propagule numbers with 44.1% and 39.5% of all propagules on sampled shoots in the 2001–2003 and 2002–2004 generations (Supplementary Table S1).

3.2.3. Original shoot indices (OSI)

The OSIs show varied reproductive organ product over the study between trees, some nearby each other (Fig. 2). On a site basis, SWR Creek was the lowest for Primordia, Bud and Fruit-OSI, but similar to the Richmond River on the Propagule-OSI (Fig. 2; Table 3). None of the site OSIs differed significantly (Table 3).

Based on data from all originally marked shoots, significant correlations were found between Primordia-, Bud- and Fruit-OSI, but not between the Propagule-OSI and any earlier stage (Table 4). Moderate, but significant, correlations were found between tree mean leaf initiations (Wilson and Saintilan, 2012) and the Primordia-, Bud-, Fruit- and Total-OSIs, but again not the Propagule-OSI (Table 4). There were no significant correlations of any OSI with tree height or trunk diameter ($D_{1.3}$ on single stemmed trees) at the end of the study (Table 4).

3.2.4. Conversion rates and propagule production

The rates of conversion of buds to advanced fruit, buds to propagules and advanced fruit to propagules was inconsistent between trees and sites (Table 2; tree data in Supplementary Table S1). Mean bud to propagule conversion did not differ significantly between sites (H = 1.29, DF = 2, P = 0.52), despite varying from north to south.

There were more propagules on originally marked shoots in the 2001–2003 reproductive cycle than for the tracked 2002–2004 cycle (Table 2; Supplementary Table S1), due to fewer propagules at SWR Creek. Totals at Marshalls Creek and the Richmond River were identical in both years, but not necessarily on the same trees. The difference between years was not significant (Wilcoxon rank sum test W = 119, DF = 1, P = 0.33). If trees with no propagule production on tracked shoots are removed, there is only a faint indication of alternating propagule generations.

Table 4
Rank correlation coefficients (Kendall's τ-b) and P values (parentheses) between the cumulative number of all primordia, buds, fruit, propagules and the Original Shoot Indices (OSI), plus correlation coefficients for the OSIs with leaf initiation rate (Wilson and Saintilan, 2012) and tree height and $D_{1.3}$ (single stemmed trees only) at the end of the study. See Section 3.2.

	Primordia-OSI	Bud-OSI	Fruit-OSI	Propagule-OSI	Total-OSI
Primordia-OSI	1	–	–	–	–
Bud-OSI	0.85 (< **0.01**)	1	–	–	–
Fruit-OSI	0.65 (< **0.01**)	0.63 (**0.02**)	1	–	–
Propagule-OSI	0.01 (1.00)	0.01 (1.00)	0.10 (0.66)	1	–
Leaf initiation	0.55 (< **0.01**)	0.49 (**0.02**)	0.42 (**0.04**)	−0.14 (0.54)	0.46 (**0.03**)
Tree height	0.09 (0.70)	0.05 (0.87)	0.16 (0.48)	0.12 (0.61)	0.09 (0.7)
$D_{1.3}$	0.22 (0.47)	0.33 (0.25)	0.22 (0.47)	0.09 (0.83)	0.39 (0.18)

4. Discussion

4.1. Phenology and length of the reproductive cycle

Phenological phases were consistent across the study area, especially in the relatively tight peaks of buds and flowers, which supports the null hypothesis of no difference, albeit with some variability within the seasonal patterns. By contrast, Clarke and Myerscough (1991) found flowering initiation in the dominant mangrove species, *A. marina*, varied by 2–3 weeks over 200 km of the central NSW coast. Wan Juliana et al. (2011) report quite different lengths of their "bud season" for *R. stylosa* at two relatively nearby sites in Malaysia and Wium-Andersen (1981) found propagule fall varied by two months for *R. mucronata* over 60 km in southern Thailand.

Beginning phenological observations at the primordium stage is rare; however, *R. stylosa* primordia peaked in August at Hinchinbrook Island (Duke et al., 1984; -18.36°, 146.15°), similar to this study. Using litterfall, Duke et al. (1984) found maximum bud fall in summer, apparently comparable to this study as ongoing bud failure during the summer bud peak was high in NSW.

Using direct shoot data, Coupland et al. (2005)'s very broad bud peak at Darwin Harbour (-12.50°, 130.83°) was in early summer, but their lowest bud numbers were in March versus May-June in NSW. Their bud (and fruit) peaks are broad as they report the percentage of sampled shoots with buds, which does not account for differing numbers of buds per inflorescence, the loss of some buds, or multiple inflorescences on a shoot. Hence, patterns are less pronounced than in shoot tracking or litterfall data.

Peak *R. stylosa* flowering in northern NSW (February-March) was comparable to north Queensland (February-March; Duke, 2002) and PNG (January-March; Leach and Burgin, 1985) and a little earlier than Fiji (March-June; Tyagi, 2004). By contrast, Coupland et al. (2005) reported peak flowering in December/January at Darwin Harbour.

The peak fall of "mature fruit" in September in north Queensland (Duke et al., 1984) is comparable to the period of high failure of advanced fruit in NSW (July-September). In the only other extra-tropical *R. stylosa* reproductive study on Okinawa, peak flowering and bud fall were in comparable seasons to NSW, but peak fruit fall appeared to be in the opposite season (Kamruzzaman et al., 2013).

Peak *R. stylosa* propagule fall was reported as February-March in north Queensland generally (Duke, 2002) and at Dunk Island (Banfield 1908; -17.95°, 146.16°) and Port Curtis (Saenger, 1982; -23.92°, 151.42°) specifically. Peak propagule fall in NSW was slightly later (April), although viable propagules fell as early as late February. In contrast to NSW and north Queensland, Coupland et al. (2005) report peak propagule fall in Darwin Harbour during the mid-year dry season. Tyagi (2004) implies propagule drop is in March in Fiji and Kamruzzaman et al. (2013) report peak propagule fall on Okinawa in a similar season (August-September) to NSW.

Coupland et al. (2005) suggest "different monsoonal regimes" may be responsible for phenological differences between Darwin Harbour and north Queensland, but climatic differences are much greater between tropical Queensland and NSW. Northern NSW is less seasonal than the tropics, but February-April is the wettest period. Duke et al. (1984) suggest dispersal advantages from high river flow during wet seasons, and most mangrove species produce disseminules during the local wet season (Saenger, 2002).

The typical time from primordia to propagule fall in *R. stylosa* in NSW (circa 19–20 months) was slightly longer than the 16–20 months at Hinchinbrook Island (Duke et al., 1984). However, some shorter cycles to meet the seasonal propagule fall were recorded in this study. The typical time from flowering to propagule fall was 12–13 months, compared to 11 months in Darwin Harbour (Coupland et al., 2005) and 11–12 months in north Queensland (Duke, 2002).

The dominant *Avicennia marina* subsp. *australasica* (Walp.) J.Everett extends much further south than *R. stylosa* (to -38.75°), but experiences more dramatic latitudinal impact. Duke (1990, 2002) recorded flowering six months later and an increase in flower to fruit maturation time from 2 to 3 months to 10 months in the most southern populations of *A. marina* compared to the tropics. Any difference in maturation times between *R. stylosa* in NSW and those published for the tropics appeared small with some overlap, hence a null hypothesis of no difference between NSW and the tropics cannot be rejected. Arguably there is little import to any slightly longer maturation times due to resource restriction or other factor if the propagules fall within the same season. Kamruzzaman et al. (2013) recorded 9–10 months from flowers to propagule fall ("mature propagules") on Okinawa, interestingly shorter than in NSW and tropical Australia.

4.2. Quantitative comparisons and reproductive success

4.2.1. Organ production

The OSIs show the sum production over the study of each phase of the reproductive cycle varied between trees (e.g. observable in Fig. 2). However, there were very few significant pairwise comparisons using Wilcoxon rank sum tests and no significant site differences in any OSI were detected, suggesting intra-estuary variability was stronger than inter-site differences such as latitude. Results may be inconsistent; for example, tracked shoots at the Richmond River produced more buds but fewer fruit than those at Marshalls Creek. Sample sizes are low and propagule analyses in particular may be weakened by the low numbers (34 propagules from 1652 buds), although that is a result in itself.

All the tree [Organ]-Date Indices indicated significant inter-tree variation in primordia, fruit, bud and propagule production over the sampling dates, but only the Primordia- and Fruit-Date Indices varied significantly on a site basis. As interim stages there is no material impact on fecundity if the differences do not carry through to propagule production.

The correlations between Primordia-, Bud- and Fruit-OSI were expected, however no earlier stage correlated with the propagule stage, contradicting an intuitive idea that more buds and fruit set should mean more propagules. Loss during the fruiting stage was most responsible. Few, if any, factors predicting propagule production were detected, including no correlation with tree size and shoot growth rate. Even nearby trees with putatively similar environmental variables such as solar access and sediment differed in fecundity. Controlling factors remain obscure, as do reasons for the dominant performance of one tree (BR32), which extends beyond the tracked shoots, and was also observed in 2010 and 2016.

Inter-annual variation was not statistically significant on tracked shoots, partly due to the influence of trees with zero propagule production (Supplementary Table S1) but was observed consistent with the literature. For example, in an isolated stand on the Brunswick River, there were < 10 propagules in 2003, circa 100 in 2004 and zero in January 2016, although such differences are not as dramatic in bigger, more fruitful stands. One tree at SWR Creek (SWR5) branched relatively strongly in 2004, producing no propagules in that year compared to 8 in 2002, 13 in 2003 and 9 in 2005, conceivably because branches arise in the same axillary space as reproductive primordia. Many *A. marina* trees do not reproduce every year in NSW (Clarke and Myerscough, 1991). We thus caution against comparisons made on single year observations.

4.2.2. Bud conversion

The general finding that conversion of buds and flowers to propagules is low in *Rhizophora* is supported, perhaps due to combinations of genetic factors, inefficient pollination and prevailing conditions. Regardless, only *Avicennia* rivals *Rhizophora* for dominance as a global mangrove genus and apparently inefficient reproduction has not been a barrier to biogeographic success. The overlapping reproductive generations may be a factor; in this study, the rise in new buds mirrored the fall in existing fruit, with a simple correlation of $r = -0.81$, and maybe resource limitation, perhaps mediated by prevailing conditions, is operative.

The rates of conversion through the cycle in this study compare well with tropical studies. The bud stage is the earliest for meaningful comparison, although not often assessed. However, Coupland et al. (2006) recorded 0.5% of buds progressing to propagules in Darwin Harbour, much lower than in this study (2.1%). Bud conversion to advanced fruit of 17.2% in NSW was much higher than the 3.0% conversion to young fruit in Darwin Harbour (Coupland et al., 2006) and estimates of 7.2% for *R. mangle* and 13.0% for *R. apiculata* (Hogarth, 1999).

However, conversion of fruit to propagules was lower in this study (11.9%) than the 25% recorded by Coupland et al. (2006), although this only partially compensates for the lower bud to fruit conversion in Darwin Harbour. The greatest loss in Darwin Harbour appeared to be as buds/flowers, compared to fruit in NSW. This is unexplained, and more effective pollination in the sparse stands and isolated trees in NSW over tropical stands seems unlikely. Kamruzzaman et al. (2013) found 6.7% conversion from fruit to propagules in *R. stylosa* on Okinawa, lower than the current study, although one of their years was comparable

(11.4%).

The high bud conversion rate in NSW does not necessarily denote greater fecundity, however. Although bud number did not correlate with propagule production on a shoot scale in this study, hypothetically trees with more buds in total due to more reproductive branches, more inflorescences per branch and/or more buds per inflorescence may produce more propagules even if conversion rates are lower. Tropical data for comparison to this study are lacking, but, for example, the mean bud number per inflorescence in this study (2.7) was lower than 4–8 buds cited for Queensland (Duke, 2006; range: 1–64) and Malaysia (Mohd Nasir and Safiah Yusmah, 2007).

Proffitt and Travis (2014) found increased reproductive potential with latitude in recently expanded *R. mangle* range, but this cannot be categorically determined for *R. stylosa* despite apparently high conversion rates. There was no evidence of a latitudinal effect over the study area and a hypothesis of no increased fecundity in *R. stylosa* at the southern limits remains. Kamruzzaman et al. (2013) concluded propagule litter fall at Okinawa was comparable to tropical studies, implying neither lower nor higher reproductive production at the northern limit.

A recent warming trend (BOM, 2018b) could not have initiated colonisation or reproduction at *R. stylosa*'s southern limits, as the most southern mature tree is one of the largest trees south of the Tweed River (710 cm tall in 2005) and large trees and seedlings were present at Corindi Creek in 1980 (Floyd, 1980). However, this does not preclude growth rates and reproductive effort being enhanced by physiologically beneficial small temperature rises.

Reproduction continues at SWR Rocks and at least eight further individuals had recorded away from the mature trees by January 2016 (pers. obs.). It is expected that reproduction will continue at current rates, or with a slight increment from ongoing warming. Monthly maxima since the study (2005–2017) are warm (91% of monthly maxima are above the long-term mean; overall + 0.9 °C). The July monthly minimum has been at the long-term mean or warmer every month (overall + 0.4 °C) (data: BOM, 2018a).

"Precocious" reproduction (*sensu* Dangremond and Feller, 2016) in young *R. stylosa* was not seen during the study, nor during observations in 2010 and 2016. Based on January 2016 observations of marked 2001–2004 seedlings, an approximate minimum time range for initial (very limited) propagule delivery is 12–15 years.

The northern limit of *R. mangle* evidently has greater fluctuation between relatively warm winters and severe impactful cold episodes than at, and beyond, *R. stylosa*'s southern limit, where freezes on the immediate mangrove shore are unknown. Reproductive "anomalies" such as early or exaggerated fruiting may reflect locality- and taxon-specific factors. Perhaps *R. mangle* at its northern limits is closer to its physiological limit than *R. stylosa* is in NSW and is thus more responsive to climatic changes.

5. Conclusion

There was a tendency for SWR Creek to be lower on some measures, such as bud to propagule conversion and some [Organ]-Date and OSI indices, but generally this was due to one only tree there (a large, slowly expanding tree on waterlogged substrate). This, plus intra-estuary variation between trees on numerous parameters, argues against strong latitudinal impact on reproduction over the last 265 km of the range. The short phenological bud and flower phases were tight and peak propagule fall was regional. Endogenous or tree-level exogenous influences on reproduction must be important. There was little evidence of anomalous reproductive responses, although high bud conversion is interesting.

While there must be some link between temperature, plant growth and reproduction, and there is a correlation between temperature (latitude) and mangrove species diversity on the entire Australian east coast, the southern limit of *R. stylosa* appears not to be set physiologically, either reproductively or vegetatively (Wilson and Saintilan, 2012). This suggests caution in generalising about mangrove species responses at the limits under climate change scenarios. Non-physiological factors such as dispersal limitation need to be considered.

Declarations of interest

None.

Acknowledgements and Declaration

NCW was supported by an APA (I) postgraduate scholarship from the Australian Commonwealth Government at ACU. A Strategic Partnership with Industry for Research and Training (SPIRT) Grant to ACU from the NSW Department of Land and Water Conservation provided funding, but no control over findings. Part of the research was undertaken when NCW was at the School of Environmental Science and Management, Southern Cross University in Lismore, NSW in a visiting capacity. Dr Sahadev Sharma provided helpful information on *R. stylosa* on Okinawa. Comments and suggested edits by the anonymous reviewers were very useful.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.aquabot.2018.07.009.

References

Alongi, D.M., 2015. The impact of climate change on mangrove forests. Curr. Clim. Change Rep. 1, 30–39. https://doi.org/10.1007/s40641-015-0002-x.

Bazzaz, F.A., Ackerly, D.D., Reekie, E.G., 2000. Reproductive allocation in plants. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. CAB International, Wallington, U.K, pp. 1–29.

BOM (Bureau of Meteorology), 2018a. Climate Statistics for Australian Locations: South West Rocks (Smoky Cape Lighthouse). Accessed 2 February 2018. http://www.bom.gov.au/climate/averages/tables/cw_059030.shtml.

BOM (Bureau of Meteorology), 2018b. Annual Mean Temperature Anomaly – New South Wales/ACT (1910-2017). Accessed 2 February 2018. http://www.bom.gov.au/climate/change/index.shtml#tabs=Tracker&tracker=timeseries&tQ=graph%3Dtmean%26area%3Dnsw%26season%3D0112%26ave_yr%3D0.

Cavanaugh, K.C., Kellner, J.R., Forde, A.J., Gruner, D.S., Parker, J.D., Rodriguez, W., Feller, I.C., 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proc. Natl. Acad. Sci. U. S. A. 111, 723–727.

Christensen, B., Wium-Andersen, S., 1977. Seasonal growth of mangrove trees in southern Thailand. I. The phenology of *Rhizophora apiculata* BL. Aquat. Bot. 3, 281–286.

Clarke, P.J., Myerscough, P.J., 1991. Floral biology and reproductive phenology of *Avicennia marina* in south-eastern Australia. Aust. J. Bot. 39, 283–293.

Coupland, G.T., Paling, E.I., McGuinness, K.A., 2005. Vegetative and reproductive phenologies of four mangrove species from northern Australia. Aust. J. Bot. 53, 109–117.

Coupland, G.T., Paling, E.I., McGuinness, K.A., 2006. Floral abortion and pollination in four species of tropical mangroves from northern Australia. Aquat. Bot. 84, 151–157.

Creese, R.G., Glasby, T.M., West, G., Gallen, C., 2009. Mapping the Habitats of NSW Estuaries. Fisheries Final Report Series No. 113, Industry & Investment NSW, Nelson Bay, NSW.

Dangremond, E.M., Feller, I.C., 2016. Precocious reproduction increases at the leading edge of a mangrove range expansion. Ecol. Evol. 6, 5087–5092.

de Lima Nadia, T., Morellato, L.P.C., Machado, I.C., 2012. Reproductive phenology of a northeast Brazilian mangrove community: environmental and biotic constraints. Flora 207, 682–692.

Duke, N.C., 1990. Phenological trends with latitude in the mangrove tree Avicennia marina. J. Ecol. 78, 113–133.

Duke, N.C., 2002. Mangrove phenologies and the factors influencing them in the Australasian region. In: Lacerda, L.D. (Ed.), Mangrove Ecosystems: Function and Management. Springer, Berlin, pp. 217–233.

Duke, N.C., 2006. Australia's Mangroves: the Authoritative Guide to Australia's Mangrove Plants. University of Queensland, Brisbane.

Duke, N.C., Bunt, J.S., 1979. The genus *Rhizophora* (Rhizophoraceae) in north-eastern Australia. Aust. J. Bot. 27, 657–678.

Duke, N.C., Bunt, J.S., Williams, W.T., 1984. Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. Aust. J. Bot. 32, 87–99.

Duke, N.C., Ball, M.C., Ellison, J.C., 1998. Factors influencing biodiversity and distributional gradients in mangroves. Glob. Ecol. Biogeog. Lett. 7, 27–47.

Fernandes, M.E.B., 1999. Phenological patterns of *Rhizophora* L., *Avicennia* L. and *Laguncularia* Gaertn. f. in Amazonian mangrove swamps. Hydrobiologia 413, 53–62.

Floyd, A.G., 1980. Conservation of Black Mangrove (Rhizophora stylosa) at Corindi

Creek. NSW NPWS, Coffs Harbour, NSW.
Gill, A.M., Tomlinson, P.B., 1971. Studies on the growth of Red Mangrove (*Rhizophora mangle* L.) 3: phenology of the shoot. Biotropica 3 (2), 109–124.
Hogarth, P.J., 1999. The Biology of Mangroves. Oxford University Press, Oxford, UK.
Hutchings, P., Saenger, P., 1987. Ecology of Mangroves. University of Queensland Press, Brisbane.
Juncosa, A.M., 1982. Developmental morphology of the embryo and seedling of *Rhizophora mangle* L. (Rhizophoraceae). Am. J. Bot. 69, 1599–1611.
Kamruzzaman, M., Sharma, S., Kamara, M., Hagihara, A., 2013. Phenological traits of the mangrove*Rhizophora stylosa* Griff. at the northern limit of its biogeographical distribution. Wetl. Ecol. Manag. 21, 277–288.
Leach, G.J., Burgin, S., 1985. Litter production and seasonality of mangroves in Papua New Guinea. Aquat. Bot. 23, 215–224.
McLeod, A.I., 2015. Kendall Rank Correlation, Version 2.2. Accessed 5 June 2015. https://cran.r-project.org/web//packages/Kendall/Kendall.pdf.
Mehlig, U., 2006. Phenology of the red mangrove, *Rhizophora mangle* L., in the Caeté Estuary, Pará, equatorial Brazil. Aquat. Bot. 84, 158–164.
Mohd Nasir, H., Safiah Yusmah, M.Y., 2007. Distribution of *Rhizophora stylosa* in Peninsular Malaysia. J. Trop. For. Sci. 19, 57–60.
Osland, M.J., Feher, L.C., Griffith, K.T., Cavanaugh, K.C., Enwright, N.M., Day, R.H., Stagg, C.L., Krauss, K.W., Howard, R.J., Grace, J.B., Rogers, K., 2017. Climatic controls on the global distribution, abundance, and species richness of mangrove forests. Ecol. Monogr. 87 (2), 341–345. https://doi.org/10.1002/ecm.1248.
Proffitt, C.E., Travis, S., 2014. Red mangrove life history variables along latitudinal and anthropogenic stress gradients. Ecol. Evol. 4, 2352–2359.
Quisthoudt, K., Schmitz, N., Randin, C.F., Dahdouh-Guebas, F., Robert, E.M.R., Koedam, N., 2012. Temperature variation among mangrove latitudinal range limits worldwide. Trees - Struct. Funct. 26, 1919–1931.
R Core Team, 2014. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.
Ragavan, P., Saxena, A., Jayaraj, R.S.C., Mohan, P.M., Ravichandran, K., Saravanan, S., Vijayaraghavan, A., 2016. A review of the mangrove floristics of India. Taiwania 61 (3), 224–242. https://doi.org/10.6165/tai.2016.61.224.
Saenger, P., 1982. Morphological, anatomical and reproductive adaptations of Australian mangroves. In: Clough, B.F. (Ed.), Mangrove Ecosystems in Australia: Structure, Function and Management. ANU Press, Canberra, pp. 153–191.
Saenger, P., 2002. Mangrove Ecology, Silviculture and Conservation. Kluwer Academic, Dordrecht, Netherlands.
Saintilan, N., Wilson, N.C., Rogers, K., Rajkaran, A., Krauss, K.W., 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob. Change Biol. 20, 147–157.
Steinke, T.D., 1988. Vegetative and floral phenology of three mangroves in Mgeni Estuary. S. Afr. J. Bot. 54, 97–102.
Tomlinson, P.B., 1994. The Botany of Mangroves. Cambridge University Press, Cambridge, U.K.
Tomlinson, P.B., Primack, R.B., Bunt, J.S., 1979. Preliminary observations on floral biology in mangrove Rhizophoraceae. Biotropica 11, 256–277.
Tyagi, A.P., 2003. Location and interseasonal variation in flowering, propagule setting and propagule size in mangroves species of the family Rhizophoraceae. Wetl. Ecol. Manag. 11, 167–174.
Tyagi, A.P., 2004. Precipitation effect on flowering and propagule setting in mangroves of the family Rhizophoraceae. Aust. J. Bot. 52, 789–798.
Wan Juliana, W.A., Farihah, A.B., Nordatul Akmar, Z., Muhamad Razali, S., Nurhanim, M.N., 2011. Phenology of *Rhizophora* species at three Peninsular Malaysia mangrove forests. Umtas 12–17.
Wilson, N.C., 2009. The distribution, growth, reproduction and population genetics of a mangrove species, *Rhizophora stylosa* Griff. Near its southern limits in New South Wales, Australia. Sch. Arts Sci. Australian Catholic University, Sydney.
Wilson, N.C., Saintilan, N., 2012. Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. Aquat. Bot. 101, 8–17.
Wium-Andersen, S., 1981. Seasonal growth of mangrove trees in Southern Thailand. III. Phenology of *Rhizophora mucronata*Lamk. and*Scyphiphora hydrophyllacea* Gaertn. Aquat. Bot. 10, 371–376.
Yatani, K., 2014. Kruskal-Wallis and Friedman Test. Accessed 1 December 2014. http://yatani.jp/HCIstats?KruskalWallis.

Aquatic Botany 101 (2012) 8–17

Contents lists available at SciVerse ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia

Nicholas C. Wilson[a,*], Neil Saintilan[b]

[a] 'Shatterwood', 84 Stokes Road, Mount George 2424, Australia
[b] New South Wales Office of Environment and Heritage, Australia

ARTICLE INFO

Article history:
Received 4 April 2011
Received in revised form 31 January 2012
Accepted 19 March 2012
Available online 28 March 2012

Keywords:
Rhizophora stylosa
Mangrove
Latitudinal limit
Growth
Phenology
Australia

ABSTRACT

A study on the growth of *Rhizophora stylosa* Griff. was undertaken in three estuaries spanning the southernmost 265 km of its range at its latitudinal limit in eastern Australia. A shoot tracking methodology was devised to follow vegetative phenological patterns and branching and to derive indices of relative growth between trees. Despite an apparent expansionary phase in distribution and a recent increased trend in mean temperature, comparisons of growth in the three estuaries do not suggest a latitudinal cline. The phenologies of leaf gain and leaf loss are generally comparable between *R. stylosa* in New South Wales and elsewhere, as is the rate of growth assessed by leaf initiation. However, leaf longevity and the number of leaves held on the shoot appears to be overall greater in NSW than in lower latitudes, perhaps as an adaptive response to lower levels of assimilation. This study suggests that *R. stylosa* is not close to physiological limits at the end of its range, supporting a contention that its current known southern limit is not at an absolute thermal boundary.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Rhizophora stylosa Griff. is widespread in the Indo-Pacific Region, extending in the Western Pacific from South West Rocks (SWR) in the Australian state of New South Wales (NSW) to Fiji and the Marshall Islands and north to the Ryukyu Islands (Hsueh and Lee, 2000; Vannucci, 2002; Duke, 2006). It extends in a less prominent manner through SE Asia to the Indian Ocean, with a likely western limit of the Andaman Islands (Lakshmi et al., 2002; Vannucci, 2002).

In Australia, *R. stylosa* extends from South West Rocks Creek (SWR Creek) (−30.88°; 153.03°) (Wilson, 2009) north around the Australian coast to about Yardie Creek (−22.32°; 113.81°) near Exmouth Gulf in Western Australia (Pedretti and Paling, 2000). It is regarded as the ubiquitous northern Australian mangrove species and can dominate large areas (Duke, 2006). The distribution of *R. stylosa* in NSW is sporadic and only rarely ubiquitous in discrete stands. There are relatively numerous but separate stands on the estuary of the Tweed River (the border between NSW and Queensland) and lower numbers in 15 other known estuaries south to SWR Creek. Within this range, the species appears absent from several estuaries (Wilson, 2009). NSW has a high energy coast, so mangroves are virtually confined to estuaries.

Only five NSW estuaries contain notable stands and unmistakably old trees of *R. stylosa*. Several estuaries contain only seedlings and/or saplings, indicating recent colonisation. A similar pattern is evident on a sub-estuary scale in most places; isolated young trees or small stands are present within estuaries containing larger stands. Generally, stands in NSW show evidence of recent expansion (Wilson, 2009).

There is a progressive decrease in mangrove diversity and biomass with increasing latitude along the Australian east coast, in keeping with the well-observed gradient in many biomes (Alongi, 2002). The latitudinal decline in mangrove diversity (and thus species' latitudinal limits) on continental coasts is most frequently ascribed to a differential delimiting effect of decreasing minimum temperatures on species with latitude (e.g. Davis, 1940; Macnae, 1966; Oliver, 1982; Duke, 1992; Saenger, 2002; Krauss et al., 2008). Five 'core' mangrove tree species have been definitively recorded in NSW. These are *Aegiceras corniculatum* (L.) Blanco, *Avicennia marina* subsp. *australasica* (Walp.) J.Everett, *Bruguiera gymnorhiza* (L.) Lam., *Excoecaria agallocha* L. and *R. stylosa*. *A. marina* is by far the most common species, forming much of the mangrove matrix.

Climatic influences such as solar radiation, day length, temperature, rainfall and evapotranspiration and their seasonal variability influence the growth and productivity of mangrove trees, as they do for all plants (Clough, 1992). The processes of plant growth are enzymatic, and within limits, enzymatic reactions approximately double in rate for every 10 °C rise in temperature (Bidwell, 1974). When light is sufficient, temperature changes have a moderate

* Corresponding author. Tel.: +61 429006861; fax: +61 65506655.
E-mail address: rstylosa@gmail.com (N.C. Wilson).

0304-3770/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquabot.2012.03.011

effect on photosynthesis within a normal day-time temperature range (16–29 °C), but are increasingly important when temperatures are lower and higher (Bidwell, 1974). Freezing temperatures may be damaging or fatal to *Rhizophora* (e.g. Snedaker, 1995), but the immediate coastal strip in northern NSW is essentially frost-free (BOM, 1991).

The possibility that lower temperatures may limit growth rate sufficiently for the species to be physiologically or competitively excluded from estuaries south of its current range is a starting point for this research. Evidence in support of this hypothesis might include a latitudinal cline in the growth characteristics of the species towards its current southern limit, or at least evidence of differences between growth rate at the southern limit and in tropical estuaries where the species is dominant. This study sought to test this hypothesis by examining leaf phenology and growth through leaf initiation and fall in individuals within three estuaries encompassing a 265 km range including the southern limit of the species. Comparisons within limits to published accounts from the tropics are made.

Leaf longevity is significant in various aspects of plant physiology and life history and reflects a balance between the ongoing efficiency of a leaf's carbon gain versus the carbon cost of replacing it with a new, more efficient leaf (Kikuzawa and Ackerly, 1999). In general, leaf longevity is thought to optimise carbon gain and is likely to be short when photosynthetic rates are high, when photosynthetic efficiency of leaves decreases rapidly with time, or when the construction cost of the leaf is small (Kikuzawa, 1995). Burrows (2003) reviews this topic for mangrove species.

The specific aims of this study were to:

- Determine the major vegetative phenology of *R. stylosa* at its southern limits and in two other estuaries in NSW and compare these to each other and to tropical Australia. (Null hypothesis: no difference between latitudes within NSW, or with tropical Australia.)
- Develop and measure growth rate indices based on the number of leaf emergences over time on the same shoots and compare the trees to each other and tropical Australia. (Null hypothesis: no difference between estuaries within NSW, or with tropical Australia.)
- Determine leaf longevity on the same shoots and compare these to each other and tropical Australia. (Null hypothesis: no difference between estuaries in NSW and tropical Australia.)

2. Methods

2.1. Introduction and sample selection

The *Rhizophora* vegetative shoot has a distinctive anatomy in that not only all leaves but also all branches and reproductive structures emerge from a prominent terminal bud, which is enclosed by a pair of lanceolate in-rolled stipules (Tomlinson, 1994). The bud swells and the stipules split apart and are shed on leaf emergence, leaving a pronounced annular scar ('node') which can persist for years until obscured by stem thickening. Barring herbivory, each leaf emergence produces a fixed pair of opposite leaves, which when shed leave a distinct petiolar scar. The shoot extends to a differing degree between leafing events, and this internodal extension is the sole basis for growth in *Rhizophora*.

The next pair of leaf primordia is formed in the new bud following leaf emergence, with apparently no dormancy (Gill and Tomlinson, 1971; Tomlinson, 1994). There is an obligate (but differing) period of bud development between leafing events, which is presumably some function of growing conditions. The process is predictable and the record of stipular and, to a lesser extent, petiolar scars forms the basis of the methodology used in this study, with the nodes used as fixed reference points. The primacy of the terminal bud in the growth of *Rhizophora*, the strict quantified relationship between leaf emergence from the terminal bud and leaf number, and the record left of leaves/nodes on the shoot means that a growth methodology based on shoot tracking and leafing dynamics is applicable. Node-based 'shoot tracking' methodologies similar in principle to that of this study have been used for phenological studies in *Rhizophora* since at least Gill and Tomlinson (1971) and to estimate growth rates in *Rhizophora* seedlings (e.g. Duke and Pinzon, 1992; Duarte et al., 1999).

Phenological patterns, along with leaf gain and loss as a measure of relative growth rate between trees and sites, were recorded. Leaf longevity data complement these. Reproductive phenology and success from the same shoots are reported elsewhere. A total of 45 trees were repeatedly sampled from three estuaries. These estuaries are:

- Brunswick River (−28.54°; 153.56°). This medium-sized system is the most northerly sampled. Most *R. stylosa* are found on the northern arm known as Marshalls Creek, where trees were sampled in the two main, but loose, aggregations. In addition, the two sole young mature shaded trees in the mangrove stand immediately north west of the road bridge on the main arm of the Brunswick River were sampled. (Tree code: BR[letter] for the main Brunswick arm and BR[number] for Marshalls Creek.)
- Richmond River (−28.88°; 153.59°). On this large river system, three mature trees were sampled within Mobbs Bay on the southern bank, with one mature tree and four saplings scattered on the South Ballina shoreline. Most *R. stylosa* on the Richmond River are in the sole stand in Mobbs Bay, with a few trees scattered elsewhere (Tree code: RR).
- South West Rocks Creek (SWR Creek) (−30.88°; 153.04°). This small system is the most southerly known locality of *R. stylosa*, with only two mature trees (Tree code: SWR).

Details of the estuaries can be found on OEH (2011). Tree selection was set at SWR Creek by the number available. On Marshalls Creek, sampling sought to include the range of tree sizes across the geographical coverage of the nearby main stands. All but one of the largest trees was sampled. Individuals in shade and sun were selected for smaller trees, and the choice was not random, but without intentional bias. The trees on the Richmond River were an adjunct to main sampling on the Brunswick River system. Some small trees at Mobbs Bay were abandoned following shoot damage following the onset of herbivory by Swamp Wallabies (*Wallabia bicolor*). Node data on a total of 11 seedlings were recorded at Marshalls Creek and Richmond River, but results are only briefly reported.

The climate of northern NSW is subtropical and generally mild, with a potential for hot summer days. Freezing temperatures have never been recorded on the immediate coast. There is little decline in mean annual maximum temperatures over the length of the study area, from 23.7 °C at Cape Byron to 23.2 °C at Smoky Cape Lighthouse, close to SWR Creek (BOM, 2011). Minimum temperature comparisons are unreliable due to the sensitivity of the stations to elevation and distance from the coast, but Smoky Cape has an annual minimum of 15.6 °C. The lowest monthly mean minimum is 11.2 °C in July. Annual mean rainfall is 1484.6 mm at Smoky Cape and ranges between 1340.8 mm (Wooli Beach) and 1737.0 mm (Cape Byron) in the study area (BOM, 2011).

Branches were selected to cover the girth of the tree and to include both larger and smaller branches in sun and shade. Sampling was without known bias within those categories. Different sized shoots were sampled to gauge the variability of shoot performance and thus avoid any potential bias in only selecting large

leaders. It was hypothesised that the modular growth in *Rhizophora* means all healthy shoots perform similarly, and this was able to be tested somewhat by sampling a range of branches. All large sampled trees are multi-stemmed with extensive major lateral shoot growth and main branches within 2.5 m of the ground were selected, as the reiterating branch form regardless of height means these are expanding shoots. This was for practical reasons, but also for consistency with smaller trees. The predominant central leader was always selected on small trees, along with side shoots.

2.2. Sampling and data recording techniques

On each selected shoot, a tag was fixed at the last relatively major branching point, and the number of nodes to the terminal bud was counted. The terminal bud was the 'zero' node for subsequent recording, but the initial recording was the count from the tag to the terminal node. Node gain was derived by subtraction of the initial count from the count at any subsequent time. The fixed branching pattern for *R. stylosa* is a 'trident' of branches of the central parent shoot and two oppositely arranged side-shoots (Tomlinson, 1994). Rarely only one branch forms. The central shoot and all side shoots at and above the point of the tag were named and scored independently. Branches that appeared during the study period were also scored independently, with a flexible naming and recording system that allows new data to be incorporated as needed.

Pilot data were recorded from June 2002, but all trees were marked by October 2002 and this date is used as the starting point for the comparative studies, finishing in October 2004. The inter-sampling period varied between recording dates, but averaged 73 days on the Richmond River; 73 days at SWR Creek; and 72 days at the Brunswick River sites.

Leaf marking allows for a direct investigation of leaf longevity. Leaf longevities were measured, rather than computed, in this study. An initial marking of all leaves using an indelible marker to record the date sampled on six shoots at SWR Creek in June 2002 was a test for leaf mark durability, followed by marking the terminal leaves on each sampling from December 2002. Marked leaves were tracked as the shoot grew and the sampling date at which they became the lowest remaining leaves on the shoot was recorded. This allows a minimum life span to be observed (rather than computed from leaf fall data). Given that leaves are present when marked and are still present when finally recorded, the actual longevity is greater than the conservative minima reported, by a variable time up to a few months depending on when in the inter-sampling period they formed or fell. As few marked leaves had fallen at the end of regular sampling, field trips in October and November 2005 were added for this parameter, but circumstance prevented re-sampling of two trees on the Brunswick River.

The data collected for each shoot (including new branches) at each sampling event were:

- Number of nodes (leaf emergences) since the last sampling.
- Leaf gain and leaf loss from previous date, any complete loss of newly formed leaves and the state of the current bud (very new, new, mid, old, very old). Leaf gain and loss were recorded separately, as this allows discrimination of the respective roles of leaf initiation and leaf loss in leaf dynamics.
- Any branching (which become new recording units from that point on).

2.3. Data compilation and analysis

A number of measures were devised to allow comparison between trees, including accounting for the differing number of original shoots per tree and any branching during the study. These include:

- The mean leaf gain, the mean leaf loss, and the net leaf gain or loss per original shoot between sampling dates and cumulatively over the study period. Leaf gain and leaf loss data on the original shoots allow vegetative phenological patterns to be shown. Leaf data differ slightly from node data in that node data does not account for lost leaves, whereas direct leaf count data does. The data are reported as leaf gain per shoot per day $\times$ 100.
- The mean node increase per original shoots between sampling dates and cumulatively over the study period. This is a general measure of the timing and rate of leaf emergence (growth rhythm) that can be used for comparison. Only original shoots can be used as the timing of branching varies, and branch shoots had different periods to accumulate nodes.
- A 'cumulative node index' (CNI) of the cumulative total of nodes gained per tree divided by the number of original shoots. This gives net growth performance of trees incorporating leaf initiation on both the originally marked shoots and the differing number of branches added during the study, without distinction.
- A 'cumulative net leaf index' (CLI) of the net leaf gain per tree divided by the number of original shoots. This accounts for leaf production on original shoots and branches initiated during the study, and thus incorporates leaf longevity, unlike the CNI.

Post-seedling plants were divided into two classes on the basis of height (mature tree and sapling) to seek comparability, although such divisions are somewhat arbitrary on the continuum of growth. In the field the distinction was quite clear, but the approximate cut off height was 2.5 m. Kruskal–Wallis ANOVA, plus post hoc pair-wise comparisons using Wilcoxon rank sum tests with Holm's sequential Bonferroni correction, were undertaken using R 2.13 software following Yatani (2011). Kendall's τ-*b* rank correlation was undertaken with R 2.13 using the 'Kendall' package (McLeod, 2011). Standard deviations are given on the graphs to show the spread of values, with the standard errors in the node data very small due to the large sample sizes. The node gain growth data are reported principally by site for clarity, although there is inter-tree variability within sites.

3. Results

3.1. Vegetative phenology

There were clear seasonal patterns in leaf production for mature *R. stylosa* in NSW over the study period, which are highly congruent between trees and estuaries (Fig. 1). There is a mid to late summer peak in leaf production, with varying degrees of a second, much smaller peak towards winter on some trees. There is a spring peak in leaf loss, preceding or coincident with the beginning of peak leaf production (Fig. 2). This is also congruent between trees. Net leaf gain or loss at each date for all mature trees shows a summer peak in net leaf gain and the fact that leaf gain dominates leaf loss except for a short time in spring (c. October–November), although some leaves are still produced then (Fig. 2). Overall leaf loss is lowest in winter, whilst leaf gain is lowest in winter or winter/spring.

The 11 saplings show similar seasonal patterns in leaf dynamics to mature trees, although the patterns of net leaf gain are more pronounced (Fig. 3), due to a very similar pattern of leaf gain to mature trees, but a flatter leaf loss pattern. There are more younger shoots on smaller trees, so there is not yet as great a balance between leaf gain and loss.

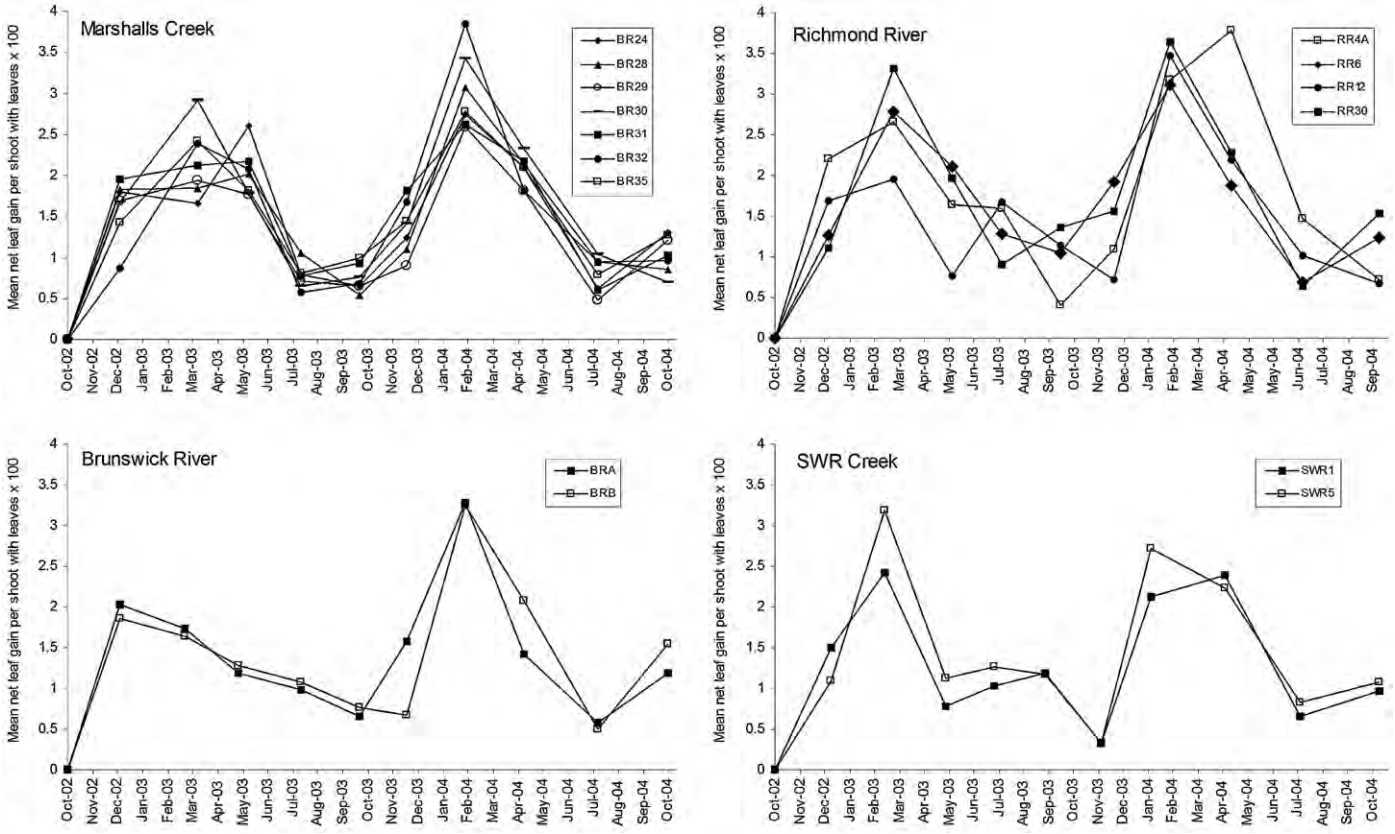


Fig. 1. Mean leaf production per shoots with leaves per day × 100 for 15 mature trees by site. Marshalls Creek and Brunswick River are different localities within the Brunswick River system.

3.2. Comparative node production between trees and sites

3.2.1. Original shoots

Node gain per unit time is a measure of growth rate, with the Richmond River having the highest overall site mean node gain over two years, although the site median is the same as that of Marshalls Creek (Fig. 4a). SWR Creek is the poorest performing site, although a number of trees on the Brunswick River system have comparable node gains (individual tree data in Appendix A, Fig. A.1).

The raw node gain data are not normally distributed (Anderson–Darling test; $A = 18.29$; $P \ll 0.001$). Hence, the non-parametric Kruskal–Wallis test was employed to test the

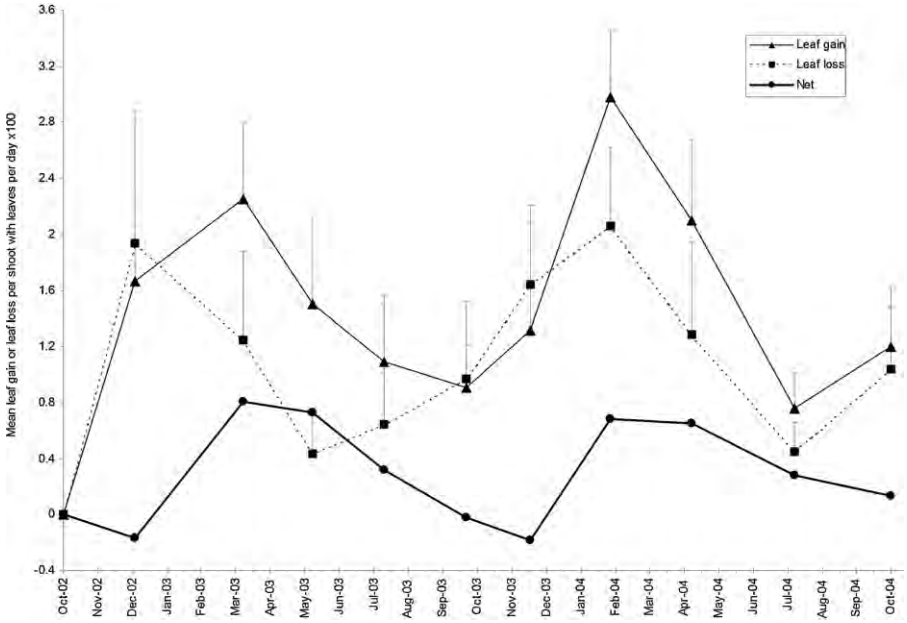


Fig. 2. Mean leaf production; mean leaf loss; and net leaf gain or loss per shoots with leaves per day × 100 for 15 mature trees collectively. Error bars are standard deviations.

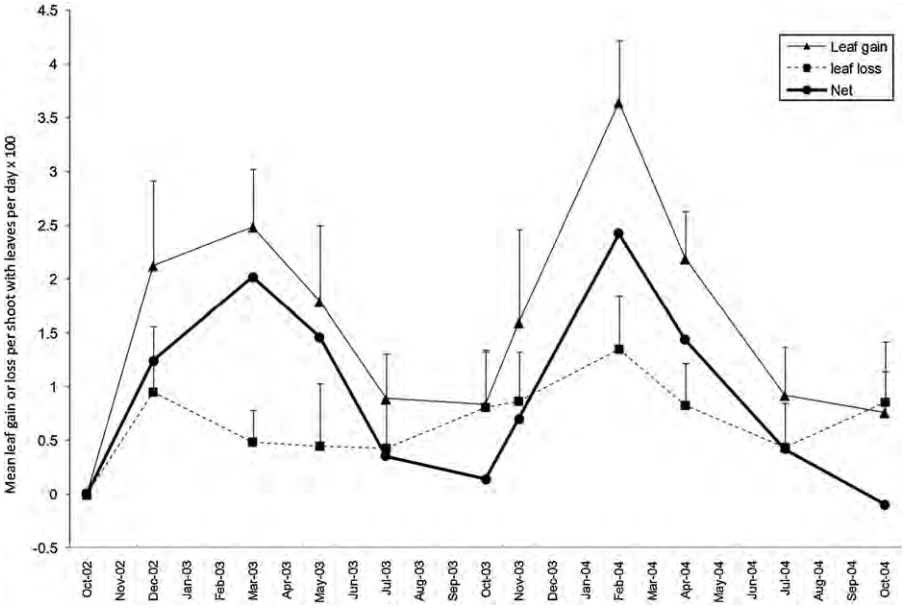


Fig. 3. Mean leaf production; mean leaf loss; and net leaf gain or loss per shoots with leaves per day × 100 for 11 sapling trees collectively. Error bars are standard deviations.

significance of overall differences in node gain on original shoots for trees as a group and for sites as a group (Zar, 1999). Both individual trees ($H = 135.12$; df = 14; $P \ll 0.001$) and the combined site data ($H = 88.29$; df = 3; $P \ll 0.001$) return highly significant results, meaning there are strong differences within the groups. Wilcoxon post hoc testing of pair-wise differences showed sites differed significantly at $P = 0.05$, except the Brunswick River and SWR Creek ($P = 0.52$). Of the 105 pair-wise comparisons in the mature tree data, 37 were significant at $P = 0.05$, suggesting a generally similar pace overall. Differences in the tree data do not accord well with latitude, as the SWR Creek and the Brunswick River sites are similar and trees frequently differed significantly within the same site.

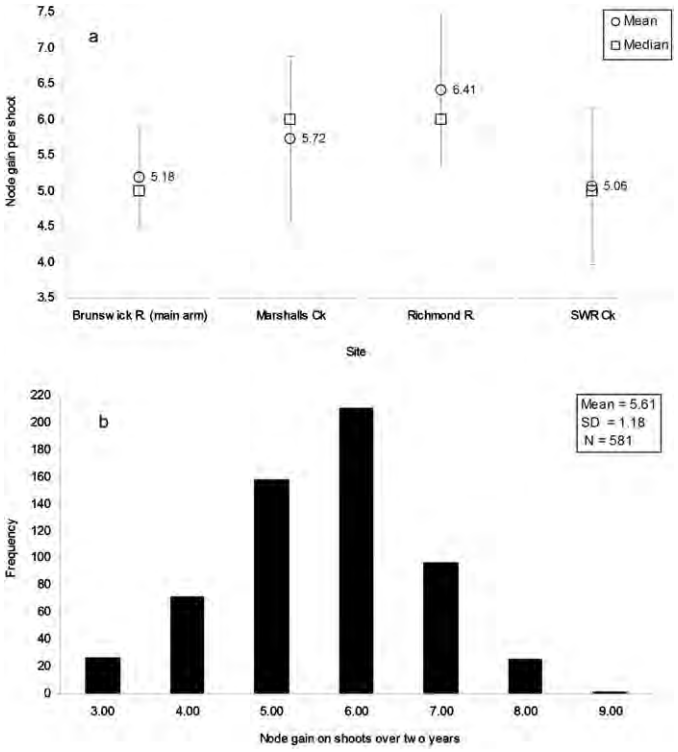


Fig. 4. (a) Mean and median node gain on originally marked shoots over two years by site for mature trees. Error bars for the mean values are standard deviations. (b) Node gain frequencies over two years for all originally marked, non-predated shoots on 15 mature trees collectively.

The mean node gain per shoot for all mature trees is 5.61 ± 1.18 over two years, but this includes some slow shoots that are clearly naturally losing vigour and some shoots where predation of the apical bud has stalled expansion before the shoot re-sprouts from reserve buds (Fig. 4b). This said, predation of the growing tip was of no consequence for most trees, although some trees, including one at the southern limit, where relatively strongly affected (Fig. A.1). A few small predated shoots died (overall 1.4%; c.f. 18% in Burrows, 2003) and were not counted. The regional rhythm of node gain on healthy, actively growing shoots on a whole-tree basis is thus about three per annum.

For saplings, the sampled trees in two estuaries are very similar in combined value (Fig. 5a). Saplings generally outperformed mature trees in node gain, with an overall mean of 6.31 ± 1.16 nodes over two years (Fig. 5b), although slower saplings overlap with mature trees (Appendix A, Fig. A.2). The overall difference between mature and sapling trees is highly significant ($H = 29.58$; df = 1; $P \ll 0.001$). The vertical leader shoot on saplings was distinctly faster (mean of 7.30 ± 0.83 nodes over two years), with side shoots often slower on smaller trees. Seedlings put on a mean of 6.55 ± 0.93 nodes over two years, with means at Marshalls Creek of 6.63 ± 0.74 nodes and the Richmond River of 6.33 ± 1.52 nodes over two years.

3.2.2. Original shoots plus branches

Branching during the study was a significant source of node and leaf gain for all trees to different degrees, especially on larger shoots. The ratio of node gain on branches to that on original shoots was greater than 0.90 for eight mature trees, meaning nearly as many nodes were produced on branches as on original shoots. There was a mean net gain on mature trees of 2.77 leaves per shoot on branches and original shoots versus 1.71 leaves per shoot on original branches only.

The 'cumulative node index' (CNI) and 'cumulative net leaf index' (CLI) notably change the ranking of trees compared to node gain on original shoots after the inclusion of node and leaf data respectively from branches (Fig. 6; Appendix A, Table A.1). Trees

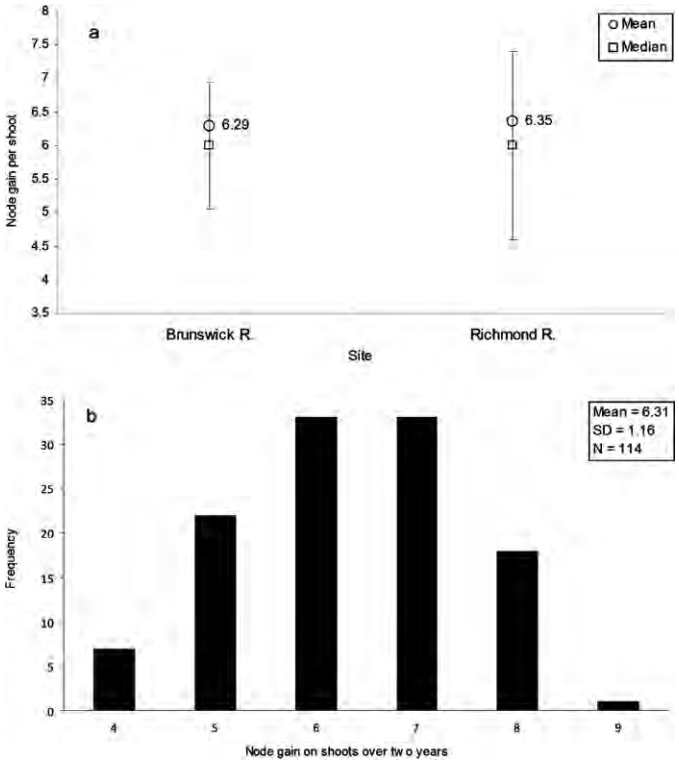


Fig. 5. (a) Mean and median node gain on originally marked shoots over two years by site for sapling trees. Error bars for the mean values are standard deviations. (b) Node gain frequencies over two years for all originally marked shoots on 11 saplings collectively.

are shown left to right by node gain on original shoots in Fig. 6. For example, one tree at SWR Creek (SWR5) is elevated in the CNI as it branched relatively strongly. There is no clear latitudinal signal evident, and no significant differences within the sites as a group for the CNI ($H = 1.23$; df = 3; $P = 0.75$). As the leaf-based CLI is a function of leaf longevity, some trees with low node gain rank highly by retaining their leaves longer. The CNI is moderately but significantly correlated with the CLI (τ-$b = 0.49$; $P = 0.02$).

3.3. Leaf longevity

The initial leaf marking trial at SWR Creek in June 2002 allowed tracking of the progressive leaf loss over 30 months to the end of regular sampling. Four leaves of 74 remained after this time, indicating their persistence. Marking of terminal leaves from December 2002 did not determine many leaf longevities by the end of normal sampling as most leaves persisted for the 22 months available. In the most dramatic case, 28 of 34 leaves marked remained on each of the two trees on the main Brunswick River arm (BRA and BRB). Following re-sampling in late 2005, a range of apparent minimum leaf life spans of 13 months to >41 months was determined, although the proportion at both extremes is small (Fig. A.3). The oldest minimum age of 41 months was for two leaves close to abscission on slow growing shoots on the southern-most individual. As they were present on the earliest sampling date the true age is greater, representing a conservative extreme for leaf longevity. Very few, if any, mature leaves were completely lost through herbivory.

The most common 'ages' are 18.5 and 19 months, then 21 and 21.5 months (Fig. A.3). This timing very generally accords to the period between peak leaf gain in one year and peak leaf loss the following year, although there are exceptions. Minimum ages between 18.5 and 21.5 months made up 47% of leaves, with 43% between 22 and 30 months. Few were younger than 18.5 months (6.3%) or older than 30 months (4.4%). Mature tree and saplings tree means vary, including within site in some cases, but there are differences in site means (Fig. 7; further data in Table A.2).

The differences between mature trees as a group were highly significant ($H = 127.48$; df = 12: $P \ll 0.001$), with 33 of 78 pair-wise comparisons being significant at $P = 0.05$. Most (18) differences were pairs with two slow trees, and there was only a weak and non-significant negative correlation between leaf longevity and node gain for mature trees (τ-$b = -0.23$; $P = 0.15$). There is longer apparent leaf life at SWR Creek than the Richmond River and Marshalls Creek (Fig. 7). The differences between sites for mature trees as a group were significant ($H = 36.49$; df = 2; $P \ll 0.001$), with all

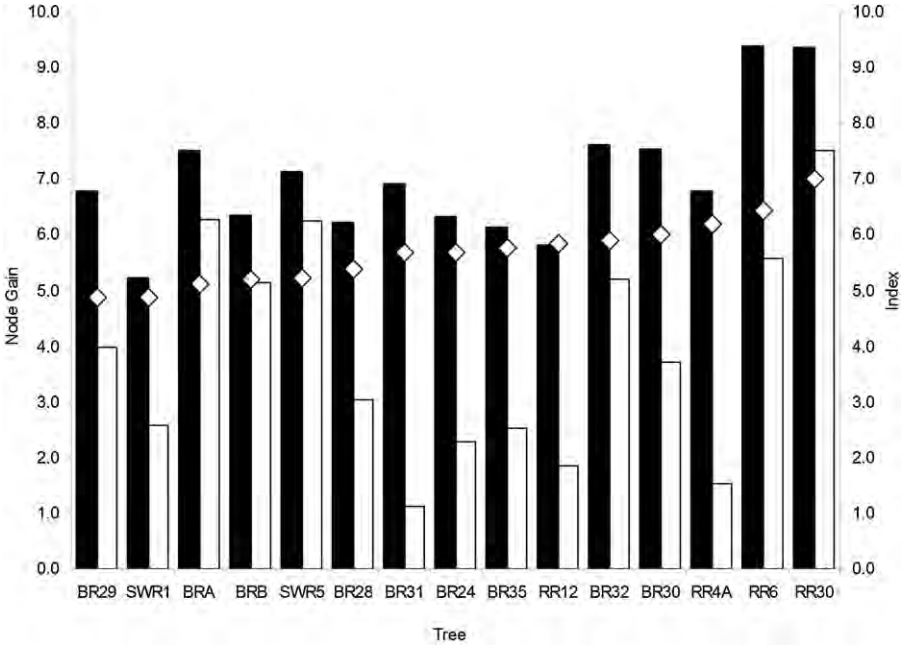


Fig. 6. Mean node gain on original marked shoots (diamonds), cumulative node index (black columns) and cumulative leaf index (white columns) for 15 mature trees. Trees are arranged from low to high mean node gain on original shoots. See text for more details.

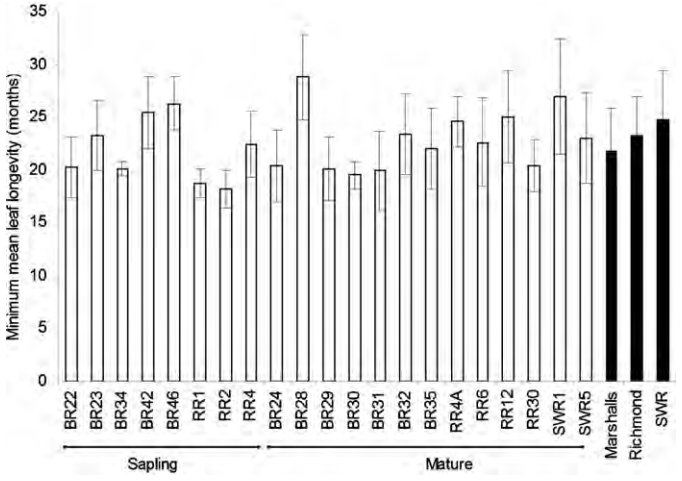


Fig. 7. Calculated mean minimum leaf ages in months for 13 mature trees and 8 saplings, along with site means for mature trees.

pair-wise comparisons being significant at $P = 0.05$, very strongly so for SWR Creek versus the other sites. Sapling trees show similar variety in leaf longevity, with the mean minimum leaf age of sapling trees (22.8 months; range: 18.2–26.3) one month shorter than mature trees (21.8 months; range: 19.5–28.8 months).

The mean number of leaves held in the rosette of leaves on the originally marked shoots was recorded once at the final regular sampling in October 2004 (Table A.2). Mature tree means ranged from 9.2 to 14.3 with the differences between all mature trees as a group being highly significant ($H = 152.08$; df = 14; $P \ll 0.001$). Most of the 41 of 105 significant pair-wise comparisons were with the high rosette leaf numbers on one tree on the Brunswick River (12 differences) and one on Marshalls Creek (9 differences). The Brunswick River had the highest site mean (13.7 ± 2.17 leaves), followed by the Richmond River (11.94 ± 1.84 leaves), SWR Creek (11.39 ± 2.10 leaves) and Marshalls Creek (10.36 ± 2.24 leaves). The differences between sites for mature trees are significant ($H = 100.89$; df = 3; $P \ll 0.001$), with all pair-wise site comparisons also significant. The correlation between the number of leaves on a shoot and leaf longevity is positive for both mature trees (τ-$b = 0.43$; $P = 0.05$) and sapling trees (τ-$b = 0.64$; $P = 0.04$).

4. Discussion

4.1. Phenology

The strong concordance in the typical late summer peak of leaf/node gain within- and between estuaries suggests a strong regional seasonal influence. Some trees differ slightly in timing between years (actual peaks may be between two sampling dates) and there are differences of degree between trees, but the seasonality is strong. Peak leaf fall is also strongly seasonal, although some leaves are lost throughout the year. Despite a typical short period of net leaf loss in late spring on mature trees, *R. stylosa* initiates leaves throughout the year at its southern limit. Upper-intertidal *C. tagal* are essentially dormant during the driest period at Hinchinbrook Island, Queensland (Qld) (−18.23°) due to stress (Duke et al., 1984), but no full seasonal stasis applies to *R. stylosa* in NSW. Leaf gain virtually always exceeds leaf loss in saplings.

Vegetative phenology is generally consistent with *Rhizophora* elsewhere as summer peaks in leafing are typical (see Wilson, 2009). Duke et al. (1984) found a bimodal summer peak in leafing for *R. stylosa* at Hinchinbrook Island, with peak leaf fall just preceding peak leaf gain, similar to the present study. Some shoots put on two nodes over the long summer in NSW, but the overall peak is unimodal. Saenger and Moverley (1985) found similar timing in *R. stylosa* peak leaf production in central Qld to NSW, with leaf fall generally coinciding with leaf production. Conacher et al. (1996) found a distinct summer peak in stressed *R. stylosa* in the Northern Territory, although only mild summer peaks were found in the studies of Coupland et al. (2005) and Leach and Burgin (1985). Seasonality in leaf fall is found in all tropical studies, although less seasonal leaf fall accompanies less seasonal leaf initiation in some places. Vegetative phenology in NSW is particularly similar to Qld, with little evidence of major shifts in phenophases down the Australian east coast, in contrast to the major phenological shifts with latitude in *A. marina* from New Guinea to South Australia (Duke, 1990).

Analysis of climatic influences on leaf dynamics is difficult as climatic parameters co-vary strongly. For example, Gwada et al. (2000) found 70% of the variation in leaf phenological traits of Okinawan *Kandelia obovata* explainable by environmental parameters, but distinguishing between temperature, humidity and day length was difficult. Still, rising temperatures are often implicated in mangrove leaf initiation in subtropical or temperate regions (e.g. Gill and Tomlinson, 1971; Duke, 1990; Gwada et al., 2000; Ha et al., 2003). Saenger and Moverley (1985) suggest *R. stylosa* ceases leaf production below 16 °C, which is lower than the mean winter maxima at and south of the southern limit. Whilst temperature effects on leafing are not precluded and might contribute to the summer peak, *R. stylosa* not only continues to leaf over winter in NSW, but there is some evidence that it does so better than in the tropics (e.g. low late winter leaf appearance in Fig. 1 in Duke et al. (1984)), perhaps relating to milder winter stress.

Some tropical studies implicate aridity as a winter leafing stressor, suggesting lowered groundwater salinity during the wet season spurs peak leaf initiation (e.g. Wium-Andersen, 1981; Coupland et al., 2005; Mehlig, 2006) or rising salinity in the dry triggers peak leaf fall (Pool et al., 1975; Slim et al., 1996). The moderate seasonal aridity and *R. stylosa*'s low intertidal position in NSW should lessen the effect compared to seasonally very arid places such as the Venezuelan sites of Suárez and Medina (2005), but perhaps also to northern Australia with a more pronounced dry season than NSW. Again, this does not preclude an influence on leafing dynamics, likely in concert with other factors, as peak leaf fall and the lowest net leaf gain do coincide broadly with the end of the relatively dry spring period in NSW. There is potentially also a degree of internal regulation of peak leaf fall if it is linked to the coming leaf gain peak, with an element of 'leaf exchanging' (Singh and Kushwaha, 2005). This is tentatively supported by the fact that leaf loss was greater in the year of greatest leaf gain, although net leaf gain was very similar between years. Some dry season deciduous tropical monsoon tree species flush leaves before the rains, indicating an endogenous influence probably mediated by day length (Williams et al., 1997; Elliott et al., 2006). If similar in mangrove species, perhaps seasonal phenologies are due to seasonal climatic stress and optima, but with some endogenous control on timing.

4.2. Growth

Shoot-tracking studies are useful in the Rhizophoraceae due to its particular anatomy, particularly in single, small trees where canopy litter trapping is not applicable. Cumulative node gain on originally marked shoots is a useful comparator, although care should be taken in interpretation, as local site factors are significant and tree age has some effect as rates on seedling and sapling trees are highest. The lack of a latitudinal cline in node gain over the study area is perhaps understandable given the moderate distance involved relative to the species' range, but does exclude a rapid falling away of viability towards the limits. The two mature trees at

SWR Creek have relatively poor node gain, but they are similar to the two trees on the Brunswick River and two on Marshalls Creek.

Shoot extension between nodes was not measured as it adds complexity without greater clarity. Extension varied from the minimum to fit new petioles (c. 1.0 cm) to c. 20 cm and did not relate directly to the rhythm of node gain. General growing conditions are likely influential, but other factors including tree size/age (large trees reduce most shoot extension), branching (which increases the next shoot extension) and shading (which increases leader shoot extension on saplings, but may decrease extension on mature shaded shoots) are evident.

Branching accelerates tree growth (but not height) by adding new shoot modules, thus extending carbon gain, particularly as young leaves are more efficient (Kikuzawa and Ackerly, 1999; Suárez, 2003). The importance of branching was demonstrated by the high proportion of leaves that accumulated on branches compared to the originally marked branches. Virtually all large trees in NSW are multi-stemmed (c.f. many tropical individuals) and the spread and filling out of peripheral shoots continues to add to such trees for a long time. Even the largest trees sampled gained leaves over the study, although trees must trend from expansion towards maintenance past a certain age. Sampling branches appears less important in sapling trees that still retain one strong vertical leader.

Branching does not invalidate node gain on original shoots as a whole-tree measure of growth rhythm as node gain on branches was shown to be very similar to that on the mother shoot. However, branching has to be incorporated in investigating growth in leaf canopies beyond the basic rhythm of shoot expansion. Typically only the original marked shoot is followed, although Gwada et al. (2000) followed original shoots and branches separately in *K. obovata*. They found a net leaf loss on original shoots, but a net gain on subsequent branches, again suggesting the importance of branching in leaf gain in the Rhizophoraceae.

Despite being unusual, single indices such as the CNI are useful in showing a whole tree picture of performance in a modular species like *R. stylosa*. The CNI further argues against growth differences over the southernmost 265 km of the range as it does not differ significantly between sites (cf. node gain on original shoots) and trees change rank in a non-ordered way. Notably, one tree at SWR Creek was elevated in the rankings as it branched strongly, supporting observation that it is an equivalent young adult tree in performance to others to the north. Branching dynamics are outside the scope here (e.g. physiological cost affecting existing shoot expansion, whether adaptive or a function of age) but are clearly important. Although less of a measure of the process of growth than the CNI due to the variability in leaf retention between trees, the CLI provides further insight by suggesting the possibility of an adaptive mechanism on some trees of retaining old leaves longer to maintain a larger photosynthetic area, rather than being capable of faster leaf initiation.

Intra-estuary differences in performance indicate that site factors are perhaps dominant on a regional scale. Site factors were not measured, but Youssef and Saenger (1999) show the local sediment variability at our study site at Mobbs Bay, Richmond River, although their conclusions on species patterning are not supported. Changes in the key parameters of sediment texture and waterlogging are easily observed and, whilst not determining *R. stylosa* presence, observation suggests relative waterlogging is a factor in differential rates of some close-by trees. Variability in *R. stylosa* node gain on a local scale has been found elsewhere (Duke et al., 1999; Burrows, 2003) and site factors are well recognised to influence growth (Alongi, 2009). Bunt (1995) interpreted local parameters, such as the salinity regime, nutrient input and topographic characteristics as important in the high variability of mangrove leaf litter fall within climatic groupings across Australia. The Richmond River is the largest, most fluvial system sampled, but it is premature to conclude that lower salinity and greater sediment and nutrient supply is a factor in the slightly faster growth there, even though freshwater supply can affect mangrove development positively at least on broad scales (Saenger, 2002).

Slightly faster node gain on seedlings and saplings to mature trees is understandable. Node gain in heavily shaded saplings was slightly lower than sun saplings, although shoot extension was greater. Shade of the mixed *A. marina* type in NSW does not prevent the establishment and early growth of *R. stylosa*, in contrast to the large literature suggesting high light is important in tropical mangrove species establishment (e.g. Ball, 2002; Pinzón et al., 2003; Krauss et al., 2008).

The repeatable *Rhizophora* growth pattern makes comparisons of node gain on originally marked shoots possible between studies, but advisedly as factors such as tree and shoot selection can influence results. In general, *R. stylosa* is relatively slow for the genus, with the published extreme being seedling *R. apiculata* with eight nodes a year (Duarte et al., 1999). Saenger and Moverley (1985) placed *R. stylosa* in a 'low leafing and shedding' class and this appears to generally hold.

Perhaps surprisingly, *R. stylosa* in NSW is comparable with tropical Australian trees. At Hinchinbrook Island, Duke et al. (1984) found 2.57 nodes per annum, below the NSW average. Although preliminary data only (N. Duke, pers. comm.), they do show only moderate rhythm in prime *R. stylosa* habitat. In more robust data from Port Curtis, Qld (−23.51°), Duke et al. (1999) found annual tree mean leaf production per shoot of 4.89–6.85 (≈2.45–3.43 nodes, assuming no leaves lost) over two years, similar to the current study. Burrows (2003) sampled *R. stylosa* shoots at Townsville, Qld (−19.16°), including shoots where the terminal bud was removed by herbivores during the study. On non-predated shoots, annual tree means at two sites of 4.24 and 4.66 nodes annualised from 13-month data were faster than the present study, but when predated shoots are included the means are comparable (2.62 and 3.17 nodes). Bud removal by herbivory is built into the node gain data in the current study and it interesting that evident lower rates of predation in NSW are elevating trees there in whole-tree node gain comparisons. The mean annual node gain on natural seedlings in NSW of 3.25 nodes is identical to node gain converted from leaf initiation in Darwin Harbour (O'Grady et al., 1996).

Clough (1992) observed 'decreasing rates of [mangrove] growth with increasing latitude along the eastern coastline of Australia' but on annual node gain on marked shoots this is equivocal for *R. stylosa*. Although a simple criterion only, it does suggest lower temperatures are not greatly significant physiologically in NSW on the rhythm of growth and/or that conditions are more frequently excessive in the tropics. There, for example, temperatures in direct sunlight are often supra-optimal for *Rhizophora* growth (Clough, 1992) and winter aridity perhaps suppresses growth more than in the subtropics. Further, ecotypic or adaptive differences over the latitudes also cannot be ruled out; Andrews and Muller (1985) found maximum assimilation of adult *R. stylosa* in situ at c. 29 °C at Hinchinbrook Island, whilst Okimoto et al. (2007) found an optimum at c. 25 °C at high latitudes in Japan.

The null hypotheses that *R. stylosa* in NSW is comparable in vegetative phenology and growth measured as node gain to the species in northern Australia, particularly on the Qld coast, is not easily rejected. *R. stylosa* clearly grows successfully at its southern limits, which suggests that SWR Creek is not a physiologically set limit. *R. stylosa*'s southern limits lacks episodic freezes and generalisations on low temperatures as the limiter, including Stuart et al. (2007)'s on freezing susceptibility contributing to *R. stylosa*'s limits do not fit well. The maximum tree size indicates suitable growing conditions at SWR Creek precede the most recent upwards trend in temperatures, notably since about 1980. Temperatures were mostly marginally above the long term mean during the

study, but it is unlikely this makes the data unrepresentative of the longer term given the relative ease of the species at its limits. Rainfall was generally below average, including drought conditions in 2002.

4.3. Leaf longevity

Leaves are persistent on *R. stylosa* in NSW, albeit with significant differences between trees. Theories of carbon economy suggest leaf longevity should be longer in sub-optimal conditions (e.g. Kikuzawa, 1995) and Alongi (2009) supports a generalisation that mangroves must have more conservative water-use strategies with increasing stress. However, node gain and leaf longevity is poorly correlated, despite the two slowest mature trees sampled having the greatest leaf longevity. If two slow trees on the Brunswick River with otherwise demonstrably long leaf longevity had been sampled the correlation may have been stronger, but on the data collected the evidence for a relationship between slower growth rhythm and increased leaf longevity is weak. The higher correlation coefficient for saplings suggests fewer complicating factors for younger trees, but the relationship is still not statistically significant. There is a more suggestive relationship for the site leaf longevity means, with a north–south decrease, although concluding a latitudinal effect on a regional scale would be premature given the small number of sampled trees at SWR Rocks and the variability within estuaries.

Rhizophora shoots trend towards a stable number of leaves in the rosette as leaf loss matches leaf gain. Leaf number on a shoot is allied to leaf longevity, and likely to leaf carbon economy, and a correlation between leaf longevity and leaf number is understandable, although the moderate coefficient indicates there are complicating factors. Two very slow trees had particularly high leaf numbers, but the relationship is not consistent throughout. Such trees score highly on the CLI, and perhaps some trees are maintaining old leaves longer to maintain a greater leaf area on shoots as a compensatory mechanism to local stress rather than slowing the rhythm of growth too much. Conclusions from this early data can only be tentative at this stage.

Although preliminary, a null hypothesis of similar leaf longevity between NSW and the tropics is poorly supported. Leaf life spans found in this study are mostly longer than those found for *Rhizophora* elsewhere (Wilson, 2009). They contrast strongly with mean turnover of 11.2 months recorded for *R. stylosa* by Coupland et al. (2005) in Darwin Harbour and Saenger (2002) at Gladstone. Coupland et al. (2005)'s data often contrast with east coast studies, but the short leaf spans at Gladstone is particularly at odds with the present study given the slow leafing rates there. Findings of 19 months at Hinchinbrook Island (Duke et al., 1984) and 15 and 21 months at Townsville (Burrows, 2003) are closer to the present study. Methodological differences or unintentional bias in tree selection might be influencing the comparison, but there is still tentative evidence that *R. stylosa* holds leaves longer at high latitudes, even if the lack of a clear relationship with growth locally muddies conclusions on whether this is adaptive.

The species holds a relatively high number of leaves on mature shoots in NSW compared to limited data elsewhere, although again whether this ecologically significant is unclear. Duke et al. (1984) found a mean of 8.2 ± 0.3 leaves per shoot on *R. stylosa* at Hinchinbrook Island, whilst Moriya et al. (1989) found means of 8.3–8.9 leaves on young trees on Iriomote Island, Japan (24.33°). Kikuzawa and Lechowicz (2006) found life time carbon gain of leaves was 'rather constant' across species and it is an intriguing possibility that total carbon assimilation of a NSW leaf may be similar to that of a tropical leaf due to its longer life. Ultimately, all this is speculative and further study on all leaf level traits would be beneficial.

Acknowledgements

The research was supported by an APA (I) scholarship from the Australian Commonwealth Government to NCW. A Strategic Partnership with Industry for Research and Training Grant to ACU from the NSW Department of Land and Water Conservation as industry partner provided the funding for the study, but no active control of methodology or findings. Part of the research was undertaken when NCW was at the School of Environmental Science and Management, Southern Cross University in Lismore, NSW in a visiting capacity. The constructive comments of two reviewers are acknowledged.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.aquabot.2012.03.011.

References

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 293, 331–349.
Alongi, D.M., 2009. The Energetics of Mangrove Forests. Springer, New York.
Andrews, T.J., Muller, G.J., 1985. Photosynthetic gas exchange of the mangrove, *Rhizophora stylosa* Griff. in its natural environment. Oecologia 653, 449–455.
Ball, M.C., 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. Trees 16, 126–139.
Bidwell, R.G.S., 1974. Plant Physiology. Macmillan, New York.
BOM (Bureau of Meteorology), 2011. Climate Data Online. http://www.bom.gov.au/climate/data/ (accessed 01.09.11).
BOM (Bureau of Meteorology), 1991. Climate of New South Wales. Commonwealth of Australia, Canberra.
Bunt, J.S., 1995. Continental-scale patterns in mangrove litter fall. Hydrobiologia, 135–140, 2951-3.
Burrows, D.W., 2003. The Role of Insect Leaf Herbivory on the Mangroves *Avicennia marina* and *Rhizophora stylosa*. Unpubl. PhD thesis. School of Tropical Biology, James Cook University, Townsville, Australia.
Clough, B.F., 1992. Primary productivity and growth of mangrove forests. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, pp. 225–249.
Conacher, C.A., O'Brien, C., Horrocks, J.L., Kenyon, R.K., 1996. Litter production and accumulation in stressed mangrove communities in the Embley River Estuary north-eastern Gulf of Carpentaria, Australia. Mar. Freshwater Res. 475, 737–743.
Coupland, G.T., Paling, E.I., McGuinness, K.A., 2005. Vegetative and reproductive phenologies of four mangrove species from northern Australia. Aust. J. Bot. 532, 109–117.
Davis, J.H., 1940. The ecology and geologic role of mangroves in Florida. Papers from the Tortuga Laboratory, Carnegie Inst. Washington Publ. No. 517, 303-412.
Duarte, C.M., Thampanya, U., Terrados, J., Geertz-Hansen, O., Fortes, M.D., 1999. The determination of the age and growth of SE Asian mangrove seedlings from internodal counts. Mangroves Salt Marshes 3, 251–257.
Duke, N.C., 2006. Australia's Mangroves: The Authoritative Guide to Australia's Mangrove Plants. University of Queensland, Brisbane.
Duke, N.C., 1992. Mangrove floristics and biogeography. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, USA, pp. 63–100.
Duke, N.C., 1990. Phenological trends with latitude in the mangrove tree *Avicennia marina*. J. Ecol. 78, 113–133.
Duke, N.C., Bunt, J.S., Williams, W.T., 1984. Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. Aust. J. Bot. 32, 87–99.
Duke, N.C., Dalhaus, O., Rupp, R.J., Burns, K.A., 1999. Gladstone field experiment – plants: impact, response and recovery of mangrove trees and seedlings. In: Duke, N.C., Burns, K.A. (Eds.), Fate and Effects of Oil and Dispersed Oil on Mangrove Ecosystems in Australia. Australian Institute of Marine Science and CRC Reef Research Centre, Townsville.
Duke, N.C., Pinzon, Z.S., 1992. Aging *Rhizophora* seedlings from leaf scar nodes: a technique for studying recruitment and growth in mangrove forests. Biotropica 24 (2a), 173–186.
Elliott, S., Baker, J.P., Borchert, R., 2006. Leaf flushing during the dry season: the paradox of Asian monsoon forests. Global Ecol. Biogeogr. 153, 248–257.
Gill, A.M., Tomlinson, P.B., 1971. Studies on the growth of Red Mangrove *Rhizophora mangle* L. 3. Phenology of the shoot. Biotropica 32, 109–124.
Gwada, P., Makoto, T., Uezu, Y., 2000. Leaf phenological traits in the mangrove *Kandelia candel* L. Druce. Aquat. Bot. 681, 1–14.
Ha, H.T., Duarte, C.M., Tri, N.H., Terrados, J., Borum, J., 2003. Growth and population dynamics during early stages of the mangrove *Kandelia candel* in Halong Bay, North Viet Nam. Estuar. Coast. Shelf Sci. 583, 435–444.
Hsueh, M.-L., Lee, H.-H., 2000. Diversity and distribution of the mangrove forests in Taiwan. Wetlands Ecol. Manage. 8, 233–242.
Kikuzawa, K., 1995. The basis for variation in leaf longevity of plants. Plant Ecol. 1211, 89–100.

Kikuzawa, K., Lechowicz, J.M., 2006. Toward synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain, and the gross primary production of forests. Am. Nat. 1683, 373–383.
Kikuzawa, K., Ackerly, D., 1999. Significance of leaf longevity in plants. Plant Species Biol. 141, 39–45.
Krauss, K.W., Lovelock, C.E., McKee, K.L., Lopez-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: a review. Aquat. Bot. 892, 105–127.
Lakshmi, M., Parani, M., Parida, A., 2002. Molecular phylogeny of mangroves IX: molecular marker assisted intra-specific variation and species relationships in the Indian mangrove tribe Rhizophoreae. Aquat. Bot. 743, 201–217.
Leach, G.J., Burgin, S., 1985. Litter production and seasonality of mangroves in Papua New Guinea. Aquat. Bot. 233, 215–224.
Macnae, W., 1966. Mangroves in eastern and southern Australia. Aust. J. Bot. 14, 67–104.
McLeod, A.I., 2011. Kendall Rank Correlation. http://127.0.0.1:29820/library/Kendall/html/Kendall.html (accessed 05.12.11).
Mehlig, U., 2006. Phenology of the red mangrove, *Rhizophora mangle* L., in the Caeté Estuary, Pará, equatorial Brazil. Aquat. Bot. 84, 158–164.
Moriya, H., Komiyma, A., Ogino, K., 1989. Specific characteristics of vegetative and reproductive shoot development of mangrove trees in Iriomote Island. Galaxea 8, 69–77.
OEH (NSW Office of Environment and Heritage), 2011. Estuaries of NSW: physical characteristics, tidal surveys and hydrographic surveys. http://www.environment.nsw.gov.au/estuaries/list.htm (accessed 1.09.11).
O'Grady, A.P., McGuinness, K.A., Eamus, D., 1996. The abundance and growth of *Avicennia marina* and *Rhizophora stylosa* in the low shore zone of Darwin Harbour, Northern Territory. Aust. J. Ecol. 21, 272–279.
Okimoto, Y., Nose, A., Katsuta, Y., Tateda, Y., Agarie, S., Ikeda, K., 2007. Gas exchange analysis for estimating net CO_2 fixation capacity of mangrove *Rhizophora stylosa* forest in the mouth of River Fukido, Ishigaki Island, Japan. Plant Prod. Sci. 103, 303–313.
Oliver, J., 1982. The geographic and environmental aspects of mangrove communities: climate. In: Clough, B.F. (Ed.), Mangrove Ecosystems in Australia: Structure, Function and Management. Australian Institute of Marine Science, Townsville, pp. 19–30.
Pedretti, Y.M., Paling, E.I., 2000. WA Mangrove Assessment Project 1999–2000. Marine and Freshwater Research Laboratory, Environmental Science, Murdoch University, Perth.
Pinzón, Z.S., Ewel, K.C., Putz, F.E., 2003. Gap formation and forest regeneration in a Micronesian mangrove forest. J. Trop. Ecol. 192, 143–153.
Pool, D.J., Lugo, A.E., Snedaker, S.C., 1975. Litter production in mangrove forests of Southern Florida and Puerto Rico. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proc. Int. Symp. Biology and Management of Mangroves. 8–11 October 1974, Hawaii. Florida University Press, FL, pp. 213–237.
Saenger, P., 2002. Mangrove Ecology, Silviculture and Conservation. Kluwer Academic, Dordrecht, Netherlands.
Saenger, P., Moverley, J., 1985. Vegetative phenology of mangroves along the Queensland coastline. Proc. Ecol. Soc. Aust. 13, 257–265.
Singh, P.K., Kushwaha, P.C., 2005. Emerging paradigms of tree phenology in dry tropics. Curr. Sci. 896, 964–975.
Slim, F., Gwada, P., Kodjo, M., Hemminga, M.A., 1996. Biomass and litterfall of *Ceriops tagal* and *Rhizophora mucronata* in the mangrove forest of Gazi Bay, Kenya. Mar. Freshwater Res. 478, 999–1007.
Snedaker, S.C., 1995. Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. Hydrobiologia 295, 43–49.
Stuart, S.A., Choat, B., Martin, K.C., Holbrook, N.M., Ball, M.C., 2007. The role of freezing in setting the latitudinal limits of mangrove forests. New Phytol. 173, 576–583.
Suárez, N., 2003. Leaf longevity, construction, and maintenance costs of three mangrove species under field conditions. Photosynthetica 413, 373–381.
Suárez, N., Medina, E., 2005. Salinity effect on plant growth and leaf demography of the mangrove, *Avicennia germinans* L. Trees. Struct. Funct. 196, 721–727.
Tomlinson, P.B., 1994. The Botany of Mangroves. Cambridge University Press, Cambridge, U.K.
Vannucci, M., 2002. Indo-west pacific mangroves. In: Lacerda, L.D. (Ed.), Mangrove Ecosystems: Function and Management. Springer, Berlin, pp. 123–215.
Williams, J.R., Myers, A.B., Muller, J.W., Duff, A.G., Eamus, D., 1997. Leaf phenology of woody species in a north Australian tropical savanna. Ecology, 2542–2558.
Wilson, N.C., 2009. The Distribution, Growth and Population Genetics of a Mangrove Species *Rhizophora stylosa* Griff. in NSW, Australia. Unpubl. PhD Thesis, School of Arts and Sciences, Australian Catholic University, Sydney.
Wium-Andersen, S., 1981. Seasonal growth of mangrove trees in Southern Thailand III. Phenology of *Rhizophora mucronata* Lamk. and *Syphiphora hydrophyllacea* Gaertn. Aquat. Bot. 10, 371–376.
Yatani, K., 2011. Kruskal–Wallis and Friedman Test. http://yatani.jp/HCIstats?KruskalWallis (accessed 1.12.11).
Youssef, T., Saenger, P., 1999. Mangrove zonation in Mobbs Bay – Australia. Estuar. Coast. Shelf Sci. 49 (Suppl. A), 43–50.
Zar, J.H., 1999. Biostatistical Analysis, 4th edition. Prentice Hall International, Upper Saddle River, NJ.

Provided for non-commercial research and educational use only.
Not for reproduction, distribution or commercial use.

This chapter was originally published in the book *Coastal Wetlands: An Integrated Ecosystem Approach.* The copy attached is provided by Elsevier for the author s benefit and for the benefit of the author s institution, for non-commercial research, and educational use. This includes without limitation use in instruction at your institution, distribution to specific colleagues, and providing a copy to your institution s administrator.

All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution s website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

http://www.elsevier.com/locate/permissionusematerial

From Neil Saintilan, Salt Marsh–Mangrove Interactions in Australasia and the Americas.
In: Gerardo M. E. Perillo, Eric Wolanski, Donald R. Cahoon, Mark M. Brinson, editors,
Coastal Wetlands: An Integrated Ecosystem Approach.
Elsevier, 2009, p. 855. ISBN: 978-0-444-53103-2
© Copyright 2009 Elsevier B.V.
Elsevier.

Author's personal copy

CHAPTER 31

SALT MARSH–MANGROVE INTERACTIONS IN AUSTRALASIA AND THE AMERICAS

Neil Saintilan, Kerrylee Rogers, *and* Karen McKee

Contents

1. Introduction 855
2. Distribution/Geomorphic Settings – Where do Mangrove and Salt Marsh Coexist? 856
   2.1. Mangrove distribution 856
   2.2. Salt marsh distribution 858
   2.3. Coexisting mangrove and salt marsh 859
3. Long-Term Dynamics 862
   3.1. Tropical northern Australia 862
   3.2. Southeastern Australia 863
   3.3. Western Atlantic–Caribbean Region 865
4. Recent Interactions 866
   4.1. Air photographic evidence of mangrove–salt marsh dynamics in SE Australia 866
   4.2. Saltwater intrusion in Northern Australia 867
   4.3. Western Atlantic–Gulf of Mexico 867
5. Stressors Controlling Delimitation of Mangrove 869
   5.1. Geomorphic and hydrological controls 870
   5.2. Climatic controls 873
   5.3. Physicochemical factors 874
   5.4. Biotic interactions 874
6. Conclusions 875
References 876

1. INTRODUCTION

In many places in the world mangroves and salt marsh coexist and competitively interact. These interactions can be studied over a range of timescales. Stratigraphic and palynological evidence has been used to reconstruct distribution of mangrove and salt marsh communities over geological timescales with the greatest clarity emerging from the Holocene. At this scale, interactions between mangroves

Coastal Wetlands: An Integrated Ecosystem Approach
© 2009 Elsevier B.V. All rights reserved.

Author's personal copy

and salt marshes are governed by geomorphic processes, most notably patterns of sedimentation following the postglacial marine highstand.

More recently, over the historical time period, archival air photographs, and other remotely sensed images have been used to study changes in distribution of these communities over wide geographic areas. In SE Australia, the technique has revealed a consistent replacement of salt marsh by mangrove over the previous five decades.

Mangroves compete with salt marshes at the limits of their physiological tolerance. At their latitudinal extreme, the vigor of mangrove growth is constrained by cold, and survival may be dictated by frost. The landward limit of mangroves in the intertidal zone is constrained by the often severe environment of the upper intertidal zone, where low soil moisture and high salinity may prohibit seedling establishment and growth.

This chapter reviews a range of environmental variables: geomorphic, hydrologic, climatic, physicochemical, and biotic, which governs mangrove and salt marsh interactions. An emerging theme is the potential importance of climate change as a key control on dynamics: mangrove competitive advantage may well be enhanced by higher temperatures, mangroves being tropical plants and salt marshes predominantly temperate and sub-Arctic, increasing in diversity with increasing latitude (Saenger et al., 1977). Furthermore, higher sea levels could promote the landward encroachment of mangrove into salt marsh. The changing distribution of mangrove and salt marsh may serve as an important indicator of climate change impacts, a sentinel of change for the broad range of ecosystem services dependent on these habitats.

2. Distribution/Geomorphic Settings – Where do Mangrove and Salt Marsh Coexist?

2.1. Mangrove distribution

Mangroves are the typical intertidal vegetation of sheltered tropical and subtropical coastlines. However, some mangrove species will readily occupy sheltered coastlines at lower temperate latitudes (Saenger, 2002). The global distribution of mangroves has been examined on numerous occasions (Chapman, 1977; Duke et al., 1998a; Duke, 2006; Figure 1) and is primarily limited by the physiological tolerance of mangrove species to low temperature. Other factors, such as the availability of suitable habitat and climate, dispersal and establishment of propagules, continental drift, and tectonic events are also important (Duke et al., 1998a). Mangroves tend to be restricted to coastlines where mean air temperatures of the coldest month are higher than 20°C and the seasonal range is not greater than 10°C (Walsh, 1974; Chapman, 1977, from Duke et al., 1998a), which appears to correlate with the 20°C isotherm for seawater (Duke et al., 1998a).

In the Americas, distribution of mangroves roughly corresponds to the sea-surface winter isotherm of 20°C, except for the North Atlantic coast where the northern limit corresponds to the 27°C isotherm (i.e., the isotherm of the annual average for monthly maximal sea temperature where areas poleward are always cooler) (see Davy

Author's personal copy

Figure 1 Global mangrove and salt marsh distribution and the average 20°C sea-surface temperature isotherm.
Sources: Spalding et al. (1997), Long and Mason (1983), and NOAA (2007).

and Costa, 1992). The cold Humboldt and Falkland (Malvinas) currents influence sea temperatures along the western and eastern coasts of South America so that the winter 20°C isotherm occurs at different latitudes (Figure 1). Similarly, the distribution of mangroves on the west coast of Africa is more restricted than on the east coast due to the different latitudinal positions of the 20°C isotherm (Figure 1). The reduced occurrence of mangroves on the western coasts of Africa and South America also coincides with the limits of arid regions (Saenger, 2002) and implies that the development of mangroves in these regions is limited by aridity in addition to temperature (Saenger and Moverly, 1985; Smith and Duke, 1987).

However, latitude and its relationship with low temperatures and/or the occurrence of frosts are the primary explanation for the latitudinal distribution of mangroves in the Americas (Sherrod and McMillan, 1985; McMillan and Sherrod, 1986). Mangroves thus extend from about 31°N (Baja California, Peinado et al., 1994) to 3°45′S (Peru, Clusener and Breckle, 1987) on the Pacific coast and from about 29°N (Indian River Lagoon, Florida, USA) to 28°30′S (Laguna, Brazil, (Schaeffer-Novelli et al., 1990) on the Atlantic coast. The northernmost mangroves in this region occur in Bermuda (32°18′N), off the east coast of the United States, due to the warm waters of the Gulf Stream and absence of freezing temperatures; species found there include *Rhizophora mangle*, *Avicennia germinans*, and *Conocarpus erectus* (Thomas, 1993). In contrast, mangroves historically extended only to Ponce de Leon Inlet (29°04′N) on the Atlantic coast of Florida and the Mississippi River delta in the Gulf of Mexico (29°12′N) where they are periodically killed by freezing temperatures. Recent reports indicate northernmost individuals of *R. mangle* at 29°40′N (Fort Matanzas, FL, USA) (Zomlefer et al., 2006) and of *A. germinans* at 30°01.012′N (Indian River Lagoon, FL, USA) (I.C. Feller, pers. comm.).

Author's personal copy

Exceptions to the distribution pattern of mangrove in waters cooler than 20°C also occur around Australia and the North Island of New Zealand. In these locations, the species of mangrove with the greatest latitudinal extent is *Avicennia marina*, with its distribution extending to Corner Inlet (38°45′S) in Southeastern Australia. Explanations for the southerly distribution of *A. marina* in Australia include transmission by ocean currents or that they are relict populations that had greater poleward distributions in the past (MacNae, 1966; Duke et al., 1998a). The latter explanation is more widely accepted, particularly since *A. marina* var. *australisica* is genetically distinct from more tropical varieties, such as var. *marina* and var. *eucalyptifolia* (Duke et al., 1998a,b).

A. marina var. *australasica* is the only mangrove species found in New Zealand, and is restricted to the north island with a latitudinal limit at Kutarere (38°03′S) (Lange and Lange, 1994). Like its Australian counterpart, its southern distribution does not appear to relate to climatic factors (Lange and Lange, 1994) and may be a relict of greater poleward distributions (Mildenhall and Brown, 1987; Saenger, 2002). Due to the successful establishment of *A. marina* in more southerly locations, it has been the latitudinal distribution of mangroves in New Zealand is hypothesized to be in disequilibrium with climatic factors. Furthermore, low current velocities and large distances between suitable habitats inhibit the distribution of mangrove to the same extent observed in Australia (Lange and Lange, 1994).

2.2. Salt marsh distribution

In contrast, salt marsh may occur on many of the world's shorelines (Adam, 1990, Mendelssohn and McKee, 2000). Information about the global distribution of salt marsh species is poor and extensive detailed mapping of salt marsh has not been undertaken for some time (Chapman, 1977; Long and Mason, 1983). At a global scale, salt marsh establishes on shorelines where mangrove establishment is precluded or development is limited (Kangas and Lugo, 1990). For this reason salt marshes are most common in temperate, sub-Arctic, and Arctic zones (Long and Mason, 1983; Mitsch and Gosselink, 2000; Mendelssohn and McKee, 2000).

In North America, salt marshes occur from the southern boundary of Central America to Alaska and Canada, with greatest development in the temperate United States (Mendelssohn and McKee, 2000). The northernmost limits of salt marsh on that continent occur along the Arctic Ocean at 70°N latitude and extend southward along the Pacific shoreline of Alaska, Canada, the continental United States, Mexico, and Central America. Salt marsh also occurs along the shoreline of Hudson Bay (55°N) and the Atlantic coasts of Canada and the United States, extending along the Gulf of Mexico into Central America where the distribution overlaps with that of mangrove vegetation. Salt marsh species can be found in Belize (16–17°N), Guyana (6–8°N), Peru/Ecuador (0–5°S), Brazil (0–32°S), Argentina (34–51°S), and Chile (40–52°S) (Table 2 in Costa and Davy, 1992).

Salt marsh vegetation can be classed into six biogeographical types: Arctic, Boreal, Temperate, West Atlantic, Dry Coast, and Tropical (Adam, 1990). A description of salt marsh vegetation in North America using this classification can be found in Mendelssohn and McKee (2000). Salt marshes in the Arctic and sub-Arctic regions are

Author's personal copy

dominated by species such as *Puccinellia phryganoides* and *Carex* spp. Boreal salt marsh along the Atlantic coast is characterized by *Spartina patens*, *S. alterniflora* in the low marsh, whereas Boreal salt marsh in the Pacific–Oceanic region, including British Columbia, contain *Triglochin maritima*, *Salicornia virginica*, and *Distichlis spicata*. Temperate salt marsh on the Atlantic coast is dominated by *S. alterniflora*, which extends southward into northern Florida. Other temperate species along the Atlantic coast include *Juncus balticus* (Boreal), *J. gerardii* (Boreal to Temperate), and *J. roemerianus* (Temperate), which also occurs along the Gulf of Mexico. Temperate salt marsh on the Pacific coast contains *Spartina foliosa*, *Salicornia virginica*, and *D. spicata*. In tropical zones, species such as *S. patens*, *Spartina spartinae*, *D. spicata* can occur, but may be replaced in hypersaline settings by succulents such as *Batis maritima*, *Borrichia frutescens*, *Suaeda maritima*, and *Sesuvium portulacastrum*.

2.3. Coexisting mangrove and salt marsh

Salt marsh typically occurs in settings where mangrove development is limited (West, 1977; Kangas and Lugo, 1990) enabling salt marsh to establish. Extensive coexisting mangrove and salt marsh communities can be found in the temperate regions of Australia, New Zealand, and southern continental United States. Salt marsh may also establish behind mangrove communities within tropical and subtropical climates where rainfall is low and soil salinities in these areas become hypersaline (Chapman, 1977; Long and Mason, 1983). In Mexico, Central America, and Florida, for example, salt marsh may occur on the margins of mangrove forests (either colonizing seaward mudflats or the saline soils on landward edges), within mangrove woodlands with more open canopies, or in disturbed areas (West, 1977; Lopez-Portillo and Ezcurra, 1989).

A distinction must be made between salt marsh vegetation typical of the low intertidal zone and that restricted to the "high marsh", that is, areas in the upper intertidal range that are characterized by dryer, more saline conditions. More specifically, it is necessary to identify salt marsh and mangrove physiographic equivalents when considering interactions between coexisting mangrove and salt marsh vegetation and future changes in climate and sea level. For example, in North America, extensive stands of the temperate low marsh dominant *S. alterniflora* can be found as far south as subtropical Florida, Louisiana, and Texas. Although *S. alterniflora* can be found throughout Latin America, its occurrence is infrequent and mainly limited to mangal fringes (Costa and Davy, 1992). Other salt marsh species such as *S. spartinae*, *D. spicata*, *B. maritima*, *Sesuvium portulacastrum*, and *Sporobolus virginicus* may be more abundant at tropical latitudes (Costa and Davy, 1992), possibly due to their greater tolerance of arid conditions and dessication. Species differences in tolerance of inundation, salinity, dessication, and frost as well as ability to acquire resources under differing stresses will determine mangrove versus salt marsh shifts in response to global drivers. The physiographic equivalent of *S. alterniflora* is *R. mangle*, but the latter cannot tolerate freezing temperatures and does not extend far into subtropical latitudes. Consequently, in the southern United States *S. alterniflora* often intergrades with *A. germinans*, which is more cold tolerant (Figure 2).

Author's personal copy

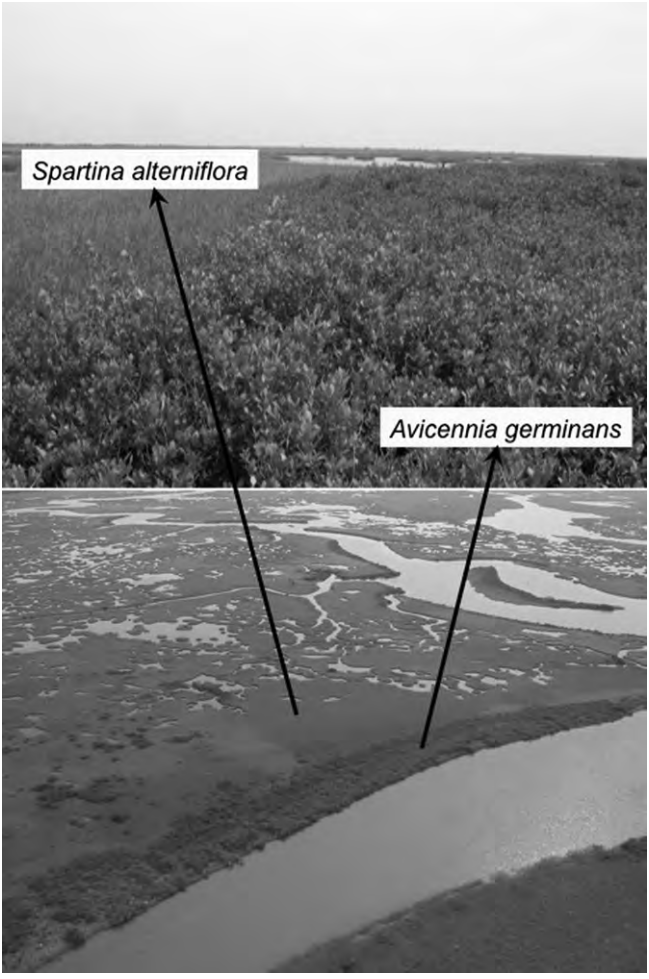


Figure 2 Ground (top) and aerial (bottom) views of a salt marsh–mangrove community in coastal Louisiana, USA. Black mangrove (*Avicennia germinans*) occurs along creekbanks and intergrades with smooth cordgrass (*Spartina alterniflora*) in the marsh interior.

Coexisting mangrove and salt marsh communities occur in a range of geomorphic settings. Along the coastline of New South Wales in Australia, mangrove and salt marsh are primarily located within drowned river valleys and barrier estuaries (Roy et al., 2001). While some salt marsh may be located within saline coastal lagoons, mangroves are generally excluded because mangrove propagule dispersal to these estuaries is restricted by the near permanent closure of the estuary mouth. Periodic extended flooding within coastal lagoons may also lead to the dieback of mangroves, yet allow the survival of salt marsh. Due to high wave energies along the southern Victorian coastline, mangrove and salt marsh are almost exclusively distributed within three coastal embayments; Port Phillip Bay, Western

Author's personal copy

Figure 3 Mangroves (*Avicennia marina*) invading a mudflat in New Zealand (Coromandel Penninsula). Marsh vegetation in foreground is *Leptocarpus similis* (jointed rush).

Port Bay and Corner Inlet. In New Zealand, mangroves are located within major embayments of the northern part of the North Island (Burns and Ogden, 1985) and may occur with species such as *Apodasmia similis* (jointed rush) (Figure 3).

Along the east coast of Florida, mangrove and salt marsh coexist in low-energy environments such as the Indian River Lagoon (Reimold, 1977; Montague and Wiegert, 1990). Along the northern coastline of the Gulf of Mexico mangrove and salt marsh may coexist within the inactive deltaic environments of the Mississippi River and chenier coastal plains in Louisiana (Patterson and Mendelssohn, 1991), in embayments along the west coast of Florida from Tampa Bay to the Cedar Keys (Kangas and Lugo, 1990; Stevens et al., 2006), and in lagoons along the southeast coast of Texas (Sherrod and McMillan, 1985; Everitt et al., 1996). In tropical Mexico, salt marshes are often associated with mangroves in coastal lagoons or near river deltas with low sediment loads (Olmsted et al., 1993). Elsewhere in Latin America, salt marsh may develop in settings that promote the development of hypersaline conditions and in disturbed mangrove areas (Costa and Davy, 1992).

The species composition of salt marsh–mangrove communities in any geographic location may vary substantially due to differences in tide range, local topography, wave energy, and temperature regime. This variation is exemplified along the southern coast of the United States. On the east coast of Florida in the Indian River Lagoon complex, a typical shoreline might be dominated by *R. mangle* or *S. alterniflora* in front of a mid-marsh mixed community of *Salicornia* spp., *D. spicata*, *Borrichia frutescens*, *B. maritima*, and *A. germinans* (Montague and Wiegert, 1990). In south Florida, *S. alterniflora* might form a narrow fringe in front of a well-developed mangrove zone (*R. mangle*, *A. germinans*, *Laguncularia racemosa*) and a back mangal zone dominated by *J. roemerianus* (Davis, 1940). On the west coast of Florida (north of Tampa Bay to the Cedar Keys), *S. alterniflora* stands contain small

Author's personal copy

stature, but abundant *A. germinans*. Similarly, the salt marsh–mangrove communities in coastal Louisiana and south Texas consist of *S. alterniflora* and *A. germinans*. The mangrove *R. mangle* occurs farther south along the Texas coast due to its greater freeze sensitivity. Geographic variation in species co-occurrence and respective inherent environmental tolerances and competitive abilities will likely determine mangrove–salt marsh interactions in any specific location.

3. Long-Term Dynamics

3.1. Tropical northern Australia

Tropical northern Australia is drained by several macrotidal rivers, each receiving seasonal floods in relation to the monsoons (Woodroffe et al., 1989). Mangroves are confined to active depositional environments, including channel banks, the edges of mid-channel islands, and prograding coastlines (Woodroffe et al., 1985). The wide upper-intertidal and supratidal flats are bare in lower rainfall areas, or covered in grasses, sedges, and, in wetter areas, Melaleuca forest (Woodroffe et al., 1989). These wide estuarine flats are known as blacksoil plains.

Beneath the blacksoil plains lay extensive mangrove peat deposits. These have been located in King Sound (Semeniuk, 1980, 1982), the Fitzroy River (Jennings, 1975), the Ord River (Thom et al., 1975), and the Daly and Alligator Rivers (Woodroffe et al., 1985). Radiocarbon dating of these mangrove facies shows a consistency in age across the estuarine plains and also between river systems. For example, in the South Alligator River, 33 radiocarbon dates returned values within a range of 5370–6860 years BP with no spatial trends (Woodroffe et al., 1985). These dates corresponded with dates returned from other systems in northern Australia, including the Fitzroy (5800–7500 years BP) and the Ord (ca. 6700 BP Thom et al., 1975). From these dates Woodroffe et al. (1985) hypothesized that extensive mangrove deposits occupied much of the estuarine plains adjacent to the macrotidal rivers near the end of the postglacial marine transgression.

Jennings (1975) had provided a climate interpretation of the extensive cover of mangrove, or "big swamp" phase in northern Australian estuaries, postulating higher rainfall as a possible mechanism. In tropical north Queensland, mangroves still occupy the entire estuarine plain in some rivers experiencing high, year-round rainfall, but can occur together with salt marsh species (Figure 4). By contrast, Woodroffe et al. (1985) presented a geomorphological explanation for this phase. In this model, continued sedimentation following sea-level stabilization raised intertidal elevations above those tolerated by mangroves, to the point that by 5500 BP most of the mangrove extent was confined to the fringes of channels. In dryer areas, mangroves gave way to hypersaline flats, while in wetter areas; upper intertidal and supratidal environments were colonized by salt-tolerant grasses and sedges.

The more detailed investigation by Woodroffe et al. (1985) had shown that the relationship between sedimentation and sea level was the driver of mangrove–salt marsh/saltflat dynamics at the scale of the Holocene, at least in northern Australia.

Author's personal copy

Figure 4 Salt marsh (*Distichlis* sp.) growing adjacent to a stand of mangroves (*Ceriops tagal*) in Queensland, Australia.

These studies provided a theoretical context for later work in the estuaries of southeastern Australia.

3.2. Southeastern Australia

Roy (1984) presented a model of estuarine infill for SE Australia that described phases in the availability of intertidal habitat. Under this model, the deeply incised drowned river valleys characteristic of SE Australia support little in the way of intertidal vegetation immediately following postglacial marine transgression. As these valleys infill with sediment, the fluvial bayhead delta progrades seaward, supporting wide intertidal flats. It is during this "intermediate" stage of infill that estuaries support the greatest extent of mangrove and salt marsh. With the completion of infill floodplains accrete above intertidal elevations, flow is channelized throughout the length of the estuary, and intertidal habitats are restricted to channel fringes and cutoff embayments.

The Roy (1984) model assumes stable sea level following the cessation of the postglacial marine transgression at approximately 6500 BP. Recent dating of encrusting organisms at several locations in New South Wales have suggested that mid-Holocene sea levels may have been somewhat higher (50–150 cm) than present levels (Baker and Haworth, 1997, 2000), an observation which might explain the widespread occurrence of potentially acid sulfate soils above current sea levels on estuarine floodplains (Wilson, 2005). Were mangroves more widely distributed in the mid-Holocene than at present?

Early work on the interactions between mangrove and salt marsh in eastern Australia was dominated by succession theory. Pidgeon (1940) saw mangroves as the initial colonizers of exposed estuarine mudflat under conditions of extreme

Author's personal copy

salinity and saturation. Mangroves were seen as active land builders, which accumulated sediment amongst aerial roots, inviting invasion by subsequent colonizers.

> Saltmarsh plants, the first of which are *Salicornia australis, Suaeda australis* and *Samolus repens*, invade the landward margin of the mangrove area. With subsequent silt accumulation the mangroves are forced further out into the estuary and in their place a saltmarsh is formed.
>
> Pidgeon (1940, p. 224)

Under this model, continued accretion led to colonization by salt-tolerant grasses (*Sporobolus virginicus*), followed by the rush *Juncus* spp., then *Casuarina glauca*. As freshwater conditions replace saline, Eucalyptus invades, with the "climax" community appearing as a mixed Eucalypt forest (Pidgeon, 1940). Evidence supporting this dynamic succession was seen as the occurrence of "relict species in more advanced zones" and the active invasion of *Juncus* into the *Sarcocornia* meadow.

The succession model can be tested by coring within the salt marsh in search of relict mangrove peat material. To this end, Mitchell and Adam (1989a) retrieved shallow sediment cores from several salt marshes in Botany Bay and the Georges River, in the Sydney region. Their coring failed to find any evidence of previous occupation of the salt marsh habitat by mangrove, and suggested a model which had salt marsh species as primary colonizers, followed by invasion by mangrove. This model accorded with observations of initial colonization of newly created intertidal flats by salt marsh on the northern foreshore of Botany Bay, and the spreading of mangroves into the salt marsh zone at various intertidal locations in the Sydney region (Mitchell and Adam, 1989b).

The Hawkesbury River in central NSW is a large drowned river valley in an intermediate phase of infill. Unlike the macrotidal estuaries of tropical northern Australia, the Hawkesbury supports a diverse array of vegetation on depositional terraces through its tidal length of some 106 km. There is no "big swamp" phase, nor does there appear to have been at any point in the Holocene or late Pleistocene. Present-day intertidal flats support widespread mangrove in the central reaches of the estuary. Seaward of these, mudflats exposed at low tide are unvegetated. Headward, intertidal flats are dominated by salt marsh, principally *Juncus kraussii*. Saintilan (1997) suggested that gradual infill has led to the replacement of mangrove with salt marsh on successive intertidal flats as the river progrades seaward within its valley.

Evidence for this model of geomorphically driven vegetation succession is found in the stratigraphy of intertidal flats currently occupied by salt marsh. Using techniques similar to those of Mitchell and Adam (1989b), Saintilan and Hashimoto (1999) found mangrove peats well preserved 20–30 cm beneath the present-day marsh surface, at the approximate elevation of contemporary mangrove root systems. Beneath these peats, estuarine shells dated to approximately 5000 years BP. The age of the mangrove peats varied with distance from the edge of wide intertidal flats, from 1200 to 1700 years BP at the upslope fringes of the flats to 500 years BP close to the current mangrove/salt marsh boundary, suggesting gradual infill.

Author's personal copy

Mangrove root material retrieved from beneath salt marsh in small creeks in southern NSW told a similar story. Mangrove root material dating to 1300 BP in Currambene Creek and 1900 BP in Cararma Inlet were retrieved from beneath the contemporary salt marsh (Saintilan and Wilton, 2001). The lack of any significant fluvial input into Cararma Inlet suggested tidal reworking of aeolian and washover deposits as the most likely mechanism for infill. Within Currambene, preserved mangrove root material was more sporadic, and the suggestion was made that channel migration had erased evidence of prior mangrove occupation in some locations. At neither site was there evidence of widespread mangrove colonization earlier than 3000 BP, though more headward estuarine floodplains were not sampled.

3.3. Western Atlantic–Caribbean Region

Early work in Florida and the Caribbean Region was also influenced by succession theory and the concept of mangroves as "land-builders" (Spackman et al., 1966; Cohen and Spackman, 1977). Davis (1940) proposed that mangrove–salt marsh zonation in Florida reflected ecological succession and seaward progradation by mangroves as sea level rose. However, Egler (1952); Thom (1967) and others later challenged both the zonation–succession interpretation and the idea that mangroves were geological agents capable of building land. Egler (1952) presented evidence that mangroves had retreated landward during sea-level rise, invading freshwater habitats in the Everglades. More recent work in the Caribbean has shown that mangroves growing in sediment-deficient settings can build vertically via peat formation (Woodroffe, 1981, 1983; Cameron and Palmer, 1995; Macintyre et al., 1995, 2004; McKee and Faulkner, 2000; Toscano and Macintyre, 2003; McKee et al., 2007). In some cases, mangrove peat deposits reach 10 m in thickness, and radiocarbon dating shows that this biogenic accretion has kept pace with sea-level rise (e.g., Twin Cays and Tobacco Range, Belize) (Macintyre et al., 2004; McKee et al., 2007).

Paleostratigraphic evidence of fluctuations in mangrove and salt marsh dominance is limited for the Western Atlantic–Caribbean Region and generally does not record the interplay between these specific vegetation types. Early work in Florida showed basal freshwater peat beneath mangrove peat in the modern Everglades–mangrove complex, suggesting mangrove invasion of freshwater marsh during sea-level rise (Cohen and Spackman, 1977). Some of the deepest and oldest peat deposits occur in Belize where basal peats have been radiocarbon dated to about 8000 Cal BP (Toscano and Macintyre, 2003; Macintyre et al., 2004; McKee et al., 2007). Most of these studies identified mangrove-derived peat throughout the stratigraphic profile and no components were identified as "salt marsh" peat. Work by Woodroffe (1981, 1983) at Grand Cayman also showed predominately mangrove peat in radiocarbon dated cores. These latter observations show the continued dominance of mangroves throughout the Holocene despite changes in sea level.

Other locations, including Jamaica (Digerfeldt and Hendry, 1987) and Trinidad (Ramcharan, 2004), show fluctuations between mangroves and brackish water

Author's personal copy

sedges (e.g., *Cladium* sp.) or freshwater species, respectively. In the Negril Swamp, Jamaica, radiocarbon dated cores show sedge (*Cladium* sp.) peat at the base (ca. 7000–8000 Cal BP) and interspersed at intervals with mangrove peat (*Rhizophora* or *Rhizophora–Conocarpus*) or mixtures of *Cladium–Rhizophora* or *Cladium–Conocarpus* peat (Digerfeldt and Hendry, 1987). Pollen records from a late Holocene core on the Mexican Caribbean coast (Quintana Roo) showed mangroves dominating during humid periods and *Conocarpus erectus* and nonmangrove taxa dominating during drier periods, for example, that coincided with the decline in the Mayan culture (Islebe and Sanchez, 2002).

4. Recent Interactions

4.1. Air photographic evidence of mangrove–salt marsh dynamics in SE Australia

On the basis of the stratigraphic evidence described above the trend in SE Australia over the later Holocene has been one of salt marsh replacing mangrove with the infilling of estuaries, and mangrove occupying freshly accreted habitat. This pattern has been consistent across a range of settings, from drowned river valleys (Saintilan and Hashimoto, 1999) to smaller barrier estuaries (Saintilan and Wilton, 2001). The pattern presents a contrast to trends identified from more recent times from air photographic records. Numerous studies from SE Australia have demonstrated the encroachment of mangrove into upper-intertidal salt marsh.

Saintilan and Williams (2000) cited 28 surveys that demonstrated salt marsh loss to mangrove encroachment over the period covered by archival air photographs (usually 1940s – present). The trend is apparent across all east coast bioregions and a range of geomorphic settings. Within southern Queensland, Pleistocene sand barriers protect wide, shallow backbarrier deposits which support extensive mangrove and salt marsh. Mangrove encroachment into salt marsh in these environments is well documented (McTainsh et al., 1986; Hyland and Butler, 1988; Morton, 1994; Manson et al., 2003). In northern NSW, mangroves and salt marshes occupy the mouths of large rivers. While losses of mangrove and salt marsh to agriculture have been extensive (West, 1993), mangroves are encroaching upon salt marsh and some agricultural pastures (Saintilan, 1998). In central coast NSW, widespread losses of salt marsh to mangrove have been reported from both shallow coastal lakes (Winning, 1990) and drowned river valleys (Mitchell and Adam, 1989a,b; Evans and Williams, 1997; Williams and Watford, 1997; Williams et al., 1999; McLoughlin, 2000; Haworth, 2002; Williams and Meehan, 2004). South coast NSW estuaries, mostly smaller "barrier" estuaries (Roy et al., 2001) have shown similar trends with a median loss of approximately 40% of the salt marsh to mangrove encroachment (Meehan, 1997; Chafer, 1998; Saintilan and Wilton, 2001).

Within Victoria, salt marshes and mangroves occupy the shorelines of large coastal embayments. Here, loss of salt marsh to mangrove encroachment has been

Author's personal copy

consistent though less dramatic. Declines of 5–12% of salt marsh to mangrove encroachment have been reported for the salt marshes of Western Port Bay (Rogers et al., 2005b) and losses have also been noted for Corner Inlet (Vanderzee, 1988) and the Gulf St. Vincent in South Australia (Burton, 1982). Within New Zealand, the proliferation of mangrove is more commonly described as a seaward colonisation (Cragg et al., 2001; Park, 2001; Morrisey et al., 2003) though landward encroachment has been noted (Burns and Ogden, 1985).

4.2. Saltwater intrusion in Northern Australia

Marked geomorphological changes to estuaries and coastal plains in Northern Australia over the past 50 years have been associated with saltwater intrusion in the Alligator River Region (Winn et al., 2006) and Mary River (Knighton et al., 1991; Mulrennan and Woodroffe, 1998). The gradual extension of tidal influence along stream channels, the expansion of tidal creeks and the formation of new tidal creeks (Winn et al., 2006) is linked to the encroachment of mangrove and saline mudflats into freshwater vegetation (Finlayson et al., 1998), localized scour and dieback within Melaleuca forests, accretion of sediment on floodplains (Knighton et al., 1991; Woodroffe and Mulrennan, 1993; Bell et al., 2001), changes in subsurface hydrology (Jolly and Chin, 1992) and land cover changes (Ahmad and Hill, 1995; Bell et al., 2001). Changes since 1950 are significant with bare saline mudflats on the East Alligator River exhibiting a ninefold increase and an associated loss of 64% of Melaleuca forests by 2000 (Winn et al., 2006). More than 17,000 ha of freshwater vegetation have been adversely affected on the Mary River and a further 35–40% of floodplains are immediately vulnerable to intrusion (Mulrennan and Woodroffe, 1998).

A single cause for saltwater intrusion has not been identified (Mulrennan and Woodroffe, 1998). Instead, it is apparent that factors such as drier-than-average monsoonal conditions, low-frequency and low-intensity cyclonic events, and above average ocean water levels (Winn et al., 2006) facilitate extension of tidal influence into freshwater environments, while tributary development, large tidal range, small elevation differences over floodplains, and uncontrolled feral buffalo promote the expansion of tidal influence (Knighton et al., 1991). Due to the desiccation of floodplain sediments in the dry seasons, the process of saltwater intrusion now appears to be internally driven and is likely to continue until an equilibrium state is reached between floodplain elevation and tidal influence (Mulrennan and Woodroffe, 1998; Winn et al., 2006).

4.3. Western Atlantic–Gulf of Mexico

Information on historical shifts in salt marsh and mangrove vegetation in the Western Atlantic–Gulf of Mexico region is limited to site-specific observations (Lonard and Judd, 1985; Sherrod and McMillan, 1985; McMillan and Sherrod,

Author's personal copy

1986; Montague and Wiegert, 1990; Montague and Odum, 1997; McKee et al., 2004; Stevens et al., 2006). In the northern Gulf of Mexico, the persistence and spread of mangroves is controlled mainly by temperature (Sherrod and McMillan, 1985; Stevens et al., 2006) although hydroperiod, sedimentation, salinity, and nutrients as well as propagule dispersal and predation determine local patterns of establishment and spread (Patterson and Mendelssohn, 1991; Patterson et al., 1993, 1997). In coastal Louisiana, for example, mangroves tend to dominate shorelines of tidal creeks, and salt marsh occupies the interior position.

The *A. germinans* zone is characterized by higher elevation, salinity and soil bulk density, whereas the *S. alterniflora* zone is lower in elevation with greater flooding and reducing soils (Patterson and Mendelssohn, 1991). Exclusion of *A. germinans* from the interior marsh zone has been attributed to limited retention of and higher predation on propagules (Patterson et al., 1997) and plant competition in combination with greater flooding stress (Patterson et al., 1993).

Periodic freezes have killed or damaged mangroves allowing expansion of salt marsh, most recently during the 1980s (McMillan and Sherrod, 1986; Montague and Wiegert, 1990; Montague and Odum, 1997; Stevens et al., 2006). Stevens et al. (2006) review reports of major damage to mangroves in Florida as a result of severe freezes in 1962, 1977, 1981, 1983, 1985, 1989, and 1996. *A. germinans* has some capacity to recover from freeze damage through coppicing (stump sprouting), but periodic damage results in a stunted, scrub-like growth form. In Louisiana, the last severe freeze that caused widespread dieback of mangroves (*A. germinans*) occurred in December, 1989 (K.L. McKee, pers. obs.). Although *A. germinans* can recover from mild freezes, the 1989 event killed mature trees. However, propagules that had already dispersed survived this freeze and appeared to be the primary means by which the population reestablished. Thousands of propagules were observed establishing in the months after the freeze, and their viability was further confirmed in greenhouse culture (K.L. McKee, unpublished data.). The resistance of *A. germinans* propagules in Louisiana to freezing temperatures is consistent with previous studies of cold tolerance of this species (Markley et al., 1982; Norman et al., 1984; Sherrod et al., 1986).

Most observations indicate that salt marsh replaces freeze-killed mangroves in the Gulf of Mexico within 4–5 years (Stevens et al., 2006). However, relatively mild winters and the lack of severe freezes in recent years has allowed mangrove expansion in Florida (Stevens et al., 2006) and Louisiana (K.L. McKee, pers. obs.). Mangroves have expanded (average of 21% increase in cover) at the Cedar Keys, Florida (29°08′N) between 1995 and 1999 during a period free from severe freezes (Stevens et al., 2006). Recent mangrove expansion in coastal Louisiana, USA, has been attributed to a drought-induced, widespread dieback of *S. alterniflora* during 2000 (McKee et al., 2004). Over 40,000 ha of salt marsh were severely damaged with areas up to 5 km^2 reduced to mudflat. However, *A. germinans* was unaffected and even thrived during and after this marsh dieback event (Figure 5).

Author's personal copy

Figure 5 Salt marsh (*Spartina alterniflora*) dieback in coastal Louisiana, USA (top). Black mangrove (*Avicennia germinans*) was unaffected and later became dominant in some dieback areas (bottom).

5. Stressors Controlling Delimitation of Mangrove

Mangroves commonly exhibit a gradual reduction in development with latitude (Lot et al., 1975; Saenger and Snedaker, 1993; Saenger, 2002) and stunted forms at their latitudinal limit may be due to an increasingly stressful environment (Schaeffer-Novelli et al., 1990). Kangas and Lugo (1990) hypothesize that without "stress," in their case frost stress, mangrove vegetation is competitively superior and coastlines would be dominated by mangrove. However, field observations of salt marsh dieback in coastal Louisiana, USA, and *A. germinans* expansion into areas formerly occupied by *S. alterniflora* (McKee et al., 2004) suggest that at subtropical latitudes some mangrove species are competitively inferior. In addition, greenhouse

Author's personal copy

and field experiments show that *S. alterniflora* competitively inhibits growth of *A. germinans* (Patterson et al., 1993; McKee and Rooth, 2008). Where mangrove and salt marsh coexist, environmental stressors control the delimitation of mangrove so that these communities typically form three zones: a seaward zone dominated by mangrove, a landward transition zone containing both mangrove (possibly stunted) and salt marsh, and an interior zone dominated by salt marsh. Numerous stressors, including geomorphic, hydrological and climatic controls, physicochemical factors, and biotic interactions may act to delimit mangrove establishment (Patterson et al., 1993, 1997; McKee and Rooth, 2008) and enable salt marsh development within the interior of marshes. In some extreme environments, however, marsh vegetation may facilitate mangrove recruitment through propagule trapping and/or amelioration of stressful soil conditions (McKee and Rooth, 2008).

5.1. Geomorphic and hydrological controls

Inundation by tides is not an ecophysiological requirement of mangroves and salt marshes, but it is a typical feature and plays an important role by limiting excessive buildup of salts within soils (Saenger, 2002) and distributing mangrove and salt marsh propagules (Adam, 1990; Clarke, 1993). Indeed, inundation may play a significant role in mangrove and salt marsh zonation as tidal flushing may act to alter soil salinity (Patterson and Mendelssohn, 1991) and control the transport of propagules along an elevation gradient (Adam, 1990; Patterson et al., 1997; Saenger, 2002). The hydrologic role of inundation is largely controlled by the geomorphology of a marsh so that inundation frequency and water volume is negatively proportional to land elevation. However, the relative positions of salt marsh and mangrove vegetation along a topographic gradient varies with geographic region and the species involved. In the northern Gulf of Mexico, mangroves coincide and compete with low marsh species such as *S. alterniflora*, which are highly flood tolerant (Patterson and Mendelssohn, 1991; Patterson et al., 1993, 1997). In these communities, mangroves (*A. germinans*) occupy the higher elevation creek banks and salt marsh species dominate the interior, lower elevation areas. In other locations, low elevation sites are commonly inhabited by mangrove, are inundated more frequently, and receive higher water volumes, while higher elevations are commonly inhabited by salt marsh. The latter pattern can be found in coexisting mangrove and salt marsh communities in Australia as well as in Florida, USA (Montague and Wiegert, 1990). In the latter case, the low elevation sites along shorelines are dominated by *R. mangle* and higher elevations are occupied by high marsh species such as *B. maritima*, *D. spicata*, *Borrichia frutescens*, and *Salicornia* spp.; the upland transition may be occupied by *J. roemerianus*, *Spartina bakerii*, or *S. patens* (Montague and Wiegert, 1990).

Adaptations to cope with submergence and high salt environments are evident within both mangrove and salt marsh species (summarized in Adam, 1990; Saenger, 2002) and species tolerance to submergence and salinity are hypothesized to cause the zonation of plants observed within marshes. Numerous studies have demonstrated the role of salinity in causing mangrove species to segregate (Ball, 1988a,b, 2002; Lin and Sternberg, 1992; Ball and Pidsley, 1995; López-Hoffman et al., 2006)

Author's personal copy

and coexist with temporal salinity variation (Ball, 1998). However for salt marsh, Adam (1990) argues that since soil salinity varies spatially and temporally, zonation may be more readily explained on the basis of species tolerance to frequency and duration of submergence. Furthermore, while soil salinity and tidal regime are important factors, these factors do not appear to explain observed distributions of salt marsh species across the intertidal zone (Silvestri et al., 2005). The zonation of coexisting mangrove and salt marsh communities in Sydney (Clarke and Hannon, 1971) and Brazil (Santos et al., 1997, cited in Saenger, 2002) were found to be salinity based, with species exhibiting definable salt tolerances (Clarke and Hannon, 1971) and their distribution being determined by a salinity model based on topographic level and upland runoff (Santos et al., 1997). While causes of mangrove and salt marsh zonation remain incompletely understood (Snedaker, 1982; Adam, 1990), it is evident that zonation, soil salinity and submergence are all maintained along elevation gradients and is likely to contribute to the distribution of mangrove and salt marsh vegetation (Snedaker, 1982; Saenger, 2002).

Zonation as a consequence of differential dispersal of mangrove propagules has also been proposed. This is primarily based on the concept of tidal sorting of propagules proposed by Rabinowitz (1975, 1978a,b,c) for mangroves in Panama. However, the relationship between propagule size and zonation has not been supported for mangroves in other locations (Ball, 1980; Saenger, 1982; McKee, 1995a) In addition, differential dispersal and survival of propagules with tides has not been established for salt marsh species and since many salt marsh species are able to vegetatively propagate the contribution of tides to dispersal is likely to be limited (Adam, 1990).

Regardless of the role of tidal sorting of propagules in zonation, tides do distribute mangrove propagules and it is likely that zonation of mangrove to salt marsh may be related to differential seedling mortality at different tidal levels (Ellison and Farnsworth, 1993). High soil salinity decreases the rate of pericarp shedding by mangrove propagules, thereby limiting survival (Downton, 1982; Clarke and Myerscough, 1991). Thus, higher soil salinities and reduced inundation frequency, common in the high marsh, causes mangrove propagules to desiccate and suffer high mortality (Clarke and Allaway, 1993). However, work in the northern Gulf of Mexico found that mortality of *A. germinans* propagules was associated with excessive flooding and damage by predators in low marsh areas, resulting in decay and loss of viability (Patterson et al., 1997).

Observed interactions between mangrove and salt marsh globally have highlighted the role of hydrology and geomorphology in increasing the dispersal and survival of mangrove propagules and seedlings. For example, a strong relationship has been found between relative sea-level rise and the upslope migration of mangrove into salt marsh environments in Southeastern Australia (Rogers, 2004). In this case, relative sea-level rise incorporates both geomorphological and hydrological changes and may be altered by eustatic sea-level rise, which relates to changes in the volume of water within oceans through the melting of ice caps and thermal expansion of water; and/or surface elevation changes of the land through surface processes of vertical accretion or subsurface processes of subsidence and autocompaction.

Author's personal copy

Hydrological changes due to global warming has caused global sea level to increase by 1.0–2.0 mm/year in the 20th century the rate of sea-level rise is predicted to accelerate toward 2,100 (Solomon et al., 2007). Recent studies of relative sea-level trends for salt marshes in Tasmania and New Zealand show higher rates over the past century (2.5–3.1 mm/year) compared to the previous four centuries (Gehrels et al., 2007). Numerous studies predict that global sea-level rise will cause a shift in the boundary between mangrove and salt marsh (Snedaker, 1995; Blasco et al., 1996) and indeed the study of Rogers et al. (2006) related sea-level changes to the expansion of mangroves in Southeastern Australia. However, changes to the water levels inundating a marsh may also occur due to altered tidal prisms resulting from engineering works, such as dredging of estuary entrances. These hydrological changes may increase the mean water level and/or alter the tidal range within a marsh, thereby altering soil salinity and increasing the distribution potential of mangrove propagules. Both reduced soil salinities and increased inundation promote the survival of mangrove within salt marsh and increases their competitive potential.

Geomorphological changes to marsh elevation alter the inundation frequency and duration within a marsh and may occur as a result of surface processes such as vertical accretion. Increased sediment availability and vertical accretion within estuaries has been hypothesized as a mechanism promoting mangrove encroachment of salt marsh in Southeastern Australia (summarized by Saintilan and Williams, 1999; McLoughlin, 2000) by creating more areas suitable for mangrove establishment and providing a soft substrate for mangrove propagule establishment within the salt marsh. Certainly the spread of mangrove along estuarine foreshores seems related to the availability of new habitat, and commonly the landward encroachment of mangrove is accompanied by seaward encroachment also. Perhaps the overall increase in population of *A. marina*, and increased fecundity made possible by higher nutrient loads has increased propagule availability within estuaries, including the upper-intertidal environment. However, increased vertical accretion is also more likely to increase marsh elevation, reducing inundation frequency, and thereby reducing the likelihood of mangrove survival due to propagule desiccation. Further, the "fertilization" of the salt marsh from anthropogenic sources does not necessarily lead to improved mangrove colonization. Experimental fertilization of *A. marina* propagules has failed to show an impact on propagule survival (Clarke and Myerscough, 1993; Saintilan, 2003).

Rates of vertical accretion have been used as an estimate for marsh elevation and a surrogate for investigating the cause of mangrove–salt marsh interaction. This is appropriate at some sites, such as Homebush Bay and Western Port Bay, Australia, where salt marsh surface elevation is maintained primarily by vertical accretion (Rogers et al., 2005a,b). However, this assumption is not always true. Recent literature has highlighted the role of belowground processes in altering marsh elevations (Cahoon et al., 1999, 2006; McKee et al., 2007). Processes such as subsidence, soil compaction, plant productivity and dieback, groundwater availability, and tidal flooding interact to alter soil volumes over a range of spatial and temporal scales.

Author's personal copy

The relationship between marsh elevations and sea level has primarily been explored through the use of surface elevation tables (described by Cahoon et al., 2002). By incorporating analyses of surface processes such as vertical accretion, the belowground component of surface elevation change can be differentiated. In southeastern Australia, Surface Elevation Tables (SET) were used to show that mangrove surface elevation gain was consistently lower than salt marsh surface elevation gain despite vertical accretion being consistently higher in the mangrove zone (Rogers et al., 2005a,b, 2006). Mangrove encroachment of salt marsh in the same region has been attributed to autocompaction or subsidence, which causes the observed disequilibrium between mangrove surface elevation change and vertical accretion (Rogers et al., 2006). Those marshes with the highest rates of relative sea-level rise were those with the highest rates of mangrove encroachment (Rogers et al., 2005b). Autocompaction of sediments corresponded to a severe El Nino-related drought, and surface elevation change correlated strongly with total monthly rainfall (Rogers et al., 2005a), the Southern Oscillation Index and groundwater depth (Rogers and Saintilan, 2008). This research is consistent with other studies of surface elevation and groundwater (Schmidt and Burgman, 2003; Watson, 2004; Whelan et al., 2005) and suggests that rainfall and subsequent groundwater recharge plays a significant role in determining interannual variability in surface elevation with respect to sea level.

5.2. Climatic controls

Climatic factors are commonly proposed to promote or limit the survival of mangrove within coexisting mangrove and salt marsh communities as a result of extreme low temperatures and frost causing the death of mangrove, or rainfall influencing soil salinity.

Many tropical and subtropical plants exhibit physiological dysfunction and damage in response to chilling temperatures (van Steenis, 1968) and this appears to be the case for mangroves (McMillan, 1975; Markley et al., 1982; McMillan and Sherrod, 1986; Kangas and Lugo, 1990; Olmsted et al., 1993). Freeze sensitivity is particularly apparent along the Gulf and Atlantic coasts of North America as discussed in the previous section. In the northern Gulf of Mexico, mangroves tend to expand during periods of mild winters (Stevens et al., 2006) and when weather extremes or other factors stress or eliminate salt marsh (McKee et al., 2004). When mangroves are periodically damaged or killed by freezes, salt marsh quickly regains dominance (Stevens et al., 2006). Consequently, future changes in global climate regime and local weather patterns will likely influence the relative dominance of mangrove and salt marsh vegetation in this region.

Mangroves show greater luxuriance and species richness in high rainfall areas (Tomlinson, 1986; Hutchings and Saenger, 1987; Smith and Duke, 1987) and species distribution correlates strongly with freshwater influence from rainfall (Bunt et al., 1982), controlling for latitude. In fact, low rainfall and a shortened rainfall season in Senegal in the 1980s contributed to the decline of mangroves and increased surface areas of bare salt flats and saline grasslands (Diop et al., 1997). In addition, studies in Australia have suggested that freshening of salt marsh

Author's personal copy

environments from rainfall might promote survivorship of mangroves (McTainsh et al., 1986) and may explain the establishment of mangrove at the salt marsh–terrestrial boundary in tropical and subtropical areas of Australia (Duke, 2006).

There is other evidence that mangrove encroachment in tropical and subtropical climates may be related to rainfall trends. In these situations, the proportion of mangrove and salt marsh in estuaries is correlated to annual rainfall (Bucher and Saenger, 1991). Where salt marsh occurs, it often occupies a middle position between seaward and landward mangrove zones. Increased rainfall in recent decades has been used to explain the encroachment of tall mangrove forest into saltpan in Hinchinbrook Channel (Duke, 1995) and stunted mangrove into salt marsh in Moreton Bay (Duke, pers. comm.). Conversely, declines in rainfall have resulted in mangrove dieback in the upper intertidal environment in some locations (Duke, pers. comm.) The correlation between rainfall and the proportion of mangrove and salt marsh breaks down in New South Wales (Saintilan, 2003). Here, the upslope limit of mangrove is more consistently related to frequency of tidal inundation, and there is no landward mangrove fringe.

5.3. Physicochemical factors

Physicochemical factors have been hypothesized to limit the establishment of mangrove within salt marsh areas. In particular, mangroves may be excluded from salt marsh environments due to nutrient deficiency and/or high soil salinity within salt marshes. Salinity decreases pericarp shed and increases desiccation of mangrove propagules (Downton, 1982; Clarke and Myerscough, 1991) and may contribute to zonation of mangrove and salt marsh species due to differential species tolerance to soil salinity (summarized in Adam, 1990; Saenger, 2002) as discussed above.

Experimental fertilization of mangroves indicate that nitrogen and phosphorus limitation is common (Boto, 1983; Boto and Wellington, 1983; McKee et al., 2002) and upon fertilization mangroves exhibit increases in growth and biomass (Naidoo, 1987; Clarke and Allaway, 1993; Feller et al., 2003a,b; Lovelock et al., 2004, 2006).

However, since the effect of nutrient enrichment does not become apparent until mangrove cotyledons have been exhausted (Naidoo, 1987; Clarke and Allaway, 1993), it has less impact on early mangrove establishment within salt marsh. Saintilan (2003) confirmed that mangrove mortality within salt marsh is not reduced through nutrient enrichment of seedlings. In some geographic regions, mangrove mortality within salt marshes is the result of desiccation of propagules (Clarke and Allaway, 1993; Saintilan, 2003), which is dependent on climatic, geomorphic and hydrologic factors. However, changes in tissue chemistry by fertilization or light conditions (McKee, 1995b) could influence mangrove seedling susceptibility to herbivores.

5.4. Biotic interactions

Several studies suggest that salt marsh precedes mangrove in successional sequences due to tidal transport of mangrove propagules and shading of salt marsh by mangrove seedlings (summarized in Kangas and Lugo, 1990). Recent work by

Author's personal copy

McKee and Rooth (2007) found that establishment, survival, and growth of mangrove seedlings were facilitated by herbaceous species, *Sesuvium portulacastrum* and *D. spicata*. Both species promoted mangrove propagule trapping and ameliorated soil conditions (aeration, temperature). Alternatively, dense stands of saltbush (*Tecticornia* spp.) have been suggested to inhibit mangrove establishment in salt marshes in Western Port Bay, Australia by either shading seedlings or collecting sediments and building up the marsh surface to exclude mangrove (Rogers et al., 2005b). Similar competition has been reported between mangroves and *S. alterniflora* in marshes in Louisiana (Patterson et al., 1993; McKee and Rooth, 2008).

Plant–animal interactions are also evident within coexisting communities and differential predation of mangrove propagules by crabs is suggested as a cause of zonation within mangroves (Smith, 1987; Smith et al., 1989), but this hypothesis is not supported in other locations (McKee, 1995a; Sousa and Mitchell, 1999). A study of *A. germinans* seedlings found that predator damage to propagules (and frequent flooding) leads to decay of propagules within the *Spartina* zone in coastal Louisiana (Patterson et al., 1997).

6. Conclusions

The interaction between mangrove and salt marsh is of interest to climate change research for several reasons. Having evolved in the tropics (Chapman, 1977; Specht, 1981) mangroves are most prolific in lower latitudes and decrease in diversity and vigor toward the poles (Lot et al., 1975; Saenger and Snedaker, 1993). In contrast, salt marshes increase in floristic diversity with increasing latitude within the temperate zone (Adam, 1990), and in the absence of mangroves form the characteristic intertidal vegetation in these latitudes. In the predominantly temperate latitudes where the two community types coexist, salt marsh distribution is confined in part by the presence of mangrove and in part by the extreme environmental conditions of the upper intertidal zone.

Environmental variability can therefore profoundly influence the competitive interactions between mangrove and salt marsh. In southern United States, where the proliferation of mangrove is periodically checked by frost, higher temperature and decreased freeze frequency and severity could enhance the survival and growth of species such as *A. germinans*. Wider and more continuous stands of this species may be expected in the northern Gulf of Mexico and the Atlantic coast of Florida. Less cold-tolerant species, such as *R. mangle*, may be able to shift northward along the coasts of Baja, California, Texas, and Florida.

In SE Australia and New Zealand, the growth of the mangrove *A. marina* will be aided not only by increased temperatures toward its southern limit of distribution, but also by higher sea levels. Presently, the upslope limit of *A. marina* is defined by the mean high water mark. While there is continued debate over the causes of mangrove encroachment into the salt marsh of eastern Australia, there is growing evidence for a role of relative sea-level rise, evidenced by the relationship between the rate of encroachment and relative sea-level trends, and an increase rate of

Author's personal copy

relative sea-level rise in temperate Australasian salt marshes over the past century. The subtle elevation gradients defining the position of mangrove and salt marsh in these situations provide an early indication of the effects of sea-level rise in the coastal wetlands of the region. The concern in these situations is that the landward transition of salt marsh may be impeded by topographic constraints, both cultural and natural. Where feasible, thought should be given to the designation of landward "accommodation space" in anticipation of projected rates of sea-level rise, so that the full range of wetland vegetation communities can continue to coexist in these estuaries.

REFERENCES

Adam, P., 1990. Saltmarsh Ecology. Cambridge University Press, Cambridge.

Ahmad, W., Hill, G.J.E., 1995. Land cover classification of the Mary River floodplain with emphasis on the effect of saltwater intrusion. In: Davenport, C.C., Riley, S.J., Ringrose, S.M. (Eds.), Proceedings of the Second North Australian Remote Sensing and GIS Forum. Australian Government Publishing Service, Canberra, pp. 76–83.

Baker, R.G.V., Haworth, R.J., 1997. Further evidence from relic shellcrust sequences for a late Holocene higher sea level for eastern Australia. Mar. Geol. 141, 1–9.

Baker, R.G.V., Haworth, R.J., 2000. Smooth or oscillating late Holocene sea-level curve? Evidence from the palaeo-zoology of fixed biological indicators in east Australia and beyond. Mar. Geol. 163, 367–386.

Ball, M.C., 1980. Patterns of secondary succession in a mangrove forest of southern Florida. Oecologia 44(2), 226–235.

Ball, M.C., 1988a. Ecophysiology of mangroves. Trees 2, 129–142.

Ball, M.C., 1988b. Salinity tolerance in the mangroves, *Aegiceras corniculatum* and *Avicennia marina*, I. Water use in relation to growth, carbon partitioning and salt balance. Aust. J. Plant Physiol. 15, 447–464.

Ball, M.C., 1998. Mangrove species richness in relation to salinity and waterlogging: a case study along the Adelaide River Floodplain, northern Australia. Global Ecol. Biogeogr. Lett. 7, 73–82.

Ball, M.C., 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. Trees Struct. Funct. 16, 126–139.

Ball, M.C., Pidsley, S.M., 1995. Growth responses to salinity in relation to distribution of two mangrove species, *Sonnertia alba* and *S. lanceolata*, in northern Australia. Funct. Ecol. 9, 77–85.

Bell, D., Menges, C.H., Bartolo, R.E., 2001. Assessing the extent of saltwater intrusion in a tropical coastal environment using radar and optical remote sensing. Geocarto Int. 16, 1–8.

Blasco, F., Saenger, P., Janodet, E., 1996. Mangroves as indicators of coastal change. Catena 149, 1–12.

Boto, K.G., 1983. Nutrient status and other soil factors affecting mangrove productivity in northeast Australia. Wetlands 3, 45–49.

Boto, K.G., Wellington, J.T., 1983. Phosphorus and nitrogen nutritional status of a northern Australian mangrove forest. Mar. Ecol. Prog. Ser. 11, 63–69.

Bucher, D., Saenger, P., 1991. An inventory of Australian estuaries and enclosed marine waters: an overview of results. Aust. Geogr. Stud. 29, 370–381.

Bunt, J.S., Williams, W.T., Duke, N.C., 1982. Mangrove distribution in northeast Australia. J. Biogeogr. 9, 111–120.

Burns, B.R., Ogden, J., 1985. The demography of the temperate mangrove (*Avicennia marina* (Forsk.) Vierh.) at its southern limit in New Zealand. Aust. J. Ecol. 10, 125–133.

Burton, T., 1982. Mangrove changes recorded north of Adelaide. Safic 6, 8–12.

Cahoon, D.R., Day Jr., J.W., Reed, D.J., 1999. The influence of surface and shallow subsurface soil processes in wetland elevation: a synthesis. Curr. Top. Wetl. Biogeogr. 3, 72–88.

Cahoon, D.R., Hensel, P.F., Spencer, T., Reed, D.J., McKee, K.L., Saintilan, N., 2006. Wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In:

Author's personal copy

Verhoeven, J.T.A., Beltman, B., Bobbink, R., Whigham, D.F. (Eds.), Wetland Conservation and Management. Springer-Verlag, Berlin Heidelberg, pp. 271–292.
Cahoon, D.R., Lynch, J.C., Hensel, P., Boumans, R., Perez, B.C., Segura, B., Day Jr., J.W., 2002. High-precision measurements of wetland sediment elevation: I. Recent improvements to the Sedimentation-Erosion Table. J. Sediment. Res. 72, 730–733.
Cameron, C.C., Palmer, C.A., 1995. The mangrove peat of the Tobacco Range Islands, Belize Barrier Reef, Central America. Atoll Res. Bull. 431, 1–32.
Chafer, C.J., 1998. A spatio-temporal analysis of estuarine vegetation change in the Minnamurra River 1938–1997. Unpublished report to the Minnamurra Estuary Management Committee, 47pp. plus appendices.
Chapman, V.J., 1977. Introduction. In: Chapman, V.J. (Ed.), Ecosystems of the World. 1. Wet Coastal Ecosystems. Elsevier Scientific Publications Company, Amsterdam, pp. 1–29.
Clarke, P.J., 1993. Dispersal of grey mangrove (*Avicennia marina*) propagules in south-eastern Australia. Aquat. Bot. 45, 195–204.
Clarke, P.J., Allaway, W., 1993. The regeneration niche of the grey mangrove *Avicennia marina* – effects of salinity, light and sediment factors on establishment, growth and survival in the field. Oecologia 93, 548–556.
Clarke, L.D., Hannon, N.J., 1971. The mangrove swamp and saltmarsh communities of the Sydney district. IV. The significance of species interaction. J. Ecol. 59, 535–553.
Clarke, P.J., Myerscough, P.J., 1991. Buoyancy of *Avicennia marina* propagules in South-eastern Australia. Aust. J. Bot. 39, 77–83.
Clarke, P.J., Myerscough, P.J., 1993. The intertidal distribution of the grey mangrove (*Avicennia marina*) in southeastern Australia: the effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. Aust. J. Ecol. 18, 307–315.
Clusener, M., Breckle, S.W., 1987. Reasons for the limitation of mangrove along the west-coast of northern Peru. Vegetatio 68, 173–177.
Cohen, A.D., Spackman, W., 1977. Phytogenic organic sediments and sedimentary environments in the everglades-mangrove complex. Part II. The origin, description and classification of the peats of southern Florida. Palaeontographica, Abt. B 162, 71–114.
Costa, C.S.B., Davy, A.J., 1992. Coastal salt marsh communities of Latin America. In: Seeliger, U. (Ed.), Coastal Plant Communities of Latin America. Academic Press, San Diego, pp. 179–199.
Craggs, R., Hofstra, D., Ellis, J., Schwarz, A., Swales, A., Nicholls, P., Hewitt, J., Ovenden, R., Pickmere, S., 2001. Physiological responses of mangroves and saltmarsh to sedimentation. NIWA Client Report to Auckland Regional Council, ARC01268/1, 78pp.
Davis, J.H.J., 1940. The ecology and geologic role of mangroves in Florida. Pap. Tortugas Lab. 32, 311–384.
Davy, A.J., Costa, C.S.B., 1992. Development and organization of saltmarsh communities. In: Seeliger, U. (Ed.), Coastal Plant Communities of Latin America. Academic Press, San Diego, pp. 179–199.
Digerfeldt, G., Hendry, M.D., 1987. An 8000 year Holocene sea-level record from Jamaica – implications for interpretation of Caribbean reef and coastal history. Coral Reefs 5, 165–169.
Diop, E.S., Soumare, A., Diallo, N., Guisse, A., 1997. Recent changes of the mangroves of the Saloum River Estuary, Senegal. Mangroves Salt Marshes 1, 163–172.
Downton, W.J.S., 1982. Growth and osmotic relations of the mangrove *Avicennia marina*, as influenced by salinity. Aust. J. Plant Physiol. 9, 519–528.
Duke, N.C., 1995. Genetic diversity, distributional barriers and rafting continents – more thoughts on the evolution of mangroves. Hydrobiologia 295, 167–181.
Duke, N.C., 2006. Australia's Mangroves. The Authoritative Guide to Australia's Mangrove Plants. University of Queensland, Brisbane, 200pp.
Duke, N.C., Ball, M.C., Ellison, J.C., 1998a. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecol. Biogeogr. Lett. 7, 27–47.
Duke, N.C., Benzie, J.A.H., Goodall, J.A., Ballment, E.R., 1998b. Genetic structure and evolution of species in the mangrove genus *Avicennia* (Avicenniaceae) in the Indo-West Pacific. Evolution 52, 1612–1626.
Egler, F.E., 1952. Southeast saline everglades vegetation, Florida, and its management. Vegetatio Acta Geobot. 3, 213–265.

Author's personal copy

Ellison, A.M., Farnsworth, E.J., 1993. Seedling survivorship, growth, and response to disturbance in Belizean mangal. Am. J. Bot. 80, 1137–1145.

Evans, M.J., Williams, R.J., 1997. Historical distribution of estuarine wetlands at Kurnell Peninsula, Botany Bay: the need and potential for rehabilitation. Wetlands (Australia) 18, 49–54.

Everitt, J.H., Judd, F.W., Escobar, D.E., Davis, M.R., 1996. Integration of remote sensing and spatial information technologies for mapping black mangrove on the Texas gulf coast. J. Coast. Res. 12, 64–69.

Feller, I.C., McKee, K.L., Whigham, D.F., O'Neill, J.P., 2003a. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62, 145–175.

Feller, I.C., Whigham, D.F., McKee, K.L., Lovelock, C.E., 2003b. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. Oecologia 134, 405–414.

Finlayson, C.M., Bailey, B.J., Freeland, W.J., Fleming, M.R., 1998. Wetlands of the Northern Territory. In: McComb, A.J., Lake, P.S. (Eds.), The Conservation of Australian Wetlands. Surrey Beatty and Sons, Sydney, pp. 103–126.

Gehrels, R., Hayward, B., Grenfell, H., Newnham, R., Hunter, J., Southall, K., Sabaa, A., 2007. Rapid sea-level rise in Australia and New Zealand during the past century. Abstract, XVII INQUA Congress, Cairns, Australia.

Haworth, R.J., 2002. Changes in mangrove/salt-marsh distribution in the Georges River estuary, southern Sydney, 1930–1970. Wetlands (Australia) 20, 80–103.

Hutchings, P., Saenger, P., 1987. Ecology of Mangroves. University of Queensland Press, St Lucia, Queensland.

Hyland, S.J., Butler, C.T., 1988. The distribution and modification of mangroves and saltmarsh-claypans in Southern Queensland. Queensland Department of Primary Industries, Brisbane, 74pp.

Islebe, G., Sanchez, O., 2002. History of Late Holocene vegetation at Quintana Roo, Caribbean coast of Mexico. Plant Ecol. 160, 187–192.

Jennings, J.N., 1975. Desert dunes and estuarine fill in the Fitzroy estuary, north-western Australia. Catena 2, 215–262.

Jolly, P., Chin, D., 1992. Rehabilitation of the Mary River floodplains: a review of MSS and TM imagery 1972–1992. In: Davenport, C.C., Riley, S.J., Ringrose, S.M. (Eds.), Proceedings of the GIS and Environmental Rehabilitation Workshop. Australian Government Publishing Service, Canberra, pp. 43–54.

Kangas, P.C., Lugo, A.E., 1990. The distribution of mangrove and saltmarsh in Florida. Trop. Ecol. 31, 32–39.

Knighton, A.D., Mills, K., Woodroffe, C.D., 1991. Tidal-creek extension and saltwater intrusion in Northern Australia. Geology 19, 831–834.

de, Lange, W.P., de, Lange, P.J., 1994. An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicennia marina* var. resinifera) in New Zealand. J. Coast. Res. 10, 539–548.

Lin, G.H., Sternberg, L.D.S.L., 1992. Effect of growth form, salinity, nutrients and sulfide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). Aust. J. Plant Physiol. 19, 509–517.

Lonard, R.I., Judd, F.W., 1985. Effects of a severe freeze on native woody-plants in The Lower Rio-Grande Valley, Texas. Southwest. Nat. 30, 397–403.

Long, S.P., Mason, C.F., 1983. Saltmarsh Ecology. Blackie and Son Ltd, Glasgow and London.

López-Hoffman, L., DeNoye, J.L., Monroe, I.E., Shaftel, R., Anten, N.P.R., Martínez-Ramos, M., David, D., Ackerly, D.D., 2006. Mangrove seedling net photosynthesis, growth, and survivorship are interactively affected by salinity and light. Biotropica 38, 606–616.

Lopez-Portillo, J., Ezcurra, E., 1989. Response of three mangroves to salinity in two geoforms. Funct. Ecol. 3, 355–361.

Lot, H.A., Vázquez-Yánes, C., Menéndez, F., 1975. Physiognomic and floristic changes near the northern limit of mangroves in the gulf coast of Mexico. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, vol. 1. University of Florida, Gainesville, pp. 52–61.

Lovelock, C.E., Feller, I.C., Ball, M.C., Engelbrecht, B.M.J., Ewel, M.L., 2006. Differences in plant function in phosphorus- and nitrogen-limited mangrove ecosystems. New Phytol. 172, 514–522.

Author's personal copy

Lovelock, C.E., Feller, I.C., McKee, K.L., Engelbrecht, B.M.J., Ball, M.C., 2004. Experimental evidence for nutrient limitation of growth, photosynthesis, and hydraulic conductance of dwarf mangroves in Panama. Funct. Ecol. 18, 25–33.

Macintyre, I.G., Little, M.M., Littler, D.S., 1995. Holocene history of Tobacco Range, Belize, Central America. Atoll Res. Bull. 430, 1–18.

Macintyre, I.G., Toscano, M.A., Lighty, R.G., Bond, G.B., 2004. Holocene history of the mangrove islands of Twin Cays, Belize, Central America. Atoll Res. Bull. 510, 1–16.

MacNae, W., 1966. Mangroves in eastern and southern Australia. Aust. J. Bot. 14, 67–104.

Manson, F.J., Loneragan, N.R., Phinn, S.R., 2003. Spatial and temporal variation in distribution of mangroves in Moreton Bay, subtropical Australia: a comparison of pattern metrics and change detection analyses based on aerial photographs. Estuar. Coast. Shelf Sci. 57, 653–666.

Markley, J.L., McMillan, C., Thompson Jr., G.A., 1982. Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans, Laguncularia racemosa*, and *Rhizophora mangle*, from the western tropical Atlantic and Pacific Panama. Can. J. Bot. 60, 2704–2715.

McKee, K.L., 1995a. Mangrove species distribution patterns and propagule predation in Belize: an exception to the dominance-predation hypothesis. Biotropica 27, 334–345.

McKee, K.L., 1995b. Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: Response to light and nutrient availability. Am. J. Bot. 82, 299–307.

McKee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on soil elevation change. Global Ecol. Biogeogr. 16, 545–556.

McKee, K.L., Faulkner, P.L., 2000. Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize. Atoll Res. Bull. 468, 46–58.

McKee, K.L., Feller, I.C., Popp, M., Wanek, W., 2002. Mangrove isotopic ($\delta^{15}N$ and $\delta^{13}C$) fractionation across a nitrogen vs. phosphorous limitation gradient. Ecology 83, 1065–1075.

McKee, K.L., Rooth, J.E., 2007. Mangrove recruitment after forest disturbance is facilitated by herbaceaous species in the Caribbean. Ecol. Appl. 17 (6), 1678–1693.

McKee, K.L., Rooth, J.E., 2008. Where temperate meets tropical: multi-factorial effects of elevated CO2, nitrogen enrichment, and competition on a mangrove-salt marsh community. Global Chang. Biol. 14, 971–984.

McKee, K.L., Mendelssohn, I.A., Materne, M.D., 2004. Acute salt marsh dieback in the Mississippi River deltaic plain: a drought-induced phenomenon? Global Ecol. Biogeogr. 13, 65–73.

McLoughlin, L., 2000. Estuarine wetlands distribution along the Parramatta River, Sydney, 1788–1940: implications for planning and conservation. Cunninghamia 6, 579–610.

McMillan, C., 1975. Adaptive differentiation to chilling in mangrove populations. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, vol. 1. University of Florida, Gainesville, pp. 62–68.

McMillan, C., Sherrod, C.L., 1986. The chilling tolerance of black mangrove, Avicennia germinans, from the Gulf of Mexico Coast of Texas, Louisiana and Florida. Contrib. Mar. Sci. 29, 9–16.

McTainsh, G., Iles, B., Saffinga, P., 1986. Spatial and temporal patterns of mangroves at Oyster Point Bay, South East Queensland, 1944–1983. Proc. R. Soc. Qld. 99, 83–91.

Meehan, A., 1997. Historical Changes in Seagrass, Mangrove and Saltmarsh Communities in Merimbula Lake and Pambula Lake. Honours Thesis, University of Wollongong.

Mendelssohn, I.A., McKee, K.L., 2000. Salt marshes and mangroves. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation. Cambridge University Press, Cambridge, pp. 501–536.

Mildenhall, D.C., Brown, L.J., 1987. An early Holocene occurrence of the mangrove *Avicennia marina* in Poverty Bay, North Island, New Zealand: its climatic and geological implications. N. Z. J. Bot. 25, 281–294.

Mitchell, M.L., Adam, P., 1989a. The relationship between mangrove and saltmarsh communities in the Sydney region. Wetlands (Australia) 8, 37–46.

Mitchell, M.L., Adam, P., 1989b. The decline of saltmarsh in Botany Bay. Wetlands (Australia) 8, 55–60.

Mitsch, W.J., Gosselink, J.G., 2000. Wetlands, third ed. John Wiley and Sons, New York.

Author's personal copy

Montague, C.L., Odum, H.T., 1997. The intertidal marshes of Florida's Gulf Coast. In: Coultas, C.L., Hsieh, Y. (Eds.), Ecology and Management of Tidal Marshes: A Model from the Gulf of Mexico. St Lucie Press, Delroy Beach, Florida, USA, pp. 1–9.

Montague, C.L., Wiegert, R.G., 1990. Salt marshes. In: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida, Orlando, pp. 481–516.

Morrisey, D.J., Skilleter, G.A., Ellis, J.I., Burns, B.R., Kemp, C.E., Burt, K., 2003. Differences in benthic fauna and sediment among mangrove (*Avicennia marina* var. *australasica*) stands of different ages in New Zealand. Estuar. Coast. Shelf Sci. 56, 581–592.

Morton, R.M., 1994. Fluctuations in wetland extent in southern Moreton Bay. In: Greenwood, J.G., Hall, N.J. (Eds.), Future Marine Science in Moreton Bay. School of Marine Science, University of Queensland: Brisbane, pp. 145–150.

Mulrennan, M.E., Woodroffe, C.D., 1998. Saltwater intrusion into the coastal plains of the Lower Mary River, Northern Territory, Australia. J. Environ. Manage. 54, 169–188.

Naidoo, G., 1987. Effects of salinity and nitrogen on growth and water relations in the mangrove *Avicennia marina* (Forsk.) Vierh. New Phytol. 107, 317–325.

NOAA, 2007. Sea Surface Temperature (SST) contour charts. Prepared by National Oceanic and Atmospheric Administration (NOAA) Satellites and Information. http://www.osdpd.noaa.gov/PSB/EPS/SST/contour.html. Accessed date. 12 December 2007.

Norman, H., McMillan, C., Thompson, G.A., 1984. Phosphatidylglycerol molecular species in chilling-sensitive and chilling-resistant populations of *Avicennia germinans* (L.) L. Plant Cell Physiol. 25, 1437–1444.

Olmsted, I., Dunevitz, H., Platt, W.J., 1993. Effects of freezes on tropical trees in Everglades National Park Florida, USA. Trop. Ecol. 34, 17–34.

Park, S., 2001. Bay of Plenty maritime wetlands database. Environment of the Bay of Plenty. Environment Bay of Plenty Regional Council, Whakatane, New Zealand, Environmental Report 2000/21.

Patterson, C.S., Mendelssohn, I.A., 1991. A comparison of physicochemical variables across plant zones in a mangal/salt marsh community in Louisiana. Wetlands 11, 139–161.

Patterson, S., McKee, K.L., Mendelssohn, I.A., 1997. Effects of tidal inundation and predation on Avicennia germinans seedling establishment and survival in a sub-tropical mangal/salt marsh community. Mangroves Salt Marshes 1, 103–111.

Patterson, C.S., Mendelssohn, I.A., Swenson, E.M., 1993. Growth and survival of Avicennia germinans seedlings in a mangal/salt marsh community in Louisiana, U.S.A. J. Coast. Res. 9, 801–810.

Peinado, M., Alcaraz, F., Delgadillo, J., De La Cruz, M., Alvarez, J., Aguirre, L.J., 1994. The coastal salt marshes of California and Baja California. Plant Ecol. 110, 55–66.

Pidgeon, I.M., 1940. The ecology of the central coast area of New South Wales III. Types of Primary Succession. Proc. Linnaean Soc. NSW 65, 221–249.

Rabinowitz, D., 1975. Planting experiments in mangrove swamps of Panama. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, vol. 1. University of Florida, Gainesville, pp. 385–393.

Rabinowitz, D., 1978a. Dispersal properties of mangrove propagules. Biotropica 10, 47–57.

Rabinowitz, D., 1978b. Mortality and initial propagule size in seedlings in Panama. J. Ecol. 66, 45–51.

Rabinowitz, D., 1978c. Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationships of dispersal and zonation. J. Biogeogr. 5, 113–133.

Ramcharan, E.K., 2004. Mid-to-late Holocene sea level influence on coastal wetland development in Trinidad. Quat. Int. 120, 145–151.

Reimold, R.J., 1977. Mangals and salt marshes of eastern United States. In: Chapman, V.J. (Ed.), Ecosystems of the World. 1. Wet Coastal Ecosystems. Elsevier Scientific Publications Company, Amsterdam, pp. 157–166.

Rogers, K., 2004. Mangrove and saltmarsh surface elevation dynamics in relation to environmental variables in Southeastern Australia. A Thesis submitted in fulfillment of the requirements of the degree of Doctor of Philosophy from University of Wollongong, 270pp.

Rogers, K., Saintilan, N., 2008. Relationships between surface elevation and groundwater in mangrove forests of SE Australia. J. Coast. Res. 24, 63–69.

Author's personal copy

Rogers, K., Saintilan, N., Cahoon, D.R., 2005a. Surface elevation dynamics in a regenerating mangrove forest, Homebush Bay, Australia. Wetl. Ecol. Manage. 13, 587–598.

Rogers, K., Saintilan, N., Heijnis, H., 2005b. Monitoring of mangrove and saltmarsh resources in Westernport Bay, Australia. Estuaries 28, 551–559.

Rogers, K., Saintilan, N., Wilton, K., 2006. Vegetation change and surface elevation dynamics of the estuarine wetlands of southeast Australia. Estuar. Coast. Shelf Sci. 66, 559–569.

Roy, P.S., 1984. New South Wales estuaries – their origin and evolution. In: Thom, B.G. (Ed.), Development in Coastal Geomorphology in Australia. Academic Press, San Diego, CA, pp. 99–121.

Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of south-east Australian estuaries. Estuar. Coast. Shelf Sci. 53, 351–384.

Saenger, P., 1982. Morphological, anatomical and reproductive adaptations of Australian mangroves. In: Clough, B.F. (Ed.), Mangrove ecosystems in Australia. Australian Institute of Marine Science. Australian National University Press, Canberra, Australia, pp. 152–191.

Saenger, P., 2002. Mangrove Ecology, Silviculture and Conservation. Kluwer Academic Press, Dordrecht, Boston, London.

Saenger, P., Moverley, J., 1985. Vegetative phenology of mangroves along the Queensland coastline. Proc. Ecol. Soc. Aust. 13, 257–265.

Saenger, P., Snedaker, S.C., 1993. Pantropical trends in mangrove aboveground biomass and annual litterfall. Oecologia 96, 293–299.

Saenger, P., Specht, M.M., Specht, R.L., Chapman, V.J., 1977. Mangal and coastal saltmarsh communities in Australasia. In: Chapman, V.J. (Ed.), Ecosystems of the World I: Wet Coastal Ecosystems. Elsevier, Amsterdam, pp. 293–345.

Saintilan, N., 1997. Mangroves as successional stages on the Hawkesbury River Estuary, New South Wales. Wetlands (Australia) 16, 99–107.

Saintilan, N., 1998. Photogrammetric survey of the Tweed River wetlands. Wetlands (Australia) 17, 74–82.

Saintilan, N., 2003. The influence of nutrient enrichment upon mangrove seedling establishment and growth in the Hawkesbury River Estuary, New South Wales, Australia. Wetlands (Australia) 21, 29–35.

Saintilan, N., Hashimoto, R., 1999. Mangrove-saltmarsh dynamics on a prograding bayhead delta in the Hawkesbury River estuary, New South Wales, Australia. Hydrobiologia 413, 95–102.

Saintilan, N., Williams, R.J., 1999. Mangrove transgression into saltmarsh environments in south-east Australia. Global Ecol. Biogeogr. Lett. 8, 117–124.

Saintilan, N., Williams, R.J., 2000. The decline of saltmarshes in Southeast Australia: Results of recent surveys. Wetlands (Australia) 18, 49–54.

Saintilan, N., Wilton, K., 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetl. Ecol. Manage. 9, 409–420.

Santos, M.C.F.V., Zieman, J.C., Cohen, R.R.H., 1997. Interpreting the upper mi-littoral zonation patterns of mangroves in Maranhão (Brazil) in response to microtopography and hydrology. In: Kjerfve, B., Lacerda, L.D., Diop, E.H.S. (Eds.), Mangrove Ecosystem Studies in Latin America and Africa. UNESCO, Paris, pp. 127–144.

Schaeffer-Novelli, Y., Cintron-Molero, G., Adaime, R.R., de Camargo, T.M., 1990. Variability of mangrove ecosystems along the Brazilian Coast. Estuaries 13, 204–216.

Schmidt, D.A., Burgman, R., 2003. Time-dependent uplift and subsidence in the Santa Clara Valley, California, from a large interferometric synthetic aperture radar data set. J. Geophys. Res. Solid Earth 108, 2416.

Semeniuk, V., 1980. Mangrove zonation along an eroding coastline in King Sound, North-Western Australia. J. Ecol. 68, 789–812.

Semeniuk, V., 1982. Geomorphology and Holocene history of the tidal flats, King Sound, north-western Australia. J. R. Soc. West. Aust. 65, 47–68.

Sherrod, C.L., McMillan, C., 1985. The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. Contrib. Mar. Sci. 28, 129–140.

Author's personal copy

Sherrod, C.L., Hockaday, D.L., McMillan, C., 1986. Survival of the red mangrove *Rhizophora mangle* on the Gulf of Mexico Coast of Texas. Contributions in Marine Science 29, 27–36.
Silvestri, S., Defina, A., Marani, M., 2005. Tidal regime, salinity and salt marsh plant zonation. Estuar. Coast. Shelf Sci. 62, 119–130.
Smith, T.J., 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68, 266–273.
Smith, T.J., Chan, H.T., McIvor, C.C., Robblee, M.B., 1989. Comparisons of seed predation in tropical, tidal forests from three continents. Ecology 70, 146–151.
Smith, T.J., Duke, N.C., 1987. Physical determinants of inter-estuary variation in mangrove species richness around the tropical coastline of Australia. J. Biogeogr. 14, 9–20.
Snedaker, S.C., 1982. Mangrove species zonation: why? In: Sen, D.N., Rajpurohit, K.S. (Eds.), Contribution to the Ecology of Halophytes, vol. 2. Dr. W. Junk, The Hague, pp. 111–125.
Snedaker, S.C., 1995. Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. Hydrobiologia 295, 43–49.
Solomon, S., Quin, D., Manning, M., Marquis, M., Avery, K., Tignor, M., Miller, H., Chen, Z. (Eds.), 2007. Climate Change 2007 – The Physical Science Basis. Contribution of Working Group 1 to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge.
Sousa, W.P., Mitchell, B.J., 1999. The effect of seed predators on plant distributions: is there a general pattern in mangroves? Oikos 86, 55–66.
Spackman, W., Dolsen, C.P., Riegel, W., 1966. Phytogenic organic sediments and sedimentary environments in the Everglades-Mangrove complex. Part 1: Evidence of a transgressing sea and its effects on environments of the Shark River areas of Southwestern Florida. Palaeontographica 117, 135–152.
Spalding, M.D., Blasco, F., Field, C.D. (Eds.), 1997. World Mangrove Atlas. International Society for Mangrove Ecosystems, Okinawa.
Specht, R.L., 1981. Biogeography of halophytic angiosperms (salt-marsh, mangrove and sea-grass). In: Keast, A. (Ed.), Ecological biogeography of Australia. The Hague, Dr. W. Junk Publishers, pp. 575–589.
Stevens, P.W., Fox, S.L., Montague, C.L., 2006. The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. Wetl. Ecol. Manage. 14, 435–444.
Thom, B.G., 1967. Mangrove ecology and deltaic geomorphology: tabasco. Mexico.J. Ecol. 55, 301–343.
Thom, B.G., Wright, L.D., Coleman, J.M., 1975. Mangrove ecology and deltaic-estuarine geomorphology, Cambridge Gulf-Ord River, Western Australia. J. Ecol. 63, 203–222.
Thomas, M.L.H., 1993. Mangrove swamps in Bermuda. Atoll Res. Bull. 386, 1–18.
Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.
Toscano, M.A., Macintyre, I.G., 2003. Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated C-14 dates from *Acropora palmata* framework and intertidal mangrove peat. Coral Reefs 22, 257–270.
van Steenis, C.G.G.J., 1968. Frost in the tropics. In: Misra, R., Gopal, B. (Eds.), Recent Advances in Tropical Ecology, Part I. International Society for Tropical Ecology, Varanasi, pp. 154–167.
Vanderzee, M.P., 1988. Changes in saltmarsh vegetation as an early indicator of sea-level rise. In: Pearman, G.I. (Ed.), Greenhouse: Planning for Climate Change. CSIRO, Melbourne.
Walsh, G.E., 1974. Mangroves: a review. In: Reimhold, R.J., Queens, W.H. (Eds.), Ecology of Halophytes. Academic Press, New York, pp. 51–174.
Watson, E.B., 2004. Changing elevation, accretion, and tidal marsh plant assemblages in a South San Francisco Bay tidal marsh. Estuaries 27, 684–698.
West, R.C., 1977. Tidal salt-marsh and mangal formations of Middle and South America. In: Chapman, V.J. (Ed.), Ecosystems of the World. 1. Wet Coastal Ecosystems. Elsevier Scientific Publications Company, Amsterdam, pp. 193–213.
West, R.J., 1993. Estuarine fisheries resources of two South Eastern Australian Rivers. PhD Thesis, University of New South Wales, 173pp.
Whelan, K.R.T., Smith, T.J., Cahoon, D.R., Lynch, J.C., Anderson, G.H., 2005. Groundwater control of mangrove surface elevation: shrink and swell varies with soil depth. Estuaries 28, 833–843.

Author's personal copy

Williams, R.J., Meehan, A.J., 2004. Focusing management needs at the sub-catchment level via assessments of change in the cover of estuarine vegetation, Port Hacking, NSW, Australia. Wetl. Ecol. Manage. 12, 499–518.

Williams, R.J., Watford, F.A., 1997. Changes in the distribution of mangrove and saltmarsh in Berowra and Marramarra Creeks, 1941–1992. NSW Fisheries, Fisheries Research Institute, Cronulla, 21pp.

Williams, R.J., Watford, F.A., Balashov, V., 1999. Kooragang wetland rehabilitation project: changes in wetland fish habitats of the Lower Hunter River. NSW Fisheries, Office of Conservation, Fisheries Research Institute, Cronulla.

Wilson, B.P., 2005. Elevation of sulphurous layers in acid sulphate soils: what do they indicate about sea levels during the Holocene in eastern Australia? Catena 62, 45–56.

Winn, K.O., Saynor, M.J., Eliot, M.J., Eliot, I., 2006. Saltwater intrusion and morphologicvla change at the mouth of the East Alligator River, Northern Territory. J. Coast. Res. 22, 137–149.

Winning, G., 1990. Lake Macquarie littoral habitats study. The Wetlands Centre, Shortland, 29pp. plus appendices.

Woodroffe, C.D., 1981. Mangrove swamp stratigraphy and holocene transgression, Grand Cayman Island, West Indies. Mar. Geol. 41, 271–294.

Woodroffe, C.D., 1983. Development of Mangrove forests from a geological perspective. In: Teas, H.J. (Ed.), Tasks for Vegetation Science. Dr. W. Junk Publishers, The Hague, pp. 1–17.

Woodroffe, C.D., Chappell, J., Thom, B.G., Wallensky, E., 1989. Depositional model of a macrotidal estuary and floodplain, South Alligator River, Northern Australia. Sedimentology 36, 737–756.

Woodroffe, C.D., Mulrennan, M.E., 1993. Geomorphology of the Lower Mary River Plains, Northern Territory. Australian National University and the Conservation Commission of the Northern Territory, Darwin.

Woodroffe, C.D., Thom, B.G., Chappell, J., 1985. Development of widespread mangrove swamps in mid-Holocene times in northern Australia. Nature 317, 711–713.

Zomlefer, W.B., Judd, W.S., Giannasi, D.E., 2006. Northernmost limit of *Rhizophora mangle* (red mangrove; Rhizophoraceae) in St. Johns County, Florida. Castanea 71, 239–244.

Copyrighted Materials
Copyright © 2019 Elsevier Retrieved from app.knovel.com

PART VII

COASTAL WETLAND SUSTAINABILITY

CHAPTER

26

The Shifting Saltmarsh-Mangrove Ecotone in Australasia and the Americas

Neil Saintilan[1], *Kerrylee Rogers*[2], *Karen L. McKee*[3]

[1]Department of Environmental Sciences, Macquarie University, Sydney, NSW, Australia; [2]Geoquest, University of Wollongong, Wollongong, NSW, Australia; [3]U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA, United States

1. INTRODUCTION

Intertidal coastal wetlands, principally mangrove and saltmarsh, are among the most valuable natural ecological systems in the world (Costanza et al., 2014) providing ecological goods and services ranging from biological habitat, coastal productivity, and protection to carbon sequestration and storage (Lee et al., 2014), However, because of their position at the land–ocean interface, they are sensitive to the impacts of climate change, particularly in the many places in the world where mangroves and saltmarsh coexist and competitively interact. These interactions can be studied over a range of timescales and inform our understanding of the impacts of climate change and other anthropogenic stressors on these critically important natural systems. Stratigraphic and palynological evidence has been used to reconstruct distribution of mangrove and saltmarsh communities over geological timescales with the greatest clarity emerging from the Holocene. At this scale, interactions between mangroves and saltmarshes are governed by geomorphic processes, most notably, patterns of sedimentation following the postglacial marine high stand.

More recently, over the historical time period, archival air photographs and other remotely sensed images have been used to study changes in distribution of these communities over wide geographic areas. The decline in the area of tropical mangrove over recent decades has been well-documented (Pendleton et al., 2012; Friess and Webb, 2014), and though the rate of decline has slowed in recent years, clearance for aquaculture and palm oil agriculture continues in many parts of the world (Murdiyarso et al., 2015). At their poleward limits, the

Coastal Wetlands
https://doi.org/10.1016/B978-0-444-63893-9.00026-5

Copyright © 2019 Elsevier B.V. All rights reserved.
Donald R. Cahoon's contribution to the work is the work of a US Govt. employee and is in public domain.

trend is one of mangrove expansions, particularly where mangroves hitherto have been delimited by cold temperatures (Cavanaugh et al., 2014a). Mangrove expansion at the expense of saltmarsh has been documented in the continental USA, Central America, South America, Australia, South Africa, and China (Saintilan et al., 2014).

Mangroves compete with saltmarshes at the limits of their physiological tolerance. At their latitudinal extreme, the vigor of mangrove growth is constrained by cold, and survival may be dictated by frost. The landward limit of mangroves in the intertidal zone is constrained by the often severe environment of the upper intertidal zone, where low soil moisture and high salinity may prohibit seedling establishment and growth. Changes to environmental conditions at these extremes, including elevated temperatures, decreased frost frequency, elevated atmospheric CO_2, and higher sea levels, have the potential to alter conditions such that the growth of mangrove is favored over saltmarsh (McKee et al., 2012). The encroachment of mangrove into saltmarsh has many parallels in the encroachment of woody vegetation into grasslands in many of the world's biomes (Saintilan and Rogers, 2013).

This chapter reviews a range of environmental variables that govern mangrove and saltmarsh interactions: geomorphic, hydrologic, climatic, physicochemical, and biotic. An emerging theme is the potential importance of climate change as a key control on vegetation shifts and changes in species diversity. For example, higher temperatures may confer a competitive advantage on mangroves, which are tropical plants. Saltmarshes, which predominate at temperate and subarctic latitudes, may increase in diversity with increasing latitude (Saenger et al., 1977). Furthermore, higher sea levels could promote the landward encroachment of mangrove into saltmarsh, as could elevated levels of atmospheric CO_2 (McKee et al., 2012; Saintilan and Rogers, 2015). The changing distribution of mangrove and saltmarsh may serve as an important indicator of climate change impacts, a sentinel of change for the broad range of ecosystem services dependent on these habitats.

2. DISTRIBUTION/GEOMORPHIC SETTINGS—WHERE DO MANGROVE AND SALTMARSH COEXIST?

2.1 Mangrove Distribution

Mangroves are the typical intertidal vegetation of sheltered tropical and subtropical coastlines. However, some mangrove species will readily occupy sheltered temperate coastlines (Saenger, 2002). The global distribution of mangroves has been examined on numerous occasions (Chapman, 1977; Spalding et al., 1997a; Duke et al., 1998a; Duke, 2006; Giri et al., 2011; Fig. 26.1) and is primarily limited by the physiological tolerance of mangrove species to low temperature. Other factors, such as the availability of suitable habitat and climate, dispersal and establishment of propagules, continental drift and tectonic events, are also important (Duke et al., 1998a). Mangroves tend to be restricted to coastlines where mean air temperatures of the coldest month are higher than 20°C and the seasonal range is not greater than 10°C (Walsh, 1974; Chapman, 1977, from Duke et al., 1998a), which appears to correlate with the 20°C isotherm for seawater (Duke et al., 1998a).

In the Americas, distribution of mangroves roughly corresponds to the sea surface winter isotherm of 20°C, except for the North Atlantic coast where the northern limit corresponds to

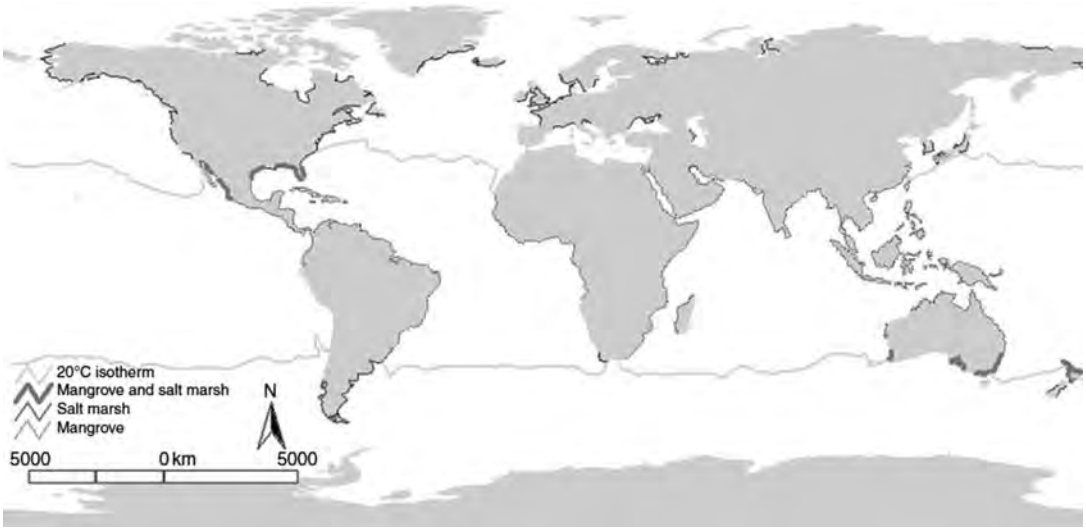


FIGURE 26.1 Global mangrove and saltmarsh distribution and the average 20°C sea surface temperature isotherm. *From Spalding, M.D., Blasco, F., Field, C.D. (Eds), 1997b. World Mangrove Atlas. International Society for Mangrove Ecosystems. Okinawa, Japan; Long, S.P., Mason, C.F., 1983. Saltmarsh Ecology. Blackie and Son Ltd., Glasgow and London; NOAA, 2007. Sea Surface Temperature (SST) Contour Charts. Prepared by National Oceanic and Atmospheric Administration (NOAA) Satellites and Information. Accessed at: http://www.osdpd.noaa.gov/PSB/EPS/SST/contour.html.*

the 27°C isotherm (i.e., the isotherm of the annual average for monthly maximal sea temperature where areas poleward are always cooler) (see Davy and Costa, 1992). The cold Humboldt and Falkland currents influence sea temperatures along the western and eastern coasts of South America so that the winter 20°C isotherm occurs at different latitudes (Fig. 26.1). Similarly, the distribution of mangroves on the west coast of Africa is more restricted than on the east coast because of the different latitudinal positions of the 20°C isotherm (Fig. 26.1). The reduced occurrence of mangroves on the western coasts of Africa and South America also coincides with the limits of arid regions (Saenger, 2002) and implies that the development of mangroves in these regions is limited by aridity in addition to temperature (Saenger and Moverley, 1985; Smith and Duke, 1987).

However, latitude and its relationship with low temperatures and/or the occurrence of frosts are the primary explanation for the latitudinal distribution of mangroves in the Americas (Sherrod and McMillan, 1985; McMillan and Sherrod, 1986). Mangroves thus extend from about 31°0′N (Baja California; Peinado et al., 1994) to 5°30′S (Peru (Clusener and Breckle, 1987)) on the Pacific coast and from 30°N (St. Augustine, Florida, USA) to 28°30′S (Laguna, Brazil (Schaeffer-Novelli et al., 1990)) on the Atlantic coast. The northernmost mangroves in this region occur in Bermuda (32°18′N), off the east coast of the United States, because of the warm waters of the Gulf Stream and absence of freezing temperatures; species found there include *Rhizophora mangle*, *Avicennia germinans*, and *Conocarpus erectus* (Thomas, 1993). In contrast, mangroves historically extended only to Ponce de Leon Inlet (29°04′N) on the Atlantic coast of Florida and the Mississippi River delta in the Gulf of Mexico (29°12′N) where they are periodically killed by freezing temperatures. Recent reports indicate northernmost individuals of *R. mangle* have extended from 29°40′N (Fort Matanzas, Florida, USA)

(Zomlefer et al., 2006) to 30°01′N, near the northernmost *A. germinans* at 30°02′N (St. Augustine, Florida, USA) (Williams et al., 2014).

Exceptions to the distribution pattern of mangrove in waters cooler than 20°C also occur around Australia and the North Island of New Zealand. In these locations, the species of mangrove with the greatest latitudinal extent is *Avicennia marina*, with its distribution extending to Corner Inlet (38°54′S) in southeastern (SE) Australia. Explanations for the more southerly distribution of *Avicennia marina* in Australia include transmission by ocean currents or that they are relict populations that had greater poleward distributions in the past (MacNae, 1966; Duke et al., 1998a). The latter explanation is more widely accepted, particularly because *Avicennia marina* var. *australasica* is genetically distinct from more tropical varieties, such as var. *marina* and var. *eucalyptifolia* (Duke et al., 1998a,b). Survival at this latitudinal extreme might be explained by the lower incidence of the heavy frosts that cause mass mortality in populations of *A. germinans* and *R. mangle* in the United States. *A. marina* and *Aegiceras corniculatum*, the next most poleward species in Australia, have smaller vessel diameters than *A. germinans* and *R. mangle*, with a consequent higher tolerance of the mild freezing more commonly encountered in southern Australia (Stuart et al., 2007).

Avicennia marina var. *australasica* is the only mangrove species found in New Zealand and is restricted to the North Island with a latitudinal limit at Kutarere (38°03′S) (Lange and de Lange, 1994). Like its Australian counterpart, its southern distribution does not appear to relate to climatic factors (Lange and de Lange, 1994) and may be a relict of greater poleward distributions (Mildenhall and Brown, 1987; Saenger, 2002). Because of the successful establishment of *Avicennia marina* in more southerly locations, the latitudinal distribution of mangroves in New Zealand is hypothesized to be in disequilibrium with climatic factors. Furthermore, low current velocities and large distances between suitable habitats inhibit the distribution of mangrove to the same extent observed in Australia (Lange and de Lange, 1994).

2.2 Saltmarsh Distribution

In contrast, saltmarsh may occur on many of the world's shorelines (Adam 1990; Mendelssohn and McKee, 2000). Information about the global distribution of saltmarsh species is poor and extensive detailed mapping of saltmarsh has not been undertaken for some time (Chapman, 1977; Long and Mason, 1983). At a global scale, saltmarsh establishes on shorelines where mangrove establishment is precluded or development is limited (Kangas and Lugo, 1990). For this reason, saltmarshes are most common in temperate, subarctic, and arctic zones (Long and Mason, 1983; Mitsch and Gosselink, 2000; Mendelssohn and McKee, 2000).

In North America, saltmarshes occur from the southern boundary of Central America to Alaska and Canada, with greatest development in the temperate United States (Mendelssohn and McKee, 2000). The northernmost limits of saltmarsh on that continent occur along the Arctic Ocean at 70°N latitude and extend southward along the Pacific shoreline of Alaska, Canada, the continental United States, Mexico, and Central America. Saltmarsh also occurs along the shoreline of Hudson Bay (55°N) and the Atlantic coasts of Canada and the United States, extending along the Gulf of Mexico into Central America where the distribution overlaps with that of mangrove vegetation. Saltmarsh species can be found in Belize

(16–17°N), Guyana (6–8°N), Peru/Ecuador (0–5°S), Brazil (0–32°S), Argentina (34–51°S), and Chile (40–52°S) (Table 12.2 in Costa and Davy, 1992).

Saltmarsh vegetation can be classed into six biogeographical types: arctic, boreal, temperate, west Atlantic, dry coast, and tropical types (Adam, 1990). A description of saltmarsh vegetation in North America using this classification can be found in Mendelssohn and McKee (2000). Saltmarshes in the Arctic and subarctic regions are dominated by species such as *Puccinellia phryganoides* and *Carex* spp. Boreal saltmarsh along the Atlantic coast is characterized by *Spartina patens*, *Spartina alterniflora* in the low marsh, whereas boreal saltmarsh in the Pacific oceanic region, including British Columbia, contain *Triglochin maritima*, *Salicornia virginica*, and *Distichlis spicata*. Temperate saltmarsh on the Atlantic coast is dominated by *S. alterniflora*, which extends southward into northern Florida. Other temperate species along the Atlantic coast include *Juncus balticus* (boreal), *Juncus gerardii* (boreal to temperate), and *Juncus roemerianus* (temperate), which also occurs along the Gulf of Mexico. Temperate saltmarsh on the Pacific coast contains *Spartina foliosa*, *Salicornia virginica*, and *D. spicata*. In tropical zones, species such as *S. patens*, *Spartina spartinae*, and *D. spicata* can occur but may be replaced in hypersaline settings by succulents such as *Batis maritima*, *Borrichia frutescens*, *Suaeda maritima*, and *Sesuvium portulacastrum*.

2.3 Coexisting Mangrove and Saltmarsh

Saltmarsh typically occurs in settings where mangrove development is limited (Kangas and Lugo, 1990; West, 1977), enabling saltmarsh to establish. Extensive coexisting mangrove and saltmarsh communities can be found in the temperate regions of Australia, New Zealand, South Africa, and southern continental USA. Saltmarsh may also establish behind mangrove communities within tropical and subtropical climates where rainfall is low and soil salinities in these areas become hypersaline (Chapman, 1977; Long and Mason, 1983). In Mexico, Central America, and Florida, for example, saltmarsh may occur on the margins of mangrove forests (either colonizing seaward mudflats or the saline soils on landward edges), within mangrove woodlands with more open canopies, or in disturbed areas (West, 1977; Lopez-Portillo and Ezcurra, 1989).

A distinction must be made between saltmarsh vegetation typical of the low intertidal zone and that restricted to the "high marsh," i.e., areas in the upper intertidal range that are characterized by dryer and more saline conditions. More specifically, it is necessary to identify saltmarsh and mangrove physiographic equivalents when considering interactions between coexisting mangrove and saltmarsh vegetation and future changes in climate and sea level. For example, in North America, extensive stands of the temperate low-marsh–dominant *S. alterniflora* can be found as far south as subtropical Florida, Louisiana, and Texas. Although *S. alterniflora* can be found throughout Latin America, its occurrence is infrequent and mainly limited to mangal fringes (Costa and Davy, 1992). Other saltmarsh species such as *S. spartinae*, *D. spicata*, *B. maritima*, *S. portulacastrum*, and *Sporobolus virginicus* may be more abundant at tropical latitudes (Costa and Davy, 1992), possibly because of their greater tolerance of arid conditions and desiccation. Species differences in tolerance of inundation, salinity, desiccation, and frost as well as ability to acquire resources under differing stresses will determine mangrove versus saltmarsh shifts in response to global drivers. The physiographic equivalent of *S. alterniflora* is *R. mangle*, but

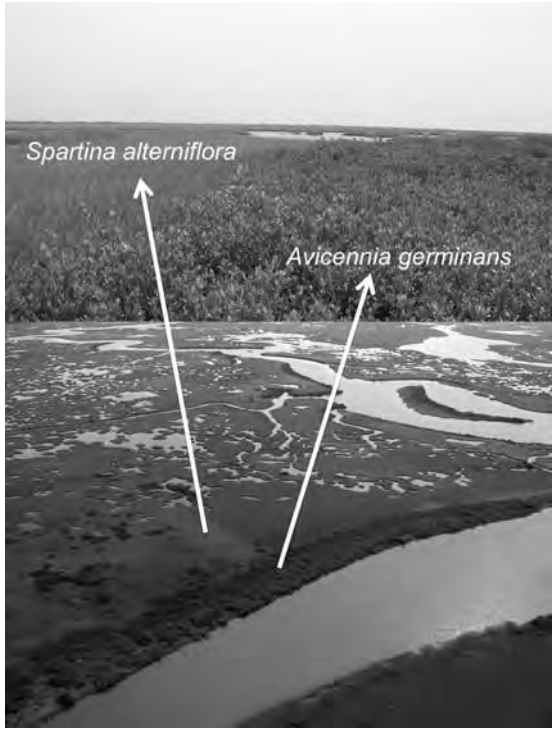


FIGURE 26.2 Ground (top) and aerial (bottom) views of a saltmarsh-mangrove community in coastal Louisiana, USA. Black mangrove (*Avicennia germinans*) occurs along creekbanks and intergrades with smooth cordgrass (*Spartina alterniflora*) in the marsh interior.

the latter cannot tolerate freezing temperatures and does not extend far into subtropical latitudes. Consequently, in the southern USA, *S. alterniflora* often intergrades with *A. germinans*, which is more cold tolerant (Fig. 26.2).

Coexisting mangrove and saltmarsh communities occur in a range of geomorphic settings. Along the coastline of New South Wales (NSW) in Australia, mangrove and saltmarsh are primarily located within drowned river valleys and barrier estuaries (Roy et al., 2001). Although some saltmarsh may be located within saline coastal lagoons, mangroves are generally excluded because mangrove propagule dispersal to these estuaries is restricted by the near permanent closure of the estuary mouth. Periodic extended flooding within coastal lagoons may also lead to the dieback of mangroves, yet allow the survival of saltmarsh (Mbense et al., 2016). Due to high wave energies along the southern Victorian coastline, mangrove and saltmarsh are almost exclusively distributed within three coastal embayments; Port Phillip Bay, Western Port Bay, and Corner Inlet. In New Zealand, mangroves are located within major embayments of the northern part of the North Island (Burns and Ogden, 1985) and may occur with species such as *Apodasmia similis* (jointed rush) (Fig 26.3).

Along the east coast of Florida, mangrove and saltmarsh coexist in low-energy environments such as the Indian River Lagoon (Reimold, 1977; Montague and Wiegert, 1990) and the Ponce de Leon inlet. Along the northern coastline of the Gulf of Mexico, mangrove and

FIGURE 26.3 Mangroves (*Avicennia marina*) invading a mudflat in New Zealand (Coromandel Penninsula). Marsh vegetation in foreground is *Apodasmia similis* (jointed wire rush).

saltmarsh may co-xist within the inactive deltaic environments of the Mississippi River and chenier coastal plains in Louisiana (Patterson and Mendelssohn, 1991), in embayments along the west coast of Florida from Tampa Bay to the Cedar Key (Kangas and Lugo, 1990; Stevens et al., 2006), and in lagoons along the southeast coast of Texas (Sherrod and McMillan, 1985; Everitt et al., 1996). In tropical Mexico, saltmarshes are often associated with mangroves in coastal lagoons or near river deltas with low sediment loads (Olmsted et al., 1993). Elsewhere in Latin America, saltmarsh may develop in settings that promote the development of hypersaline conditions and in disturbed mangrove areas (Costa and Davy, 1992).

The species composition of saltmarsh-mangrove communities in any geographic location may vary substantially because of differences in tide range, local topography, wave energy, and temperature regime. This variation is exemplified along the southern coast of the United States. On the east coast of Florida in the Indian River Lagoon complex, a typical shoreline might be dominated by *R. mangle* or *S. alterniflora* in front of a mid-marsh mixed community of *Salicornia* spp., *D. spicata*, *Borrichia frutescens*, *B. maritima*, and *A. germinans* (Montague and Wiegert, 1990). In south Florida, *S. alterniflora* might form a narrow fringe in front of a well-developed mangrove zone (*R. mangle*, *A. germinans*, *L. racemosa*) and a back-mangal zone dominated by *J. roemerianus* (Davis, 1940). On the west coast of Florida (north of Tampa Bay to the Cedar Key), *S. alterniflora* stands contain small stature, but abundant *A. germinans*. Similarly, the saltmarsh-mangrove communities in coastal Louisiana and south Texas consist of *S. alterniflora* and *A. germinans*. The mangrove *R. mangle* occurs farther south along the Texas coast because of its greater freeze sensitivity. Geographic variation in species co-occurrence and respective inherent environmental tolerances and competitive abilities will likely determine mangrove–saltmarsh interactions in any specific location.

3. LONG-TERM DYNAMICS

3.1 Tropical Northern Australia

Tropical northern Australia is drained by several macrotidal rivers, each receiving seasonal floods in relation to the monsoons (Woodroffe et al., 1989). Mangroves are confined to active depositional environments, including channel banks, the edges of mid-channel islands, and prograding coastlines (Woodroffe et al., 1985). The wide upper intertidal and supratidal flats are bare in lower rainfall areas or covered in grasses, sedges, and, in wetter areas, Melaleuca forest (Woodroffe et al., 1989). These wide estuarine flats are known as black soil plains.

Beneath the black soil plains lay extensive mangrove peat deposits. These have been located in King Sound (Semeniuk, 1980, 1982), the Fitzroy River (Jennings, 1975), the Ord River (Thom et al., 1975), and the Daly and Alligator Rivers (Woodroffe et al., 1985). Radiocarbon dating of these mangrove facies shows a consistency in age across the estuarine plains and also between river systems. For example, in the South Alligator River, 33 radiocarbon dates returned values within a range of 5370−6860 years BP with no spatial trends (Woodroffe et al., 1985). These dates corresponded with dates returned from other systems in northern Australia, including the Fitzroy (5800−7500 years BP) and the Ord (circa 6700 BP Thom et al., 1975). From these dates Woodroffe et al. (1985) hypothesized that extensive mangrove deposits occupied much of the estuarine plains adjacent to the macrotidal rivers near the end of the postglacial marine transgression.

Jennings (1975) had provided a climate interpretation of the extensive cover of mangrove or "big swamp" phase in northern Australian estuaries, postulating higher rainfall as a possible mechanism. In tropical north Queensland, mangroves still occupy the entire estuarine plain in some rivers experiencing high year-round rainfall but can occur together with saltmarsh species (Fig 26.4). By contrast, Woodroffe et al. (1985) presented a geomorphological explanation for this phase. In this model, continued sedimentation following sea level stabilization raised intertidal elevations above those tolerated by mangroves to the point that by 5500 BP most of the mangrove extent was confined to the fringes of channels. In dryer areas, mangroves gave way to hypersaline flats, whereas in wetter areas, upper intertidal and supratidal environments were colonized by salt-tolerant grasses and sedges.

The more detailed investigation by Woodroffe et al. (1985) had shown that the relationship between sedimentation and sea level was the driver of mangrove-saltmarsh/saltflat dynamics at the scale of the Holocene, at least in northern Australia. These studies provided a theoretical context for later work in the estuaries of SE Australia.

3.2 Southeastern Australia

Roy (1984) presented a model of estuarine infill for SE Australia that described phases in the availability of intertidal habitat. Under this model, the deeply incised drowned river valleys characteristic of SE Australia support little in the way of intertidal vegetation immediately following postglacial marine transgression. As these valleys infill with sediment, the fluvial bayhead delta progrades seaward, supporting wide intertidal flats. It is during this "intermediate" stage of infill that estuaries support the greatest extent of mangrove and saltmarsh. With the completion of infill floodplains accrete above intertidal elevations,

FIGURE 26.4 Saltmarsh (*Distichlis* sp.) growing adjacent to a stand of mangroves (*Ceriops tagal*) in Queensland, Australia.

flow is channelized throughout the length of the estuary, and intertidal habitats are restricted to channel fringes and cutoff embayments.

The Roy (1984) model assumes stable sea levels following the cessation of the postglacial marine transgression at approximately 6500 BP. Recent dating of encrusting organisms at several locations in NSW has suggested that mid-Holocene sea levels may have been somewhat higher (50−150 cm) than present levels (Baker and Haworth, 1997, 2000), an observation that might explain the widespread occurrence of potentially acid sulfate soils above current sea levels on estuarine floodplains (Wilson, 2005). Were mangroves more widely distributed in the mid-Holocene than at present?

Early work on the interactions between mangrove and saltmarsh in eastern Australia was dominated by succession theory. Pidgeon (1940) saw mangroves as the initial colonizers of exposed estuarine mudflat under conditions of extreme salinity and saturation. Mangroves were seen as active land builders, which accumulated sediment among aerial roots, inviting invasion by subsequent colonizers.

> Saltmarsh plants, the first of which are *Salicornia australis*, *Suaeda australis*, and *Samolus repens*, invade the landward margin of the mangrove area. With subsequent silt accumulation the mangroves are forced further out into the estuary and in their place a saltmarsh is formed. ***Pidgeon (1940, p. 24)***

Under this model, continued accretion led to colonization by salt-tolerant grasses (*Sporobolus virginicus*), followed by the rush *Juncus* spp., and then *Casuarina glauca*. As freshwater conditions replace saline, Eucalyptus invades, with the "climax" community appearing as a mixed Eucalypt forest (Pidgeon, 1940). Evidence supporting this dynamic succession was

seen as the occurrence of "relict species in more advanced zones" and the active invasion of *Juncus* into the *Sarcocornia* meadow.

The succession model can be tested by coring within the saltmarsh in search of relict mangrove peat material. To this end, Mitchell and Adam (1989a) retrieved shallow sediment cores from several saltmarshes in Botany Bay and the Georges River in the Sydney region. Their coring failed to find any evidence of previous occupation of the saltmarsh habitat by mangrove and suggested a model that had saltmarsh species as primary colonizers, followed by invasion by mangrove. This model accorded with observations of initial colonization of newly created intertidal flats by saltmarsh on the northern foreshore of Botany Bay and the spreading of mangroves into the saltmarsh zone at various intertidal locations in the Sydney region (Mitchell and Adam, 1989b).

The Hawkesbury River in central NSW is a large drowned river valley in an intermediate phase of infill. Unlike the macrotidal estuaries of tropical northern Australia, the Hawkesbury supports a diverse array of vegetation on depositional terraces through its tidal length of some 106 km. There is no "big swamp" phase or there does not appear to have been at any point in the Holocene or late Pleistocene. Present-day intertidal flats support widespread mangrove in the central reaches of the estuary. Seaward of these, mudflats exposed at low tide are unvegetated. Headward, intertidal flats are dominated by saltmarsh, principally *Juncus kraussii*. Saintilan (1997) suggested that gradual infill has led to the replacement of mangrove with saltmarsh on successive intertidal flats as the river progrades seaward within its valley.

Evidence for this model of geomorphically driven vegetation succession is found in the stratigraphy of intertidal flats currently occupied by saltmarsh. Using techniques similar to those of Mitchell and Adam (1989b), Saintilan and Hashimoto (1999) found mangrove peats well preserved 20–30 cm beneath the present-day marsh surface, at the approximate elevation of contemporary mangrove root systems. Beneath these peats, estuarine shells dated to approximately 5000 years BP. The age of the mangrove peats varied with distance from the edge of wide intertidal flats, from 1200 to 1700 years BP at the upslope fringes of the flats to 500 years BP close to the current mangrove/saltmarsh boundary, suggesting gradual infill.

Mangrove root material retrieved from beneath saltmarsh in small creeks in southern NSW told a similar story. Mangrove root material dating to 1300 BP in Currambene Creek and 1900 BP in Cararma Inlet was retrieved from beneath the contemporary saltmarsh (Saintilan and Wilton, 2001). The lack of any significant fluvial input into Cararma Inlet suggested tidal reworking of aeolian and washover deposits as the most likely mechanism for infill. Within Currambene, preserved mangrove root material was more sporadic, and the suggestion was made that channel migration had erased evidence of prior mangrove occupation in some locations. At neither site was there evidence of widespread mangrove colonization earlier than 3000 BP, though more headward estuarine floodplains were not sampled.

3.3 Western Atlantic–Caribbean Region

Early work in Florida and the Caribbean region was also influenced by succession theory and the concept of mangroves as "land builders" (Spackman et al., 1966; Cohen and Spackman, 1977). Davis (1940) proposed that mangrove-saltmarsh zonation in Florida reflected ecological succession and seaward progradation by mangroves as sea level rose.

However, Egler (1952), Thom (1967), and others later challenged both the zonation–succession interpretation and the idea that mangroves were geological agents capable of building land. Egler (1952) presented evidence that mangroves had retreated landward during sea level rise, invading freshwater habitats in the Everglades. More recent work in the Caribbean has shown that mangroves growing in sediment-deficient settings can build vertically via peat formation (Woodroffe, 1981, 1983; Cameron and Palmer, 1995; Macintyre et al. 1995, 2004; McKee and Faulkner, 2000; Toscano and Macintyre, 2003; McKee et al., 2007a). In some cases, mangrove peat deposits reach 10 m in thickness, and radiocarbon dating shows that this biogenic accretion has kept pace with sea level rise (e.g., Twin Cays and Tobacco Range, Belize) (Macintyre et al., 2004; McKee et al., 2007a).

Paleostratigraphic evidence of fluctuations in mangrove and saltmarsh dominance is limited for the western Atlantic/Caribbean region and generally does not record the interplay between these specific vegetation types. Early work in Florida showed basal freshwater peat beneath mangrove peat in the modern Everglades-mangrove complex, suggesting mangrove invasion of freshwater marsh during sea level rise (Cohen and Spackman, 1977). Some of the deepest and oldest peat deposits occur in Belize where basal peats have been radiocarbon dated to about 8000 Cal BP (Toscano and Macintyre, 2003; Macintyre et al., 2004; McKee et al., 2007a). Most of these studies identified mangrove-derived peat throughout the stratigraphic profile and no components were identified as "saltmarsh" peat. Work by Woodroffe (1981, 1983) at Grand Cayman also showed predominately mangrove peat in radiocarbon dated cores. These latter observations show the continued dominance of mangroves throughout the Holocene, despite changes in sea level.

Other locations, including Jamaica (Digerfeldt and Hendry, 1987) and Trinidad (Ramcharan, 2004), show fluctuations between mangroves and brackish water sedges (e.g., *Cladium* sp.) or freshwater species, respectively. In the Negril swamp, Jamaica, radiocarbon dated cores show sedge (*Cladium* sp.) peat at the base (c. 7000–8000 Cal BP) and interspersed at intervals with mangrove peat (*Rhizophora* or *Rhizophora-Conocarpus*) or mixtures of *Cladium-Rhizophora* or *Cladium-Conocarpus* peat (Digerfeldt and Hendry, 1987). Pollen records from a late Holocene core on the Mexican Caribbean coast (Quintana Roo) showed mangroves dominating during humid periods and *Conocarpus erectus* and nonmangrove taxa dominating during drier periods, e.g., that coincided with the decline in the Mayan culture (Islebe and Sanchez, 2002).

4. RECENT INTERACTIONS

4.1 Air Photographic Evidence of Mangrove-Saltmarsh Dynamics in Southeastern Australia

On the basis of the stratigraphic evidence described above, the trend in SE Australia over the later Holocene has been one of the saltmarshes replacing mangrove with the infilling of estuaries and mangrove occupying freshly accreted habitat. This pattern has been consistent across a range of settings, from drowned river valleys (Saintilan and Hashimoto, 1999) to smaller barrier estuaries (Saintilan and Wilton, 2001). The pattern presents a contrast to trends identified from more recent times from air photographic records. Numerous studies

from SE Australia have demonstrated the encroachment of mangrove into upper intertidal saltmarsh.

Saintilan and Williams (2000) cited 28 surveys that demonstrated saltmarsh loss to mangrove encroachment over the period covered by archival air photographs (usually 1940s–present). The trend is apparent across all east coast bioregions and a range of geomorphic settings. Within southern Queensland, Pleistocene sand barriers protect wide, shallow back-barrier deposits that support extensive mangrove and saltmarsh. Mangrove encroachment into saltmarsh in these environments is well-documented (McTainsh et al., 1986; Morton, 1994; Hyland and Butler, 1988; Manson et al., 2003). In northern NSW, mangroves and saltmarshes occupy the mouths of large rivers. Although losses of mangrove and saltmarsh to agriculture have been extensive (West, 1993), mangroves are encroaching on saltmarsh and some agricultural pastures (Saintilan, 1998). In central coast NSW, widespread losses of saltmarsh to mangrove have been reported from both shallow coastal lakes (Winning, 1990) and drowned river valleys (Mitchell and Adam, 1989a,b; Williams and Watford, 1997; Evans and Williams, 1997; Williams et al., 1999; McLoughlin, 2000; Haworth, 2002; Williams and Meehan, 2004). South coast NSW estuaries, mostly smaller "barrier" estuaries (Roy et al., 2001), have shown similar trends with a median loss of approximately 40% of the saltmarsh to mangrove encroachment (Chafer, 1998; Saintilan and Wilton, 2001; Meehan, 1997).

Within Victoria, saltmarshes and mangroves occupy the shorelines of large coastal embayments. Here, loss of saltmarsh to mangrove encroachment has been consistent, though less dramatic. Declines of 5%–12% of saltmarsh to mangrove encroachment have been reported for the saltmarshes of Western Port Bay (Rogers et al., 2005b) and losses have also been noted for Corner Inlet (Vanderzee, 1988) and the Gulf St. Vincent in South Australia (Burton, 1982). Within New Zealand, the proliferation of mangrove is more commonly described as a seaward colonization (Craggs et al., 2001; Park, 2001; Morrisey et al., 2003), though landward encroachment has been noted (Burns and Ogden, 1985).

4.2 Saltwater Intrusion in Northern Australia

Marked geomorphological changes to estuaries and coastal plains in northern Australia over the past 50 years have been associated with saltwater intrusion in the Alligator River region (Winn et al., 2006) and Mary River (Knighton et al., 1991; Mulrennan and Woodroffe, 1998). The gradual extension of tidal influence along stream channels, the expansion of tidal creeks, and the formation of new tidal creeks (Winn et al., 2006) are linked to the encroachment of mangrove and saline mudflats into freshwater vegetation (Finlayson et al., 1998), localized scour and dieback within Melaleuca forests, accretion of sediment on floodplains (Knighton et al., 1991; Woodroffe and Mulrennan, 1993; Bell et al., 2001), changes in subsurface hydrology (Jolly and Chin, 1992), and land cover changes (Ahmad and Hill, 1995; Bell et al., 2001). Changes since 1950 are significant with bare saline mudflats on the East Alligator River exhibiting a ninefold increase and an associated loss of 64% of Melaleuca forests by 2000 (Winn et al., 2006). More than 17,000 ha of freshwater vegetation have been adversely affected on the Mary River and a further 35%–40% of floodplains are immediately vulnerable to intrusion (Mulrennan and Woodroffe, 1998). A concurrent seaward and landward expansion of mangrove has been observed across the Gulf of Carpentaria, coincident with

relatively rapid sea level rise and higher river discharge in the period 1987–2014 (Asbridge et al., 2015). Asbridge et al. (2016) attribute landward mangrove encroachment in this case to freshening of upper intertidal flats as a result of the combined influence of increased tidal inundation and increased wet season inundation from rivers. Mangrove mortality in the region in the period 2016–2017 reversed some to these trends, and corresponded to a period of dryer than normal monsoons and lower sea-levels (Lovelock et al. 2017; Saintilan et al. 2018).

A single cause for saltwater intrusion has not been identified (Mulrennan and Woodroffe, 1998). Instead, it is apparent that factors such as drier-than-average monsoonal conditions, low frequency and low-intensity cyclonic events, and above average ocean water levels (Winn et al., 2006) facilitate extension of tidal influence into freshwater environments, whereas tributary development, large tidal range, small elevation differences over floodplains, and uncontrolled feral buffalo promote the expansion of tidal influence (Knighton et al., 1991). Because of the desiccation of floodplain sediments in the dry seasons, the process of saltwater intrusion now appears to be internally driven and is likely to continue until an equilibrium state is reached between floodplain elevation and tidal influence (Mulrennan and Woodroffe, 1998; Winn et al., 2006).

4.3 Western Atlantic–Gulf of Mexico

Information on historical shifts in saltmarsh and mangrove vegetation in the western Atlantic–Gulf of Mexico region has been highlighted in site-specific observations (Lonard and Judd, 1985; Sherrod and McMillan, 1985; McMillan and Sherrod, 1986; Montague and Wiegert, 1990; Montague and Odum, 1997; McKee et al., 2004; Stevens et al., 2006) and more recently in regional analyses of Landsat and aerial photographic data (Cavanaugh et al., 2014a; Osland et al., 2013; Giri and Long, 2016). Mangroves have expanded by 4.3% across the region since the earliest Landsat records in 1980 (Giri and Long, 2016). In the northern Gulf of Mexico and the Atlantic Florida coast, the persistence and spread of mangroves is controlled mainly by temperature, with dieback and recovery occurring over decadal timescales (Sherrod and McMillan, 1985; Stevens et al., 2006; Osland et al., 2013, 2015; Giri and Long, 2014). Cavanaugh et al. (2014a,b) used a 28-year Landsat chronosequence to demonstrate a doubling of mangrove cover on the Florida east coast between 1984 and 2011 and associated this spread to a reduction in the frequency of days colder than −4°C. This increase has primarily been a landward expansion and "infilling" within poleward limits rather than poleward expansion (Giri and Long, 2016).

Hydroperiod, sedimentation, salinity, and nutrients as well as propagule dispersal and predation also influence local patterns of mangrove establishment and spread (Patterson and Mendelssohn, 1991; Patterson et al. 1993, 1997; Osland et al., 2014). In coastal Louisiana, for example, mangroves tend to dominate shorelines of tidal creeks, and saltmarsh occupies the interior position. The *A. germinans* zone is characterized by higher elevation, salinity, and soil bulk density, whereas the *S. alterniflora* zone is lower in elevation with greater flooding and reducing soils (Patterson and Mendelssohn, 1991).

Periodic freezes have killed or damaged mangroves, allowing expansion of saltmarsh, most recently during the 1980s (McMillan and Sherrod, 1986; Montague and Wiegert, 1990; Montague and Odum, 1997; Stevens et al., 2006). Stevens et al. (2006) review reports of major damage to mangroves in Florida as a result of severe freezes in 1962, 1977, 1981,

1983, 1985, 1989, and 1996. *A. germinans* has some capacity to recover from freeze damage through coppicing (stump sprouting), but periodic damage results in a stunted, scrub-like growth form. In Louisiana, the last severe freeze that caused widespread dieback of mangroves (*A. germinans*) occurred in December 1989 (K.L McKee pers. obs.). Although *A. germinans* can recover from mild freezes, the 1989 event killed mature trees that never recovered. However, propagules that had already dispersed survived this freeze and appeared to be the primary means by which the population reestablished. Thousands of propagules were observed establishing in the months after the freeze, and their viability was further confirmed in greenhouse culture (K.L. McKee unpublished data.). The resistance of *A. germinans* propagules in Louisiana to freezing temperatures is consistent with previous studies of cold tolerance of this species (Markley et al., 1982; Norman et al., 1984).

Most observations indicate that saltmarsh replaces freeze-killed mangroves in the Gulf of Mexico within 4–5 years (Stevens et al., 2006). However, relatively mild winters and the lack of severe freezes in recent years has allowed mangrove expansion in Florida (Stevens et al., 2006; Cavanaugh et al., 2014a,b) and Louisiana (K.L. McKee pers. obs.). Mangroves have expanded (average of 21% increase in cover) at the Cedar Key, Florida (29°08′N), between 1995 and 1999 during a period free from severe freezes (Stevens et al., 2006) and by 74% across the Texas coast between 1990 and 2010 (Armitage et al., 2015). Recent mangrove expansion in coastal Louisiana, USA, has been attributed to a drought-induced, widespread dieback of *S. alterniflora* during 2000 (McKee et al., 2004). Over 40,000 ha of saltmarsh were severely damaged with areas up to 5 km^2 reduced to mudflat. However, *A. germinans* was unaffected and even thrived during and after this marsh dieback event (Fig 26.5).

5. STRESSORS CONTROLLING DELIMITATION OF MANGROVE

Mangroves commonly exhibit a gradual reduction in development with latitude (Lot et al., 1975; Saenger and Snedaker, 1993; Saenger, 2002) and stunted forms at their latitudinal limit may be due to an increasingly stressful environment (Schaeffer-Novelli et al., 1990). Kangas and Lugo (1990) hypothesize that without "stress," in their case frost stress, mangrove vegetation is competitively superior and coastlines would be dominated by mangrove. However, field observations of saltmarsh dieback in coastal Louisiana, USA, and *A. germinans* expansion into areas formerly occupied by *S. alterniflora* (McKee et al., 2004) suggest that at subtropical latitudes some mangrove species are competitively inferior. In addition, greenhouse and field experiments show that *S. alterniflora* competitively inhibits growth of *A. germinans* (Patterson et al., 1993; McKee and Rooth, 2008). Where mangrove and saltmarsh coexist, environmental stressors control the delimitation of mangrove so that these communities typically form three zones: a seaward zone dominated by mangrove, a landward transition zone containing both mangrove (possibly stunted) and saltmarsh, and an interior zone dominated by saltmarsh. Numerous stressors, including geomorphic, hydrological and climatic controls, physicochemical factors, and biotic interactions, may act to delimit mangrove establishment (Patterson et al., 1993, 1997; McKee and Rooth, 2008) and enable saltmarsh development within the interior of marshes. In some extreme environments, however, marsh vegetation may facilitate mangrove recruitment through propagule trapping and/or amelioration of stressful soil conditions (McKee and Rooth, 2008).

FIGURE 26.5 Saltmarsh (*Spartina alterniflora*) dieback in coastal Louisiana, USA (top). Black mangrove (*Avicennia germinans*) was unaffected and later became dominant in some dieback areas (bottom).

5.1 Geomorphic and Hydrological Controls

Inundation by tides is not an ecophysiological requirement of mangroves and saltmarshes, but it is a typical feature and plays an important role by limiting excessive buildup of salts within soils (Saenger, 2002) and distributing mangrove and saltmarsh propagules (Adam, 1990; Clarke, 1993). Indeed, inundation may play a significant role in mangrove and saltmarsh zonation as tidal flushing may act to alter soil salinity (Patterson and Mendelssohn, 1991) and control the transport of propagules along an elevation gradient (Adam, 1990; Patterson et al., 1997; Saenger, 2002). The hydrologic role of inundation is largely controlled by the geomorphology of a marsh so that inundation frequency and water volume are negatively proportional to land elevation. However, the relative positions of saltmarsh and

mangrove vegetation along a topographic gradient vary with geographic region and the species involved. In the northern Gulf of Mexico, mangroves coincide and compete with low-marsh species such as *S. alterniflora*, which are highly flood tolerant (Patterson and Mendelssohn, 1991; Patterson et al., 1993, 1997). In these communities, mangroves (*A. germinans*) occupy the higher elevation creekbanks and saltmarsh species dominate the interior, lower elevation areas. In other locations, low elevation sites are commonly inhabited by mangrove, are inundated more frequently, and receive higher water volumes, whereas higher elevations are commonly inhabited by saltmarsh. The latter pattern can be found in coexisting mangrove and saltmarsh communities in Australia and in Florida, USA (Montague and Wiegert, 1990). In the latter case, the low elevation sites along shorelines are dominated by *R. mangle* and higher elevations are occupied by high-marsh species such as *B. maritima*, *D. spicata*, *B. frutescens*, and *Salicornia* spp.; the upland transition may be occupied by *J. roemerianus*, *Spartina bakeri*, or *S. patens* (Montague and Wiegert, 1990).

Adaptations to cope with submergence and high salt environments are evident within both mangrove and saltmarsh species (summarized in Adam, 1990 and Saenger, 2002), and species tolerance to submergence and salinity are hypothesized to cause the zonation of plants observed within marshes. Numerous studies have demonstrated the role of salinity in causing mangrove species to segregate (Ball, 1988a,b; Lin and Sternberg, 1992; Ball and Pidsley, 1995; Ball, 2002; López-Hoffman et al., 2006) and coexist with temporal salinity variation (Ball, 1998). However, for saltmarsh, Adam (1990) argues that because soil salinity varies spatially and temporally, zonation may be more readily explained on the basis of species tolerance to frequency and duration of submergence. Furthermore, although soil salinity and tidal regime are important factors, these factors do not appear to explain observed distributions of saltmarsh species across the intertidal zone (Silvestri et al., 2005). The zonation of coexisting mangrove and saltmarsh communities in Sydney (Clarke and Hannon, 1971) and Brazil (Santos et al., 1997, cited in Saenger, 2002) was found to be salinity based, with species exhibiting definable salt tolerances (Clarke and Hannon, 1971) and their distribution being determined by a salinity model based on topographic level and upland runoff (Santos et al., 1997). Although causes of mangrove and saltmarsh zonation remain incompletely understood (Snedaker, 1982; Adam, 1990), it is evident that zonation, soil salinity, and submergence are all maintained along elevation gradients and is likely to contribute to the distribution of mangrove and saltmarsh vegetation (Snedaker, 1982; Saenger, 2002).

Zonation as a consequence of differential dispersal of mangrove propagules has also been proposed. This is primarily based on the concept of tidal sorting of propagules proposed by Rabinowitz (1975, 1978a,b,c) for mangroves in Panama. However, the relationship between propagule size and zonation has not been supported for mangroves in other locations (Ball, 1980; McKee, 1995a; Sousa et al., 2007) In addition, differential dispersal and survival of propagules with tides has not been established for saltmarsh species, and because many saltmarsh species are able to vegetatively propagate, the contribution of tides to dispersal is likely to be limited (Adam, 1990).

Regardless of the role of tidal sorting of propagules in zonation, tides do distribute mangrove propagules and it is likely that zonation of mangrove to saltmarsh may be related to differential seedling mortality at different tidal levels (Ellison and Farnsworth, 1993). High soil salinity decreases the rate of pericarp shedding by mangrove propagules, thereby

limiting survival (Downton, 1982; Clarke and Myerscough, 1991). Thus, higher soil salinities and reduced inundation frequency, common in the high marsh, cause mangrove propagules to desiccate and suffer high mortality (Clarke and Allaway, 1993). However, work in the northern Gulf of Mexico found that mortality of *A. germinans* propagules was associated with excessive flooding and damage by predators in low-marsh areas, resulting in decay and loss of viability (Patterson et al., 1997).

Observed interactions between mangrove and saltmarsh globally have highlighted the role of hydrology and geomorphology in increasing the dispersal and survival of mangrove propagules and seedlings. For example, a strong relationship has been found between relative sea level rise and the upslope migration of mangrove into saltmarsh environments in SE Australia (Rogers, 2004). In this case, relative sea level rise incorporates both geomorphological and hydrological changes and may be altered by eustatic sea level rise, which relates to changes in the volume of water within oceans through the melting of ice caps and thermal expansion of water and/or surface elevation changes of the land through surface processes of vertical accretion or subsurface processes of subsidence and autocompaction. Sea level rise has also been suggested as a primary driver of mangrove expansion within thermal limits across the US Gulf and Atlantic coasts (Krauss et al., 2011; Raabe et al., 2012; Armitage et al., 2015; Giri and Long, 2016).

Hydrological changes due to global warming has caused global sea level to increase by 1.0−2.0 mm/yr; in the 20th century, the rate of sea level rise is predicted to accelerate toward 2100 (Solomon et al., 2007). Recent studies of relative sea level trends for saltmarshes in Tasmania and New Zealand show higher rates over the past century (2.5−3.1 mm/yr) compared with the previous four centuries (Gehrels et al., 2007). Numerous studies predict that global sea level rise will cause a shift in the boundary between mangrove and saltmarsh (Snedaker, 1995; Blasco et al., 1996) and indeed the study of Rogers et al. (2006) related sea level changes to the expansion of mangroves in SE Australia. Changes to the water levels inundating a marsh may also occur because of altered tidal prisms resulting from engineering works, such as dredging of estuary entrances. These hydrological changes may increase the mean water level and/or alter the tidal range within a marsh, thereby altering soil salinity and increasing the distribution potential of mangrove propagules. Both reduced soil salinities and increased inundation promote the survival of mangrove within saltmarsh and increase their competitive potential. Along the US Gulf and Atlantic Coasts, mangrove encroachment is occurring in association with retreat of marsh seaward edges and forest-to-marsh transition, further implicating sea level rise as a major driver of change (Armitage et al., 2015; Raabe and Stumpf, 2016).

Geomorphological changes to marsh elevation alter the inundation frequency and duration within a marsh and may occur as a result of surface processes such as vertical accretion. Increased sediment availability and vertical accretion within estuaries have been hypothesized as mechanisms promoting mangrove encroachment of saltmarsh in SE Australia (summarized by Saintilan and Williams, 1999 and McLoughlin, 2000) by creating more areas suitable for mangrove establishment and providing a soft substrate for mangrove propagule establishment within the saltmarsh. Certainly the spread of mangrove along estuarine foreshores seems related to the availability of new habitat, and commonly the landward encroachment of mangrove is accompanied by seaward encroachment also. Perhaps the overall increase in population of *A. marina* and increased fecundity made possible by higher

nutrient loads has increased propagule availability within estuaries, including the upper intertidal environment. However, increased vertical accretion is also more likely to increase marsh elevation, reducing inundation frequency and thereby reducing the likelihood of mangrove survival due to propagule desiccation. Furthermore, the "fertilization" of the saltmarsh from anthropogenic sources does not necessarily lead to improved mangrove colonization. Experimental fertilization of *A. marina* propagules has failed to show an impact on propagule survival (Clarke and Myerscough, 1993; Saintilan, 2003).

Rates of vertical accretion have been used as an estimate for marsh elevation and a surrogate for investigating the cause of mangrove–saltmarsh interaction. This is appropriate at some sites, such as Homebush Bay and Western Port Bay, Australia, where saltmarsh surface elevation is maintained primarily by vertical accretion (Rogers et al., 2005a,b). However, this assumption is not always true. Recent literature has highlighted the role of belowground processes in altering marsh elevations (Cahoon et al., 1999, 2006; McKee et al., 2007a). Processes such as subsidence, soil compaction, plant productivity and dieback, groundwater availability, and tidal flooding interact to alter soil volumes over a range of spatial and temporal scales.

The relationship between marsh elevations and sea level has primarily been explored through the use of surface elevation tables (SETs) (described by Cahoon et al., 2002). By incorporating analyses of surface processes such as vertical accretion, the belowground component of surface elevation change can be differentiated. In SE Australia, SETs were used to show that mangrove surface elevation gain was consistently lower than saltmarsh surface elevation gain, despite vertical accretion being consistently higher in the mangrove zone (Rogers et al., 2005a,b, 2006). Mangrove encroachment of saltmarsh in the same region has been attributed to autocompaction or subsidence, which causes the observed disequilibrium between mangrove surface elevation change and vertical accretion (Rogers et al., 2006). Howard et al. (2016) found a similar association between mangrove encroachment and soil subsidence at the 10000 Island National Wildlife Refuge in Florida. Across the SE Australian sites, those marshes with the highest rates of relative sea level rise were those with the highest rates of mangrove encroachment (Rogers et al., 2005b). Autocompaction of sediments corresponded to a severe El Nino-related drought; and surface elevation change correlated strongly with total monthly rainfall (Rogers et al., 2005a), the Southern Oscillation Index, and groundwater depth (Rogers and Saintilan, 2008). This research is consistent with other studies of surface elevation and groundwater (Schmidt and Burgman, 2003; Watson, 2004; Whelan et al., 2005) and suggests that rainfall and subsequent groundwater recharge play a significant role in determining interannual variability in surface elevation with respect to sea level.

5.2 Climatic Controls

Climatic factors are commonly proposed to promote or limit the survival of mangrove within coexisting mangrove and saltmarsh communities as a result of extreme low temperatures and frost causing the death of mangrove or rainfall influencing soil salinity.

Many tropical and subtropical plants exhibit physiological dysfunction and damage in response to chilling temperatures (van Steenis, 1968) and this appears to be the case for mangroves (McMillan, 1975; Markley et al., 1982; McMillan and Sherrod, 1986; Kangas and Lugo, 1990; Olmsted et al., 1993). Freeze sensitivity is particularly apparent along the Gulf

and Atlantic coasts of North America, and the distribution of *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle* corresponds to their tolerance of freezing frequency and intensity under experimental conditions (Cavanaugh et al., 2015). In these locations, mangroves tend to expand during periods of mild winters (Stevens et al., 2006; Giri and Long, 2014; Cavanaugh et al., 2014a) and when weather extremes or other factors stress or eliminate saltmarsh (McKee et al., 2004). When mangroves are periodically damaged or killed by freezes, saltmarsh quickly regains dominance (Stevens et al., 2006). Consequently, future changes in global climate regime and local weather patterns, in particular a reduction in extreme daily minima, will likely influence the relative dominance of mangrove and saltmarsh vegetation in this region. Osland et al. (2013) used downscaled future climate projections for 2070–2100 to suggest that a 2–4°C temperature rise would lead to mangrove replacing 95% of saltmarsh in Louisiana, 100% in Texas, and 60% in Florida. Cavanaugh et al. (2015) projected a northern expansion in Florida over the next 50 years of 160, 110, and 120 km for *A. germinans*, *R. mangle*, and *L. racemosa*, respectively. Rapid colonization at poleward limits may be facilitated by the "precocious reproduction" of individuals along the invasion front, with observations of younger *R. mangle* reproducing and producing larger propagules at the leading edge of the expanding range in Florida (Dangremond and Feller, 2016).

Mangroves show greater luxuriance and species richness in high rainfall areas (Tomlinson, 1986; Hutchings and Saenger, 1987; Smith and Duke, 1987), and species distribution correlates strongly with freshwater influence from rainfall (Bunt et al., 1982), controlling for latitude. An aridity gradient extending across the Texan coastline from the Louisiana border to Texas–Mexico border strongly influences the degree of vegetative cover, and small changes in freshwater delivery in regions with mean annual rainfall below ~995 mm/yr can profoundly influence the relative extent of mangrove, saltmarsh and hypersaline flat (Osland et al., 2016), and the dominance of graminoid and succulent vegetation in the saltmarsh (Osland et al., 2014). Low rainfall and a shortened rainfall season in Senegal in the 1980s contributed to the decline of mangroves and increased surface areas of bare saltflats and saline grasslands (Diop et al., 1997). In addition, studies in Australia have suggested that freshening of saltmarsh environments from rainfall might promote survivorship of mangroves (McTainsh et al., 1986) and may explain the establishment of mangrove at the saltmarsh-terrestrial boundary in tropical and subtropical areas of Australia (Duke, 2006).

There is other evidence that mangrove encroachment in tropical and subtropical climates may be related to rainfall trends. In these situations, the proportion of mangrove and saltmarsh in estuaries is correlated to annual rainfall (Bucher and Saenger, 1991). Where saltmarsh occurs, it often occupies a middle position between seaward and landward mangrove zones. Increased rainfall in recent decades has been used to explain the encroachment of tall mangrove forest into salt pan in Hinchinbrook Channel (Duke, 1995) and stunted mangrove into saltmarsh in Moreton Bay (Duke, pers. comm.). Conversely, declines in rainfall have resulted in mangrove dieback in the upper intertidal environment in some locations, most notably in the Gulf of Carpentaria during the usually dry 2015–16 monsoon (Duke pers. comm.) The correlation between rainfall and the proportion of mangrove and saltmarsh breaks down in NSW (Saintilan, 2003). Here, the upslope limit of mangrove is more consistently related to frequency of tidal inundation, and there is no landward mangrove fringe.

5.3 Physicochemical Factors

Physicochemical factors have been hypothesized to limit the establishment of mangrove within saltmarsh areas. In particular, mangroves may be excluded from saltmarsh environments because of nutrient deficiency and/or high soil salinity within saltmarshes. Salinity decreases pericarp shed and increases desiccation of mangrove propagules (Downton, 1982; Clarke and Myerscough, 1991) and may contribute to zonation of mangrove and saltmarsh species because of differential species tolerance to soil salinity (summarized in Adam, 1990 and Saenger, 2002) as discussed above.

Experimental fertilization of mangroves indicates that nitrogen and phosphorus limitation is common (Boto, 1983; Boto and Wellington, 1983; McKee et al., 2002) and on fertilization mangroves exhibit increases in growth and biomass (Naidoo, 1987; Clarke and Allaway, 1993; Feller et al. 2003a,b; Lovelock et al. 2004, 2006; Simpson et al., 2013).

However, because the effect of nutrient enrichment does not become apparent until mangrove cotyledons have been exhausted (Naidoo, 1987; Clarke and Allaway, 1993), it has less impact on early mangrove establishment within saltmarsh. Saintilan (2003) confirmed that mangrove mortality within saltmarsh is not reduced through nutrient enrichment of seedlings. In some geographic regions, mangrove mortality within saltmarshes is the result of desiccation of propagules (Clarke and Allaway, 1993; Saintilan, 2003), which is dependent on climatic, geomorphic, and hydrologic factors. However, changes in tissue chemistry by fertilization or light conditions (McKee, 1995a,b) could influence mangrove seedling susceptibility to herbivores.

5.4 Biotic Considerations and Interactions

Several studies suggest that saltmarsh precedes mangrove in successional sequences because of tidal transport of mangrove propagules and shading of saltmarsh by mangrove seedlings (summarized in Kangas and Lugo, 1990). Work by McKee et al. (2007b) found that establishment, survival, and growth of mangrove seedlings were facilitated by herbaceous species, *Sesuvium portulacastrum* and *Distichlis spicata*. Both species promoted mangrove propagule trapping and ameliorated soil conditions (aeration, temperature). Peterson and Bell (2012) demonstrated that *Sporobolus virginicus* had a far greater capacity than *S. portulacastrum* and *B. maritima* to retain propagules of *A. germinans*. Alternatively, dense stands of saltbush (*Tecticornia* spp.) have been suggested to inhibit mangrove establishment in saltmarshes in Western Port Bay, Australia (Rogers et al., 2005b), with similar competition being reported between mangroves and *S. alterniflora* in marshes in Louisiana (Patterson et al., 1993; McKee and Rooth, 2008) and Texas (Guo et al., 2013), though the extent of this suppression may decrease in higher latitudes (Guo et al., 2013). Several mechanisms have been advanced, including shading seedlings, competition for nutrients (Guo et al., 2013; Simpson et al., 2013), or facilitated accretion (Rogers et al., 2005b). Experimental data presented by Peterson and Bell (2015) suggest that succulent saltmarsh vegetation may not be as efficient at trapping and retaining mangrove propagules during the ebb tide as graminoid vegetation.

Plant–animal interactions are also evident within coexisting communities, and differential predation of mangrove propagules by crabs is suggested as a cause of zonation within mangroves (Smith, 1987; Smith et al., 1989), but this hypothesis is not supported in other locations

(McKee, 1995a; Sousa and Mitchell, 1999). A study of *A. germinans* seedlings found that predator damage to propagules (and frequent flooding) leads to decay of propagules within the *Spartina* zone in coastal Louisiana (Patterson et al., 1997).

Once established, tall *A. germinans* are more resistant and resilient to freeze-induced mortality than smaller individuals (Osland et al., 2015). This observation suggests that nonlinear responses of mangrove expansion to declining frost frequency may occur. As poleward individuals grow taller between successive frosts, a greater number reach the required "escape height," providing the basis for subsequent expansion (Osland et al., 2015). Anthropogenic modification of nutrient status of soils and atmospheric CO_2 may enhance this trend as suggested in terrestrial woody encroachment models (Bond and Midgley, 2000; Saintilan and Rogers, 2015).

5.5 Ecosystem Effects

The broad-scale transition of intertidal vegetation from saltmarsh to mangrove represents a change in the physical structure and composition of above- and belowground plant material with potential ecosystem-scale effects. Comeaux et al. (2012) describe two mechanisms whereby mangrove colonization may increase the resistance of coastal marshland to rising sea levels. First, mangroves may facilitate vertical elevation gain more efficiently than saltmarsh, through more efficient trapping of sediment and vertical displacement as the root system expands (Friess et al., 2012). Second, the comparative density of mangrove above- and belowground root mass may facilitate soil cohesive strength while also dampening wave energy (Comeaux et al., 2012).

Comeaux et al. (2012) used radiometric dating of marsh systems in Texas to suggest a higher rate of accretion in the mangrove. This is supported by Surface Elevation Table-Marker Horizon (SET-MH) observations where mangroves and saltmarsh coexist (Rogers et al. 2006, 2013, 2014), though hydroperiod is a confounding factor in SE Australia, where saltmarsh consistently occupies higher elevations. The volume and nature of carbon sequestered by the wetland may also change as saltmarsh transitions to mangrove. In the Gulf of Mexico, studies have focused on saltmarshes recently encroached by mangroves, with some showing an increase in carbon sequestration to root mass (Bianchi et al., 2013; Osland et al., 2012) and others showing no significant change (Perry and Mendelssohn, 2009; Henry and Twilley, 2013; Doughty et al., 2016). In SE Australia, where longer chronosequences of transition may be studied, Kelleway et al. (2016) showed an increase in carbon gain, but only after several decades. This may indicate that the gain is due to the relative recalcitrant nature of mangrove carbon compared with saltmarsh (Bianchi et al., 2013). Relative sequestration potential may be altered by climate change, though the increased mineralization effected by elevated temperatures may be offset by decreased mineralization of carbon resulting from increased hydroperiod (Lewis et al., 2014).

6. CONCLUSIONS

The interaction between mangrove and saltmarsh is of interest to climate change research for several reasons. Having evolved in the tropics (Chapman, 1977; Specht, 1981), mangroves are most prolific in lower latitudes and decrease in diversity and vigor toward the poles

(Lot et al., 1975; Saenger and Snedaker, 1993). By contrast, saltmarshes increase in floristic diversity with increasing latitude within the temperate zone (Adam, 1990) and in the absence of mangroves form the characteristic intertidal vegetation in these latitudes. In the predominantly temperate latitudes where the two community types coexist, saltmarsh distribution is confined in part by the presence of mangrove and in part by the extreme environmental conditions of the upper intertidal zone.

Environmental variability can therefore profoundly influence the competitive interactions between mangrove and saltmarsh. In southern United States, where the proliferation of mangrove is periodically checked by frost, higher temperature and decreased freeze frequency and severity could enhance the survival and growth of species such as *A. germinans*. Wider and more continuous stands of this species may be expected in the northern Gulf of Mexico and the Atlantic coast of Florida. Less cold-tolerant species, such as *R. mangle*, may be able to shift northward along the coasts of Baja, California, Texas, and Florida.

In SE Australia and New Zealand, the growth of the mangrove *A. marina* will be aided not only by increased temperatures toward its southern limit of distribution but also by higher sea levels. Presently, the upslope limit of *A. marina* is defined by the mean high water mark. While there is continued debate over the causes of mangrove encroachment into the saltmarsh of eastern Australia, there is growing evidence for a role of relative sea level rise, evidenced by the relationship between the rate of encroachment and relative sea level trends, and an increased rate of relative sea level rise in temperate Australasian saltmarshes over the past century. The subtle elevation gradients defining the position of mangrove and saltmarsh in these situations provide an early indication of the effects of sea level rise in the coastal wetlands of the region. The concern in these situations is that the landward transition of saltmarsh may be impeded by topographic constraints, both cultural and natural. Where feasible, thought should be given to the designation of landward "accommodation space" in anticipation of projected rates of sea level rise so that the full range of wetland vegetation communities can continue to coexist in these estuaries.

References

Adam, P., 1990. Saltmarsh Ecology. Cambridge University Press, Cambridge.

Ahmad, W., Hill, G.J.E., 1995. Land cover classification of the Mary River floodplain with emphasis on the effect of saltwater intrusion. In: Davenport, C.C., Riley, S.J., Ringrose, S.M. (Eds.), Proceedings of the Second North Australian Remote Sensing and GIS Forum. Australian Government Publishing Service, Canberra, Australia, pp. 76–83.

Armitage, A.R., Highfield, W.E., Brody, S.D., Louchouarn, P., 2015. The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. PLoS One 10 (5), e0125404.

Asbridge, E., Lucas, R., Accad, A., Dowling, R., 2015. Mangrove response to environmental changes predicted under varying climates: case studies from Australia. Current Forestry Reports 1 (3), 178–194.

Asbridge, E., Lucas, R., Ticehurst, C., Bunting, P., 2016. Mangrove response to environmental change in Australia's Gulf of Carpentaria. Ecology and Evolution 6 (11), 3523–3539.

Baker, R.G.V., Haworth, R.J., 1997. Further evidence from relic shellcrust sequences for a late Holocene higher sea level for eastern Australia. Marine Geology 141, 1–9.

Baker, R.G.V., Haworth, R.J., 2000. Smooth or oscillating late Holocene sea-level curve? Evidence from the palaeozoology of fixed biological indicators in east Australia and beyond. Marine Geology 163, 367–386.

Ball, M.C., 1980. Patterns of secondary succession in a mangrove forest of southern Florida. Oecologia 44 (2), 226–235.

Ball, M.C., 1988a. Ecophysiology of mangroves. Trees 2, 129–142.
Ball, M.C., 1988b. Salinity tolerance in the mangroves, *Aegiceras corniculatum* and *Avicennia marina*, I. Water use in relation to growth, carbon partitioning and salt balance. Australian Journal of Plant Physiology 15, 447–464.
Ball, M.C., 1998. Mangrove species richness in relation to salinity and waterlogging: a case study along the Adelaide River Floodplain, northern Australia. Global Ecology and Biogeography Letters 7, 73–82.
Ball, M.C., Pidsley, S.M., 1995. Growth responses to salinity in relation to distribution of two mangrove species, *Sonnertia alba* and *S. lanceolata*, in northern Australia. Functional Ecology 9, 77–85.
Ball, M.C., 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. Trees - Structure and Function 16, 126–139.
Bell, D., Menges, C.H., Bartolo, R.E., 2001. Assessing the extent of saltwater intrusion in a tropical coastal environment using radar and optical remote sensing. Geocarto International 16, 1–8.
Bianchi, T.S., Allison, M.A., Zhao, J., Li, X., Comeaux, R.S., Feagin, R.A., Kulawardhana, R.W., 2013. Historical reconstruction of mangrove expansion in the Gulf of Mexico: linking climate change with carbon sequestration in coastal wetlands. Estuarine, Coastal and Shelf Science 119, 7–16.
Blasco, F., Saenger, P., Janodet, E., 1996. Mangroves as indicators of coastal change. Catena 149, 1–12.
Bond, W.J., Midgley, G.F., 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology 6 (8), 865–869.
Boto, K.G., 1983. Nutrient status and other soil factors affecting mangrove productivity in northeast Australia. Wetlands 3, 45–49.
Boto, K.G., Wellington, J.T., 1983. Phosphorus and nitrogen nutritional status of a northern Australian mangrove forest. Marine Ecology Progress Series 11, 63–69.
Bucher, D., Saenger, P., 1991. An inventory of Australian estuaries and enclosed marine waters: an overview of results. Australian Geographic Studies 29, 370–381.
Bunt, J.S., Williams, W.T., Duke, N.C., 1982. Mangrove distribution in northeast Australia. Journal of Biogeography 9, 111–120.
Burns, B.R., Ogden, J., 1985. The demography of the temperate mangrove (*Avicennia marina* (Forsk.) Vierh.) at its southern limit in New Zealand. Australian Journal of Ecology 10, 125–133.
Burton, T., 1982. Mangrove changes recorded north of Adelaide. Safic 6, 8–12.
Cahoon, D.R., Day Jr., J.W., Reed, D.J., 1999. The influence of surface and shallow subsurface soil processes in wetland elevation: a synthesis. Current Topics in Wetland Biogeography 3, 72–88.
Cahoon, D.R., Lynch, J.C., Hensel, P., Boumans, R., Perez, B.C., Segura, B., Day Jr., J.W., 2002. High-precision measurements of wetland sediment elevation: I. Recent improvements to the Sedimentation-Erosion Table. Journal of Sedimentary Research 72, 730–733.
Cahoon, D.R., Hensel, P.F., Spencer, T., Reed, D.J., McKee, K.L., Saintilan, N., 2006. Wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In: Verhoeven, J.T.A., Beltman, B., Bobbink, R., Whigham, D.F. (Eds.), Wetland Conservation and Management. Springer-Verlag, Berlin Heidelberg, pp. 271–292.
Cameron, C.C., Palmer, C.A., 1995. The mangrove peat of the Tobacco range islands, Belize barrier reef, Central America. Atoll Research Bulletin 431, 1–32.
Cavanaugh, K.C., Kellner, J.R., Forde, A.J., Gruner, D.S., Parker, J.D., Rodriguez, W., Feller, I.C., 2014a. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proceedings of the National Academy of Sciences of the United States of America 111 (2), 723–727.
Cavanaugh, K.C., Kellner, J.R., Forde, A.J., Gruner, D.S., Parker, J.D., Rodriguez, W., Feller, I.C., 2014b. Reply to Giri and Long: freeze-mediated expansion of mangroves does not depend on whether expansion is emergence or reemergence. Proceedings of the National Academy of Sciences of the United States of America 111 (15), E1449.
Cavanaugh, K.C., Parker, J.D., Cook-Patton, S.C., Feller, I.C., Williams, A.P., Kellner, J.R., 2015. Integrating physiological threshold experiments with climate modeling to project mangrove species' range expansion. Global Change Biology 21 (5), 1928–1938.
Chafer, C.J., 1998. A Spatio-temporal Analysis of Estuarine Vegetation Change in the Minnamurra River 1938-1997, 47 p., plus appendices. Unpublished report to the Minnamurra Estuary Management Committee.
Chapman, V.J., 1977. Introduction. In: Chapman, V.J. (Ed.), Ecosystems of the World. 1. Wet Coastal Ecosystems. Elsevier Scientific Publications Company, Amsterdam, pp. 1–29.

Clarke, L.D., Hannon, N.J., 1971. The mangrove swamp and saltmarsh communities of the Sydney district. IV. The significance of species interaction. Journal of Ecology 59, 535–553.
Clarke, P.J., 1993. Dispersal of grey mangrove (*Avicennia marina*) propagules in south-eastern Australia. Aquatic Botany 45, 195–204.
Clarke, P.J., Allaway, W., 1993. The regeneration niche of the grey mangrove *Avicennia marina* – effects of salinity, light and sediment factors on establishment, growth and survival in the field. Oecologia 93, 548–556.
Clarke, P.J., Myerscough, P.J., 1991. Buoyancy of *Avicennia marina* propagules in south-eastern Australia. Australian Journal of Botany 39, 77–83.
Clarke, P.J., Myerscough, P.J., 1993. The intertidal distribution of the grey mangrove *(Avicennia marina)* in south-eastern Australia: the effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. Australian Journal of Ecology 18, 307–315.
Clusener, M., Breckle, S.W., 1987. Reasons for the limitation of mangrove along the west-coast of northern Peru. Vegetatio 68, 173–177.
Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S., Turner, R.K., 2014. Changes in the global value of ecosystem services. Global Environmental Change 26, 152–158.
Cohen, A.D., Spackman, W., 1977. Phytogenic organic sediments and sedimentary environments in the everglades-mangrove complex. Part II. The origin, description and classification of the peats of southern Florida. Palaeontographica, Abteilung B 162, 71–114.
Comeaux, R.S., Allison, M.A., Bianchi, T.S., 2012. Mangrove expansion in the Gulf of Mexico with climate change: implications for wetland health and resistance to rising sea levels. Estuarine. Coastal and Shelf Science 96, 81–95.
Costa, C.S.B., Davy, A.J., 1992. Coastal salt marsh communities of Latin America. In: Seeliger, U. (Ed.), Coastal Plant Communities of Latin America. Academic Press, San Diego, USA, pp. 179–199.
Craggs, R., Hofstra, D., Ellis, J., Schwarz, A., Swales, A., Nicholls, P., Hewitt, J., Ovenden, R., Pickmere, S., 2001. Physiological Responses of Mangroves and Saltmarsh to Sedimentation. NIWA Client Report to Auckland Regional Council. ARC01268/1, 78p.
Dangremond, E.M., Feller, I.C., 2016. Precocious reproduction increases at the leading edge of a mangrove range expansion. Ecology and Evolution 6 (14), 5087–5092.
Davis, J.H.J., 1940. The ecology and geologic role of mangroves in Florida. Papers from Tortugas Laboratory 32, 311–384.
Davy, A.J., Costa, C.S.B., 1992. Development and organization of saltmarsh communities. In: Seeliger, U. (Ed.), Coastal Plant Communities of Latin America. Academic Press, San Diego, pp. 179–199.
Digerfeldt, G., Hendry, M.D., 1987. An 8000 year Holocene sea-Level record from Jamaica - implications for interpretation of Caribbean reef and coastal history. Coral Reefs 5, 165–169.
Diop, E.S., Soumare, A., Diallo, N., Guisse, A., 1997. Recent changes of the mangroves of the Saloum river estuary, Senegal. Mangroves and Salt Marshes 1, 163–172.
Doughty, C.L., Langley, J.A., Walker, W.S., Feller, I.C., Schaub, R., Chapman, S.K., 2016. Mangrove range expansion rapidly increases coastal wetland carbon storage. Estuaries and Coasts 39 (2), 385–396.
Downton, W.J.S., 1982. Growth and osmotic relations of the mangrove *Avicennia marina*, as influenced by salinity. Australian Journal of Plant Physiology 9, 519–528.
Duke, N.C., 1995. Genetic diversity, distributional barriers and rafting continents – more thoughts on the evolution of mangroves. Hydrobiologia 295, 167–181.
Duke, N.C., 2006. Australia's Mangroves. The Authoritative Guide to Australia's Mangrove Plants. University of Queensland, Brisbane, 200 p.
Duke, N.C., Ball, M.C., Ellison, J.C., 1998a. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecology and Biogeography Letters 7, 27–47.
Duke, N.C., Benzie, J.A.H., Goodall, J.A., Ballment, E.R., 1998b. Genetic structure and evolution of species in the mangrove genus *Avicennia* (Avicenniaceae) in the Indo-West Pacific. Evolution 52, 1612–1626.
Egler, F.E., 1952. Southeast saline everglades vegetation, Florida, and its management. Vegetatio Acta Geobotanica 3, 213–265.
Ellison, A.M., Farnsworth, E.J., 1993. Seedling survivorship, growth, and response to disturbance in Belizean mangal. American Journal of Botany 80, 1137–1145.
Evans, M.J., Williams, R.J., 1997. Historical distribution of estuarine wetlands at Kurnell Peninsula, Botany Bay: the need and potential for rehabilitation. Wetlands (Australia) 18, 49–54.

Everitt, J.H., Judd, F.W., Escobar, D.E., Davis, M.R., 1996. Integration of remote sensing and spatial information technologies for mapping black mangrove on the Texas gulf coast. Journal of Coastal Research 12, 64–69.

Feller, I.C., Whigham, D.F., McKee, K.L., Lovelock, C.E., 2003b. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. Oecologia 134, 405–414.

Feller, I.C., McKee, K.L., Whigham, D.F., O'Neill, J.P., 2003a. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62, 145–175.

Finlayson, C.M., Bailey, B.J., Freeland, W.J., Fleming, M.R., 1998. Wetlands of the northern territory. In: McComb, A.J., Lake, P.S. (Eds.), The Conservation of Australian Wetlands. Surrey Beatty and Sons, Sydney, pp. 103–126.

Friess, D.A., Webb, E.L., 2014. Variability in mangrove change estimates and implications for the assessment of ecosystem service provision. Global Ecology and Biogeography 23 (7), 715–725.

Friess, D.A., Krauss, K.W., Horstman, E.M., Balke, T., Bouma, T.J., Galli, D., Webb, E.L., 2012. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. Biological Reviews 87 (2), 346–366.

Gehrels, R., Hayward, B., Grenfell, H., Newnham, R., Hunter, J., Southall, K., Sabaa, A., 2007. Rapid Sea-level Rise in Australia and New Zealand during the Past Century. Abstract, XVII INQUA Congress, Cairns Australia.

Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T., Masek, J., Duke, N., 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Global Ecology and Biogeography 20 (1), 154–159.

Giri, C.P., Long, J., 2014. Mangrove reemergence in the northernmost range limit of eastern Florida. Proceedings of the National Academy of Sciences of the United States of America 111, E1447–E1448.

Giri, C., Long, J., 2016. Is the geographic range of mangrove forests in the conterminous United States really expanding? Sensors 16 (12), 2010.

Guo, H., Zhang, Y., Lan, Z., Pennings, S.C., 2013. Biotic interactions mediate the expansion of black mangrove (*Avicennia germinans*) into salt marshes under climate change. Global Change Biology 19 (9), 2765–2774.

Haworth, R.J., 2002. Changes in mangrove/salt-marsh distribution in the Georges River estuary, southern Sydney, 1930-1970. Wetlands (Australia) 20, 80–103.

Henry, K.M., Twilley, R.R., 2013. Soil development in a coastal Louisiana wetland during a climate-induced vegetation shift from salt marsh to mangrove. Journal of Coastal Research 29 (6), 1273–1283.

Howard, R.J., Day, R.H., Krauss, K.W., From, A.S., Allain, L., Cormier, N., 2016. Hydrologic restoration in a dynamic subtropical mangrove-to-marsh ecotone. Restoration Ecology 25 (3), 471–482.

Hutchings, P., Saenger, P., 1987. Ecology of Mangroves. University of Queensland Press, St Lucia, Queensland, Australia.

Hyland, S.J., Butler, C.T., 1988. The Distribution and Modification of Mangroves and Saltmarsh-claypans in Southern Queensland. Queensland Department of Primary Industries, Brisbane, 74 p.

Islebe, G., Sanchez, O., 2002. History of late holocene vegetation at Quintana Roo, Caribbean coast of Mexico. Plant Ecology 160, 187–192.

Jennings, J.N., 1975. Desert dunes and estuarine fill in the Fitzroy estuary, north-western Australia. Catena 2, 215–262.

Jolly, P., Chin, D., 1992. Rehabilitation of the Mary River floodplains: a review of MSS and TM imagery 1972-1992. In: Davenport, C.C., Riley, S.J., Ringrose, S.M. (Eds.), Proceedings of the GIS and Environmental Rehabilitation Workshop. Australian Government Publishing Service, Canberra, Australia, pp. 43–54.

Kangas, P.C., Lugo, A.E., 1990. The distribution of mangrove and saltmarsh in Florida. Tropical Ecology 31, 32–39.

Kelleway, J.J., Saintilan, N., Macreadie, P.I., Skilbeck, C.G., Zawadzki, A., Ralph, P.J., 2016. Seventy years of continuous encroachment substantially increases 'blue carbon'capacity as mangroves replace intertidal salt marshes. Global Change Biology 22 (3), 1097–1109.

Krauss, K.W., From, A.S., Doyle, T.W., Doyle, T.J., Barry, M.J., 2011. Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Islands region of Florida, USA. Journal of Coastal Conservation 15 (4), 629–638.

Knighton, A.D., Mills, K., Woodroffe, C.D., 1991. Tidal-creek extension and saltwater intrusion in Northern Australia. Geology 19, 831–834.

Lange, W.P., de Lange, P.J., 1994. An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicennia marina* var. resinifera) in New Zealand. Journal of Coastal Research 10, 539–548.

Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Diele, K., Fromard, F., Koedam, N., Marchand, C., Mendelssohn, I., Mukherjee, N., Record, S., 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. Global Ecology and Biogeography 23, 726–743.

Lewis, D.B., Brown, J.A., Jimenez, K.L., 2014. Effects of flooding and warming on soil organic matter mineralization in *Avicennia germinans* mangrove forests and Juncus roemerianus salt marshes. Estuarine. Coastal and Shelf Science 139, 11–19.

Lin, G.H., Sternberg, L.D.S.L., 1992. Effect of growth form, salinity, nutrients and sulfide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). Australian Journal of Plant Physiology 19, 509–517.

Lonard, R.I., Judd, F.W., 1985. Effects of a severe freeze on native woody-plants in the lower Rio-Grande valley, Texas. Southwestern Naturalist 30, 397–403.

Long, S.P., Mason, C.F., 1983. Saltmarsh Ecology. Blackie and Son Ltd, Glasgow and London.

López-Hoffman, L., DeNoye, J.L., Monroe, I.E., Shaftel, R., Anten, N.P.R., Martínez-Ramos, M., David, D., Ackerly, D.D., 2006. Mangrove seedling net photosynthesis, growth, and survivorship are interactively affected by salinity and light. Biotropica 38, 606–616.

Lopez-Portillo, Ezcurra, E., 1989. Response of three mangroves to salinity in two geoforms. Functional Ecology 3, 355–361.

Lot, H.A., Vázquez-Yánes, C., Menéndez, F., 1975. Physiognomic and floristic changes near the northern limit of mangroves in the gulf coast of Mexico. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, vol. 1. University of Florida, Gainesville, pp. 52–61.

Lovelock, C.E., Feller, I.C., McKee, K.L., Engelbrecht, B.M.J., Ball, M.C., 2004. Experimental evidence for nutrient limitation of growth, photosynthesis, and hydraulic conductance of dwarf mangroves in Panama. Functional Ecology 18, 25–33.

Lovelock, C.E., Feller, I.C., Ball, M.C., Engelbrecht, B.M.J., Ewel, M.L., 2006. Differences in plant function in phosphorus- and nitrogen-limited mangrove ecosystems. New Phytologist 172, 514–522.

Lovelock, C.E., Feller, I.C., Reef, R., Hickey, S., Ball, M.C., 2017. Mangrove dieback during fluctuating sea levels. Scientific Reports 7 (1), 1680.

Macintyre, I.G., Toscano, M.A., Lighty, R.G., Bond, G.B., 2004. Holocene history of the mangrove islands of Twin Cays, Belize, Central America. Atoll Research Bulletin 510, 1–16.

Macintyre, I.G., Little, M.M., Littler, D.S., 1995. Holocene history of Tobacco range, Belize, Central America. Atoll Research Bulletin 430, 1–18.

MacNae, W., 1966. Mangroves in eastern and southern Australia. Australian Journal of Botany 14, 67–104.

Manson, F.J., Loneragan, N.R., Phinn, S.R., 2003. Spatial and temporal variation in distribution of mangroves in Moreton Bay, subtropical Australia: a comparison of pattern metrics and change detection analyses based on aerial photographs. Estuarine, Coastal and Shelf Science 57, 653–666.

Markley, J.L., McMillan, C., Thompson Jr., G.A., 1982. Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans, Laguncularia racemosa*, and *Rhizophora mangle*, from the western tropical Atlantic and Pacific Panama. Canadian Journal of Botany 60, 2704–2715.

Mbense, S., Rajkaran, A., Bolosha, U., Adams, J., 2016. Rapid colonization of degraded mangrove habitat by succulent salt marsh. South African Journal of Botany 107, 129–136.

McKee, K.L., 1995a. Mangrove species distribution patterns and propagule predation in Belize: an exception to the dominance-predation hypothesis. Biotropica 27, 334–345.

McKee, K.L., 1995b. Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. American Journal of Botany 82, 299–307.

McKee, K.L., Cahoon, D.R., Feller, I.C., 2007a. Caribbean mangroves adjust to rising sea level through biotic controls on soil elevation change. Global Ecology and Biogeography 16, 545–556.

McKee, K.L., Faulkner, P.L., 2000. Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize. Atoll Research Bulletin 468, 46–58.

McKee, K.L., Feller, I.C., Popp, M., Wanek, W., 2002. Mangrove isotopic (δ^{15}N and δ^{13} C) fractionation across a nitrogen vs. phosphorous limitation gradient. Ecology 83, 1065–1075.

McKee, K.L., Mendelssohn, I.A., Materne, M.D., 2004. Acute salt marsh dieback in the Mississippi River deltaic plain: a drought-induced phenomenon? Global Ecology and Biogeography 13, 65–73.

McKee, K.L., Rogers, K., Saintilan, N., 2012. Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In: Middleton, B. (Ed.), Global Change and the Function and Distribution of Wetlands. Springer, pp. 63–96.

McKee, K.L., Rooth, J.E., 2008. Where temperate meets tropical: multi-factorial effects of elevated CO_2, nitrogen enrichment, and competition on a mangrove-salt marsh community. Global Change Biology 14, 1–14.

McKee, K.L., Rooth, J.E., Feller, I.C., 2007b. Mangrove recruitment after forest disturbance is facilitated by herbaceaous species in the Caribbean. Ecological Applications 17 (6), 1678–1693.

McLoughlin, L., 2000. Estuarine wetlands distribution along the Parramatta river, Sydney, 1788-1940: implications for planning and conservation. Cunninghamia 6, 579–610.

McMillan, C., 1975. Adaptive differentiation to chilling in mangrove populations. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, vol. 1. University of Florida, Gainesville, pp. 62–68.

McMillan, C., Sherrod, C.L., 1986. The chilling tolerance of black mangrove, Avicennia germinans, from the Gulf of Mexico Coast of Texas, Louisiana and Florida. Contributions in Marine Science 29, 9–16.

McTainsh, G., Iles, B., Saffinga, P., 1986. Spatial and temporal patterns of mangroves at Oyster point Bay, south east Queensland, 1944-1983. Proceedings of the Royal Society of Queensland 99, 83–91.

Meehan, A., 1997. Historical Changes in Seagrass, Mangrove and Saltmarsh Communities in Merimbula Lake and Pambula Lake (Honours thesis). University of Wollongong.

Mendelssohn, I.A., McKee, K.L., 2000. Salt marshes and mangroves. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation. Cambridge University Press, Cambridge, pp. 501–536.

Mildenhall, D.C., Brown, L.J., 1987. An early Holocene occurrence of the mangrove *Avicennia marina* in Poverty Bay, North Island, New Zealand: its climatic and geological implications. New Zealand Journal of Botany 25, 281–294.

Mitchell, M.L., Adam, P., 1989a. The relationship between mangrove and saltmarsh communities in the Sydney region. Wetlands (Australia) 8, 37–46.

Mitchell, M.L., Adam, P., 1989b. The decline of saltmarsh in Botany Bay. Wetlands (Australia) 8, 55–60.

Mitsch, W.J., Gosselink, J.G., 2000. Wetlands, third ed. John Wiley and Sons, New York.

Montague, C.L., Wiegert, R.G., 1990. Salt marshes. In: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida, Orlando, pp. 481–516.

Montague, C.L., Odum, H.T., 1997. The intertidal marshes of Florida's Gulf Coast. In: Coultas, C.L., Hsieh, Y. (Eds.), Ecology and Management of Tidal Marshes. A model from the Gulf of Mexico St Lucie Press, pp. 1–9, 334 pp.

Morrisey, D.J., Skilleter, G.A., Ellis, J.I., Burns, B.R., Kemp, C.E., Burt, K., 2003. Differences in benthic fauna and sediment among mangrove (*Avicennia marina* var. *australasica*) stands of different ages in New Zealand. Estuarine, Coastal and Shelf Science 56, 581–592.

Morton, R.M., 1994. Fluctuations in wetland extent in southern Moreton Bay. In: Greenwood, J.G., Hall, N.J. (Eds.), Future Marine Science in Moreton Bay. School of Marine Science, University of Queensland, Brisbane, pp. 145–150.

Mulrennan, M.E., Woodroffe, C.D., 1998. Saltwater intrusion into the coastal plains of the lower Mary River, northern territory, Australia. Journal of Environmental Management 54, 169–188.

Murdiyarso, D., Purbopuspito, J., Kauffman, J.B., Warren, M.W., Sasmito, S.D., Donato, D.C., Kurnianto, S., 2015. The potential of Indonesian mangrove forests for global climate change mitigation. Nature Climate Change 5 (12), 1089–1092.

Naidoo, G., 1987. Effects of salinity and nitrogen on growth and water relations in the mangrove *Avicennia marina* (Forsk.) Vierh. New Phytologist 107, 317–325.

Norman, H., McMillan, C., Thompson, G.A., 1984. Phosphatidylglycerol molecular species in chilling-sensitive and chilling-resistant populations of *Avicennia germinans* (L.) L. Plant and Cell Physiology 25, 1437–1444.

NOAA, 2007. Sea Surface Temperature (SST) Contour Charts. Prepared by National Oceanic and Atmospheric Administration (NOAA) Satellites and Information. Accessed at: http://www.osdpd.noaa.gov/PSB/EPS/SST/contour.html.

Olmsted, I., Dunevitz, H., Platt, W.J., 1993. Effects of freezes on tropical trees in everglades National Park Florida, USA. Tropical Ecology 34, 17–34.

Osland, M.J., Enwright, N., Day, R.H., Doyle, T.W., 2013. Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. Global Change Biology 19 (5), 1482–1494.

Osland, M.J., Enwright, N., Stagg, C.L., 2014. Freshwater availability and coastal wetland foundation species: ecological transitions along a rainfall gradient. Ecology 95 (10), 2789–2802.
Osland, M.J., Day, R.H., From, A.S., McCoy, M.L., McLeod, J.L., Kelleway, J.J., 2015. Life stage influences the resistance and resilience of black mangrove forests to winter climate extremes. Ecosphere 6 (9), 1–15.
Osland, M.J., Enwright, N.M., Day, R.H., Gabler, C.A., Stagg, C.L., Grace, J.B., 2016. Beyond just sea-level rise: considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. Global Change Biology 22 (1), 1–11.
Osland, M.J., Spivak, A.C., Nestlerode, J.A., Lessmann, J.M., Almario, A.E., Heitmuller, P.T., Russell, M.J., Krauss, K.W., Alvarez, F., Dantin, D.D., Harvey, J.E., 2012. Ecosystem development after mangrove wetland creation: plant–soil change across a 20-year chronosequence. Ecosystems 15 (5), 848–866.
Park, S., 2001. Bay of Plenty Maritime Wetlands Database. Environment of the Bay of Plenty. Environmental Report 2000/21.
Patterson, C.S., Mendelssohn, I.A., 1991. A comparison of physicochemical variables across plant zones in a mangal/salt marsh community in Louisiana. Wetlands 11, 139–161.
Patterson, C.S., Mendelssohn, I.A., Swenson, E.M., 1993. Growth and survival of Avicennia germinans seedlings in a mangal/salt marsh community in Louisiana, U.S.A. Journal of Coastal Research 9, 801–810.
Patterson, S., McKee, K.L., Mendelssohn, I.A., 1997. Effects of tidal inundation and predation on Avicennia germinans seedling establishment and survival in a sub-tropical mangal/salt marsh community. Mangroves and Salt Marshes 1, 103–111.
Peinado, M., Alcaraz, F., Delgadillo, J., De La Cruz, M., Alvarez, J., Aguirre, L.J., 1994. The coastal salt marshes of California and Baja California. Plant Ecology 110, 55–66.
Pendleton, L., Donato, D.C., Murray, B.C., Crooks, S., Jenkins, W.A., Sifleet, S., Fourqurean, J.W., Kauggman, J.B., Marba, N., Megonigal, P., 2012. Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. PLoS One 7 (9), e43542.
Perry, C.L., Mendelssohn, I.A., 2009. Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. Wetlands 29 (1), 396–406.
Peterson, J.M., Bell, S.S., 2012. Tidal events and salt-marsh structure influence black mangrove (*Avicennia germinans*) recruitment across an ecotone. Ecology 93 (7), 1648–1658.
Peterson, J.M., Bell, S.S., 2015. Saltmarsh Boundary Modulates Dispersal of Mangrove Propagules: Implications for Mangrove Migration with Sea-Level Rise. PLoS One 10 (3), e0119128.
Pidgeon, I.M., 1940. The ecology of the central coast area of New South Wales III. Types of Primary Succession. Proceedings of the Linnaean Society of New South Wales 65, 221–249.
Raabe, E.A., Roy, L.C., McIvor, C.C., 2012. Tampa Bay coastal wetlands: nineteenth to twentieth century tidal marsh-to-mangrove conversion. Estuaries and Coasts 35 (5), 1145–1162.
Raabe, E.A., Stumpf, R.P., 2016. Expansion of tidal marsh in response to sea-level rise: Gulf Coast of Florida, USA. Estuaries and Coasts 39 (1), 145–157.
Rabinowitz, D., 1975. Planting experiments in mangrove swamps of Panama. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, vol. 1. University of Florida, Gainesville, pp. 385–393.
Rabinowitz, D., 1978a. Dispersal properties of mangrove propagules. Biotropica 10, 47–57.
Rabinowitz, D., 1978b. Mortality and initial propagule size in seedlings in Panama. Journal of Ecology 66, 45–51.
Rabinowitz, D., 1978c. Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationships of dispersal and zonation. Journal of Biogeography 5, 113–133.
Ramcharan, E.K., 2004. Mid-to-late Holocene sea level influence on coastal wetland development in Trinidad. Quaternary International 120, 145–151.
Reimold, R.J., 1977. Mangals and salt marshes of eastern United States. In: Chapman, V.J. (Ed.), Ecosystems of the World. 1. Wet Coastal Ecosystems. Elsevier Scientific Publications Company, Amsterdam, pp. 157–166.
Rogers, K., 2004. Mangrove and Saltmarsh Surface Elevation Dynamics in Relation to Environmental Variables in Southeastern Australia. A thesis submitted in fulfillment of the requirements of the degree of Doctor of Philosophy from University of Wollongong, Earth and Environmental Sciences, Faculty of Science, 270 p.
Rogers, K., Saintilan, N., 2008. Relationships between surface elevation and groundwater in mangrove forests of SE Australia. Journal of Coastal Research 24, 63–69.

Rogers, K., Saintilan, N., Cahoon, D., 2005a. Surface elevation dynamics in a regenerating mangrove forest, Homebush Bay, Australia. Wetlands Ecology and Management 13, 587–598.
Rogers, K., Saintilan, N., Heijnis, H., 2005b. Monitoring of mangrove and saltmarsh resources in Westernport Bay, Australia. Estuaries 28, 551–559.
Rogers, K., Saintilan, N., Wilton, K., 2006. Vegetation change and surface elevation dynamics of the estuarine wetlands of southeast Australia. Estuarine, Coastal and Shelf Science 66, 559–569.
Rogers, K., Saintilan, N., Howe, A.J., Rodríguez, J.F., 2013. Sedimentation, elevation and marsh evolution in a south-eastern Australian estuary during changing climatic conditions. Estuarine, Coastal and Shelf Science 133, 172–181.
Rogers, K., Saintilan, N., Woodroffe, C.D., 2014. Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: implications for coastal wetland response to climate change. Estuarine. Coastal and Shelf Science 149, 46–56.
Roy, P.S., 1984. New South Wales estuaries- their origin and evolution. In: Thom, B.G. (Ed.), Development in Coastal Geomorphology in Australia. Academic Press, San Diego CA, pp. 99–121.
Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of south-east Australian estuaries. Estuarine, Coastal and Shelf Science 53, 351–384.
Saenger, P., 2002. Mangrove Ecology, Silviculture and Conservation. Kluwer Academic Press, Dordrecht, Boston, London.
Saenger, P., Moverley, J., 1985. Vegetative phenology of mangroves along the Queensland coastline. Proceedings of the Ecological Society of Australia 13, 257–265.
Saenger, P., Snedaker, S.C., 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. Oecologia 96, 293–299.
Saenger, P., Specht, M.M., Specht, R.L., Chapman, V.J., 1977. Mangal and coastal saltmarsh communities in Australasia. In: Chapman, V.J. (Ed.), Ecosystems of the World I: Wet Coastal Ecosystems. Elsevier, Amsterdam, pp. 293–345.
Saintilan, N., 1997. Mangroves as successional stages on the Hawkesbury River Estuary, New South Wales. Wetlands (Australia) 16, 99–107.
Saintilan, N., 1998. Photogrammetric survey of the Tweed River wetlands. Wetlands (Australia) 17, 74–82.
Saintilan, N., 2003. The Influence of Nutrient Enrichment upon Mangrove Seedling Establishment and Growth in the Hawkesbury River Estuary, New South Wales, Australia. Wetlands (Australia) 21, 29–35.
Saintilan, N., Williams, R.J., 1999. Mangrove transgression into saltmarsh environments in south-east Australia. Global Ecology and Biogeography Letters 8, 117–124.
Saintilan, N., Hashimoto, R., 1999. Mangrove-saltmarsh dynamics on a prograding bayhead delta in the Hawkesbury River estuary, New South Wales, Australia. Hydrobiologia 413, 95–102.
Saintilan, N., Williams, R.J., 2000. The decline of saltmarshes in Southeast Australia: Results of recent surveys. Wetlands (Australia) 18, 49–54.
Saintilan, N., Wilton, K., 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetlands Ecology and Management 9, 409–420.
Saintilan, N., Rogers, K., 2013. The significance and vulnerability of Australian saltmarshes: implications for management in a changing climate. Marine and Freshwater Research 64 (1), 66–79.
Saintilan, N., Wilson, N.C., Rogers, K., Rajkaran, A., Krauss, K.W., 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Global Change Biology 20 (1), 147–157.
Saintilan, N., Rogers, K., 2015. Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. New Phytologist 205 (3), 1062–1070.
Saintilan, N., Rogers, K., Kelleway, J.J., Ens, E., Sloane, D.R., 2018. Climate Change Impacts on the Coastal Wetlands of Australia, pp. 1–10.
Santos, M.C.F.V., Zieman, J.C., Cohen, R.R.H., 1997. Interpreting the upper mi-littoral zonation patterns of mangroves in Maranhão (Brazil) in response to microtopography and hydrology. In: Kjerfve, B., Lacerda, L.D., Diop, E.H.S. (Eds.), Mangrove Ecosystem Studies in Latin America and Africa. UNESCO, Paris, pp. 127–144.
Schaeffer-Novelli, Y., Cintron-Molero, G., Adaime, R.R., de Camargo, T.M., 1990. Variability of mangrove ecosystems along the Brazilian Coast. Estuaries 13, 204–216.
Schmidt, D.A., Burgman, R., 2003. Time-dependent uplift and subsidence in the Santa Clara Valley, California, from a large interferometric synthetic aperture radar data set. Journal of Geophysical Research – Solid Earth 108, 2416.

Semeniuk, V., 1980. Mangrove zonation along an eroding coastline in King Sound, North-Western Australia. Journal of Ecology 68, 789–812.
Semeniuk, V., 1982. Geomorphology and Holocene history of the tidal flats, King Sound, north-western Australia. Journal of the Royal Society of Western Australia 65, 47–68.
Sherrod, C.L., McMillan, C., 1985. The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. Contributions in Marine Science 28, 129–140.
Silvestri, S., Defina, A., Marani, M., 2005. Tidal regime, salinity and salt marsh plant zonation. Estuarine, Coastal and Shelf Science 62, 119–130.
Simpson, L.T., Feller, I.C., Chapman, S.K., 2013. Effects of competition and nutrient enrichment on *Avicennia germinans* in the salt marsh-mangrove ecotone. Aquatic Botany 104, 55–59.
Smith, T.J., 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68, 266–273.
Smith, T.J., Duke, N.C., 1987. Physical determinants of inter-estuary variation in mangrove species richness around the tropical coastline of Australia. Journal of Biogeography 14, 9–20.
Smith, T.J., Chan, H.T., McIvor, C.C., Robblee, M.B., 1989. Comparisons of seed predation in tropical, tidal forests from three continents. Ecology 70, 146–151.
Snedaker, S.C., 1982. Mangrove species zonation: why?. In: Sen, D.N., Rajpurohit, K.S. (Eds.), Contribution to the Ecology of Halophytes, vol. 2. Dr. W. Junk, The Hague, pp. 111–125.
Solomon, S., Quin, D., Manning, M., Marquis, M., Avery, K., Tignor, M., Miller, H., Chen, Z. (Eds.), 2007. Climate Change 2007- the Physical Science Basis. Contribution of Working Group 1 to the Fourth Assessment Report of the IPCC. Cambridge University Press.
Snedaker, S.C., 1995. Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. Hydrobiologia 295, 43–49.
Sousa, W.P., Kennedy, P.G., Mitchell, B.J., Ordóñez L, B.M., 2007. Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure? Ecological Monographs 77 (1), 53–76.
Sousa, W.P., Mitchell, B.J., 1999. The effect of seed predators on plant distributions: is there a general pattern in mangroves? Oikos 86, 55–66.
Spackman, W., Dolsen, C.P., Riegel, W., 1966. Phytogenic organic sediments and sedimentary environments in the Everglades-Mangrove complex. Part 1: Evidence of a transgressing sea and its effects on environments of the Shark River areas of Southwestern Florida. Palaeontographica 117, 135–152.
Spalding, M.D., Blasco, F., Field, C.D., 1997a. World mangrove atlas. International Society for Mangrove Conservation, National Council for Scientific Research, Paris.
Spalding, M.D., Blasco, F., Field, C.D., 1997b. World Mangrove Atlas. International Society for Mangrove Ecosystems, Okinawa, Japan.
Specht, R.L., 1981. Biogeography of halophytic angiosperms (salt-marsh, mangrove and sea-grass). Ecological biogeography of Australia. Dr. W. Junk bv Publishers, The Hague, pp. 575–589.
Stevens, P.W., Fox, S.L., Montague, C.L., 2006. The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. Wetlands Ecology and Management 14, 435–444.
Stuart, S.A., Choat, B., Martin, K.C., Holbrook, N.M., Ball, M.C., 2007. The role of freezing in setting the latitudinal limits of mangrove forests. New Phytologist 173 (3), 576–583.
Thom, B.G., 1967. Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. Journal of Ecology 55, 301–343.
Thom, B.G., Wright, L.D., Coleman, J.M., 1975. Mangrove ecology and deltaic-estuarine geomorphology, Cambridge Gulf-Ord River, Western Australia. Journal of Ecology 63, 203–222.
Thomas, M.L.H., 1993. Mangrove swamps in Bermuda. Atoll Research Bulletin 386, 1–18.
Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.
Toscano, M.A., Macintyre, I.G., 2003. Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated C-14 dates from *Acropora palmata* framework and intertidal mangrove peat. Coral Reefs 22, 257–270.
Van Steenis, C.G.G.J., 1968. Frost in the tropics. In: Misra, R., Gopal, B. (Eds.), Recent Advances in Tropical Ecology, Part I. International Society for Tropical Ecology, Varanasi, India, pp. 154–167.
Vanderzee, M.P., 1988. Changes in saltmarsh vegetation as an early indicator of sea-level rise. In: Pearman, G.I. (Ed.), Greenhouse: Planning for Climate Change. CSIRO, Melbourne.
Walsh, G.E., 1974. Mangroves: a review. In: Reimhold, R.J., Queens, W.H. (Eds.), Ecology of Halophytes. Academic Press, New York, pp. 51–174.

Watson, E.B., 2004. Changing elevation, accretion, and tidal marsh plant assemblages in a South San Francisco Bay tidal marsh. Estuaries 27, 684–698.

West, R.C., 1977. Tidal salt-marsh and mangal formations of Middle and South America. In: Chapman, V.J. (Ed.), Ecosystems of the World. 1. Wet Coastal Ecosystems. Elsevier Scientific Publications Company, Amsterdam, pp. 193–213.

West, R.J., 1993. Estuarine Fisheries Resources of Two South Eastern Australian Rivers (Ph.D. thesis). University of New South Wales, 173 p.

Whelan, K.R.T., Smith, T.J., Cahoon, D.R., Lynch, J.C., Anderson, G.H., 2005. Groundwater control of mangrove surface elevation: Shrink and swell varies with soil depth. Estuaries 28, 833–843.

Williams, A.A., Eastman, S.F., Eash-Loucks, W.E., Kimball, M.E., Lehmann, M.L., Parker, J.D., 2014. Record northern-most endemic mangroves on the United States Atlantic Coast with a note on latitudinal migration. Southeastern Naturalist 13 (1), 56–63.

Williams, R.J., Meehan, A.J., 2004. Focusing management needs at the sub-catchment level via assessments of change in the cover of estuarine vegetation, Port Hacking, NSW, Australia. Wetlands Ecology and Management 12, 499–518.

Williams, R.J., Watford, F.A., 1997. Changes in the Distribution of Mangrove and Saltmarsh in Berowra and Marramarra Creeks, 1941-1992. NSW Fisheries, Fisheries Research Institute, Cronulla, 21 p.

Williams, R.J., Watford, F.A., Balashov, V., 1999. Kooragang Wetland Rehabilitation Project: Changes in Wetland Fish Habitats of the Lower Hunter River. NSW Fisheries, Office of Conservation, Fisheries Research Institute, Cronulla.

Wilson, B.P., 2005. Elevation of sulphurous layers in acid sulphate soils: what do they indicate about sea levels during the Holocene in eastern Australia? Catena 62, 45–56.

Winn, K.O., Saynor, M.J., Eliot, M.J., Eliot, I., 2006. Saltwater intrusion and morphologicvla change at the mouth of the East Alligator River, Northern Territory. Journal of Coastal Research 22, 137–149.

Winning, G., 1990. Lake Macquarie Littoral Habitats Study. The Wetlands Centre, Shortland, 29 p., plus appendices.

Woodroffe, C.D., 1981. Mangrove swamp stratigraphy and holocene transgression, Grand Cayman Island, West Indies. Marine Geology 41, 271–294.

Woodroffe, C.D., 1983. Development of Mangrove forests from a geological perspective. In: Teas, H.J. (Ed.), Tasks for Vegetation Science. Dr. W. Junk Publishers, The Hague, pp. 1–17.

Woodroffe, C.D., Chappell, J., Thom, B.G., Wallensky, E., 1989. Depositional model of a macrotidal estuary and flood-plain, South Alligator River, Northern Australia. Sedimentology 36, 737–756.

Woodroffe, C.D., Thom, B.G., Chappell, J., 1985. Development of widespread mangrove swamps in mid-Holocene times in northern Australia. Nature 317, 711–713.

Woodroffe, C.D., Mulrennan, M.E., 1993. Geomorphology of the Lower Mary River Plains, Northern Territory. Australian National University and the Conservation Commission of the Northern Territory, Darwin.

Zomlefer, W.B., Judd, W.S., Giannasi, D.E., 2006. Northernmost limit of *Rhizophora mangle* (red mangrove; Rhizophoraceae) in St. Johns County, Florida. Castanea 71, 239–244.

Global Change Biology

Global Change Biology (2014) **20**, 147–157, doi: 10.1111/gcb.12341

Mangrove expansion and salt marsh decline at mangrove poleward limits

NEIL SAINTILAN*, NICHOLAS C. WILSON†, KERRYLEE ROGERS‡, ANUSHA RAJKARAN§ and KEN W. KRAUSS¶

NSW Department of Premier and Cabinet, Office of Environment and Heritage, PO Box A290, Sydney South, NSW 1232, Australia, †Forest Science Institute of South Vietnam, 1 Pham Van Hai Street, Tan Binh District, Ho Chi Minh City, Vietnam, ‡School of Earth and Environmental Science, University of Wollongong, Northfields Ave, Wollongong 2522, Australia, §Department of Botany, Rhodes University, PO Box 94, Grahamstown 6140, South Africa, ¶National Wetlands Research Center, US Geological Survey, Lafayette, LA 70506, USA

Abstract

Mangroves are species of halophytic intertidal trees and shrubs derived from tropical genera and are likely delimited in latitudinal range by varying sensitivity to cold. There is now sufficient evidence that mangrove species have proliferated at or near their poleward limits on at least five continents over the past half century, at the expense of salt marsh. *Avicennia* is the most cold-tolerant genus worldwide, and is the subject of most of the observed changes. *Avicennia germinans* has extended in range along the USA Atlantic coast and expanded into salt marsh as a consequence of lower frost frequency and intensity in the southern USA. The genus has also expanded into salt marsh at its southern limit in Peru, and on the Pacific coast of Mexico. Mangroves of several species have expanded in extent and replaced salt marsh where protected within mangrove reserves in Guangdong Province, China. In south-eastern Australia, the expansion of *Avicennia marina* into salt marshes is now well documented, and *Rhizophora stylosa* has extended its range southward, while showing strong population growth within estuaries along its southern limits in northern New South Wales. *Avicennia marina* has extended its range southwards in South Africa. The changes are consistent with the poleward extension of temperature thresholds coincident with sea-level rise, although the specific mechanism of range extension might be complicated by limitations on dispersal or other factors. The shift from salt marsh to mangrove dominance on subtropical and temperate shorelines has important implications for ecological structure, function, and global change adaptation.

Keywords: Australia, climate change, mangrove, range expansion, salt marsh, South Africa, South America, temperature, USA

Received 23 January 2013 and accepted 25 June 2013

Introduction

The increase in global average surface temperature of 0.74 °C (1906–2005) (Solomon *et al*., 2007) has already caused shifts in the structure and distribution of ecological communities at a variety of scales (Walther *et al*., 2002; Parmesan & Yohe, 2003). Arctic shrubs have advanced northward in response to decreases in intensity of freezing (Sturm *et al*., 2001), and an advance in range has been demonstrated for butterfly species (up to 200 km) (Parmesan *et al*., 1999) as well as birds (an average of 20 km for 12 bird species in Britain) (Thomas & Lennon, 1999). Minimum temperatures globally are increasing at twice the rate of maximum temperatures (Walther *et al*., 2002). In temperate climates, increasing temperature and decreasing intensity and frequency of frost are likely to cause transitions in the distribution of temperature sensitive higher plants (Bakkenes *et al*., 2002; Loarie *et al*., 2008), which in many instances provide structural habitat and organic carbon to organisms and ecosystems.

In many ways, mangroves are ideal species for monitoring the impacts of global climate change on vegetated habitats. Mangroves are sensitive to several global environmental conditions undergoing change, including enhanced atmospheric CO_2 (McKee & Rooth, 2008), sea level (Woodroffe, 1990; McKee *et al*., 2007), temperature (Alongi, 2008), and rainfall (Semeniuk, 2013). All mangrove species are hydrochorous and thus often have some potential for dispersal to new localities by sea currents and drift (see Friess *et al*., 2012; Van der Stocken *et al*., 2013). Mangroves are conspicuous and can be identified from aerial photography at a scale represented in easily accessible geographic applications such as Google Earth (www.google.com/earth/index.html) and Nearmap (www.nearmap.com), displaying an emergent canopy above salt marsh in temperate and

Correspondence: Neil Saintilan, tel. 612 9995 5631, fax 612 9995 5924, e-mail: neil.saintilan@environment.nsw.gov.au

© 2013 John Wiley & Sons Ltd

subtropical intertidal environments, although on-ground verification may be required when grading to freshwater woody vegetation. They are an important habitat for estuarine, nearshore and terrestrial biota (Nagelkerken *et al.*, 2008), and play a critical role in coastal environments in stabilising shorelines (Gedan *et al.*, 2011), and sequestering atmospheric carbon (Chmura *et al.*, 2003; Donato *et al.*, 2011).

Temperature has long been considered the primary limit to the latitudinal range of mangroves. Walsh (1974) postulated that this poleward threshold corresponded to a mean monthly atmospheric temperature of 20 °C for the coldest month. Duke *et al.* (1998) more accurately identified the winter position of the 20 °C isotherm for sea surface temperature (SST) as corresponding to the latitudinal limit in both hemispheres (Fig. 1), although SST and air temperature at the latitudinal limit of individual species and genera may vary between continents (Quisthoudt *et al.*, 2012). While mean temperatures provide a correlative explanation for mangrove distribution, quantifying minimum temperature requirements (and measures of extreme winter events) provide an even better mechanistic approach for quantifying thresholds (Osland *et al.*, 2013). That mangroves will shift their distribution after meeting minimum temperature thresholds in response to changing climate is well attested by the fossil record. Mangrove species distribution has changed in concert with small changes in temperature since the early Holocene. For example, a slight cooling following the mid-Holocene highstand (6000 years BP) is associated with the less common occurrence of Rhizophoraceae in northern NSW (Hashimoto *et al.*, 2006), and the loss of *Avicennia marina* from the Poverty Bay-East Cape region of New Zealand (Mildenhall, 1994).

However, caution should be exercised in interpreting changes in distribution and latitudinal limits solely to temperature. The effects of temperature upon mangroves are mediated by interactions with other aspects of global change (e.g., CO_2, precipitation, sea-level rise, nutrients). Geomorphic changes in response to rising, and then stabilising sea level exerted the strongest control on mangrove extent over the Holocene (e.g., Grindrod *et al.*, 1999; Hashimoto *et al.*, 2006). Both fluctuating sea levels and temperature regimes have vastly influenced mangrove distributions globally since much older geological time frames than the Holocene (Sherrod & McMillan, 1985; Ellison *et al.*, 1999). Contemporary distributions are shaped by suitable intertidal habitat, and the capacity of floating propagules to access these locations. Impediments to colonization therefore include unfavorable ocean currents, closed estuary entrances, or on arid and hard-rock coastlines, an absence of estuaries with depositional environments suitable for mangrove establishment (Saintilan *et al.*, 2009). Such impediments have slowed the filling of potential niche as defined by temperature thresholds for many species (Quisthoudt *et al.*, 2012).

Several publications have postulated that mangroves will migrate to higher latitudes, replacing salt marsh as

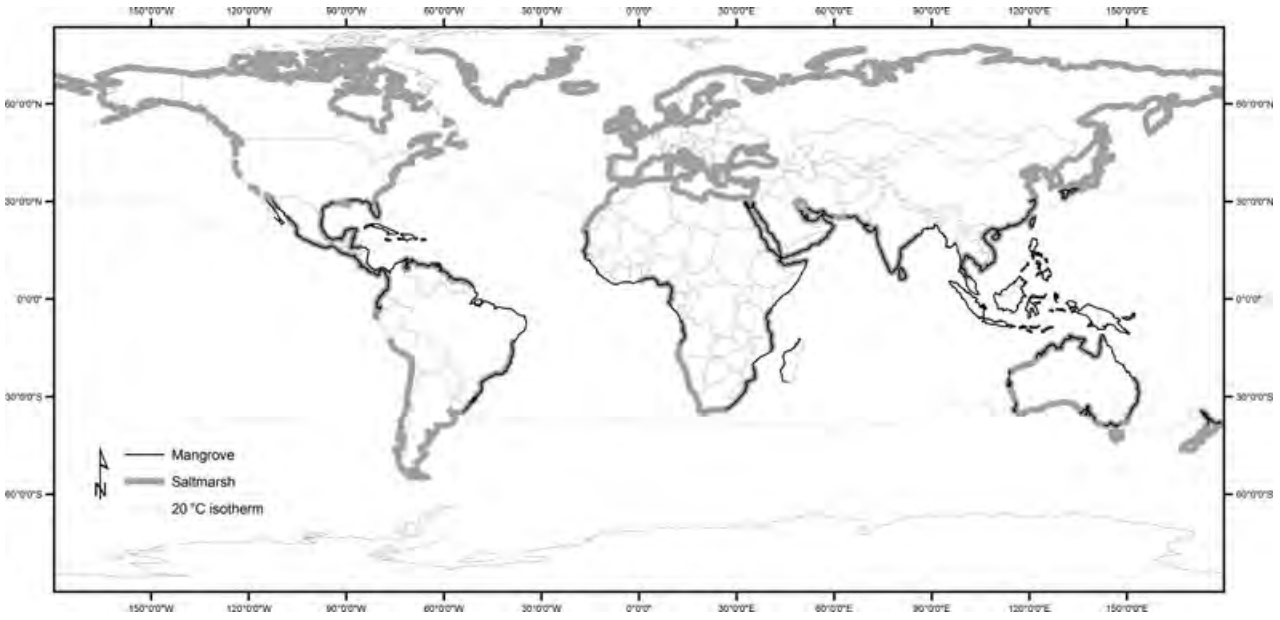


Fig. 1 Global mangrove and salt marsh distribution and the average 20 °C sea-surface temperature isotherm. Sources: Spalding (2012), Hoekstra *et al.* (2010), and NOAA (2013).

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

an outcome of global warming (Woodroffe & Grindrod, 1991; Field, 1995; Gilman *et al*., 2008). However, assessments of changes in mangrove extent at poleward limits are restricted to a few site specific studies. In this paper, we use published historic records of occurrence and distribution limits, contemporary published surveys, and our own observations to provide a global synthesis of evidence for proliferation and extension of mangroves at poleward limits. Mangroves are absent from Europe and the Mediterranean Sea but coexist with salt marsh in temperate settings in Asia, Africa, Australia/New Zealand, North America, and South America.

Materials and methods

We present a synthesis of literature from four continents detailing changes in the distribution of mangroves. In some cases, we provide additional analyses using remote sensing, field survey and local expert observations. We used Google Earth Pro (www.google.com/earth/index.html) to confirm occurrence within estuaries and poleward extent in each of the focus regions using the most recent available imagery. These images included photography of Cedar Keys, Florida (imagery dated 19 January 2012), Virilla estuary, Peru (imagery dated 19 January 2010, DigitalGlobe), and Piura estuary, Peru (imagery dated 10 February 2011, DigitalGlobe). We also used Google Earth Pro's polygon area function to estimate the extent of mangroves where these had expanded from the time of previously published estimates, including an update of the estimates in Stevens *et al.* (2006) for the US Gulf Coast, and the area of mangroves in Piura, Peru. We interpreted mangrove and salt marsh using techniques defined in Wilton & Saintilan (2000). Our identification of mangroves in Vichayal, Peru using Google Earth Pro was confirmed by photographs provided by Edwin Gerardo and Manuel Ravelo.

Results

Northern hemisphere

North America. Mangroves occupied intertidal locations in the southeastern USA at least as far back as the early Eocene Epoch (ca. 45 Million years BP), but those fossil deposits were associated with a vastly different coastline boundary driven by a warmer climate and higher sea level (Berry, 1916, 1924; Westgate & Gee, 1990). Mangrove forests from the Eocene Epoch likely occurred at densities similar to those seen in modern-day Neotropical mangrove forests, just much farther north (Sherrod & McMillan, 1985; Gee, 2001). The first fossil evidence of *Avicennia* in the Caribbean appeared in the late Miocene Epoch (ca. 10 Million years BP), and by the mid-Pliocene Epoch (ca. 3.5 Million years BP) multiple mangrove genera were evident (Graham, 1995). A prominent lack of mangrove fossil evidence along the northern Gulf just preceding the Pleistocene Epoch (ca. 11 700 years BP) until 3000–4000 years BP (from Holocene peat deposits in south Florida) suggests an eradication event for mangroves along the northern Gulf of Mexico, perhaps related to colder temperatures when mangroves were aligned in distribution closer to the equator (Sherrod & McMillan, 1985).

At the northern limits of present-day mangrove extent in the Gulf of Mexico, population extent has, in the recent past, been periodically reduced by frost (McMillan & Sherrod, 1986), with heavy frost in 1983 and 1989 leading to 95–98% loss amongst several of the northernmost populations (Lonard & Judd, 1991; Everitt *et al*., 1996; Montague & Odum, 1997). This observation prompted Snedaker (1995) to suggest that periodic heavy frost would limit northern expansion for some time. Ecotypic differences in cold tolerance among natural mangrove populations in the Gulf do have the potential to buffer this impact somewhat. This is especially true for populations of *Avicennia germinans* (McMillan, 1971); those populations growing along the Texas coast were especially tolerant to freezing among others surveyed in the wider Caribbean region (Markley *et al*., 1982). However, in more than 20 years since the 1989 freeze event, winters have been sufficiently mild to allow rapid expansion of mangroves at their northern limits into salt marsh, documented in Texas (Comeaux *et al*., 2012; Bianchi *et al*., 2013), Louisiana (Perry & Mendelssohn, 2009; Alleman & Hester, 2011; Pickens & Hester, 2011) and Florida (Stevens *et al*., 2006).

Avicennia germinans coverage increased from 57 ha in 1986 to 1182 ha in 2006 in Louisiana, but fluctuated from a maximum documented coverage of approximately 2180 ha in 1983 before the freeze of that same year (Giri *et al*., 2011). By another account, *A. germinans* increased in abundance by nearly fivefold between 2002 and 2009 within the Louisiana deltaic plain (Michot *et al*., 2010). Populations of *A. germinans* seem to be regulated strongly by air temperatures of −6.7 to −8.9 °C or less (Lonard & Judd, 1991; Stevens *et al*., 2006; Osland *et al*., 2013). This threshold is more restrictive for other Neotropical mangrove species (Lugo and Patterson Zucca, 1977; Krauss *et al*., 2008). For instance, there was no reported survival of transplanted *Rhizophora mangle* seedlings after the 1983 freeze in Texas (Sherrod *et al*., 1986), and embolism is a common consequence of temperatures slightly below 0 °C in the same species (Fig. 2a and b). Likewise, *Laguncularia racemosa* trees are highly susceptible to repetitive freeze-induced dieback events (Fig. 2c), although re-sprouting from the base is a common response in both *L. racemosa* and *A. germinans*.

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

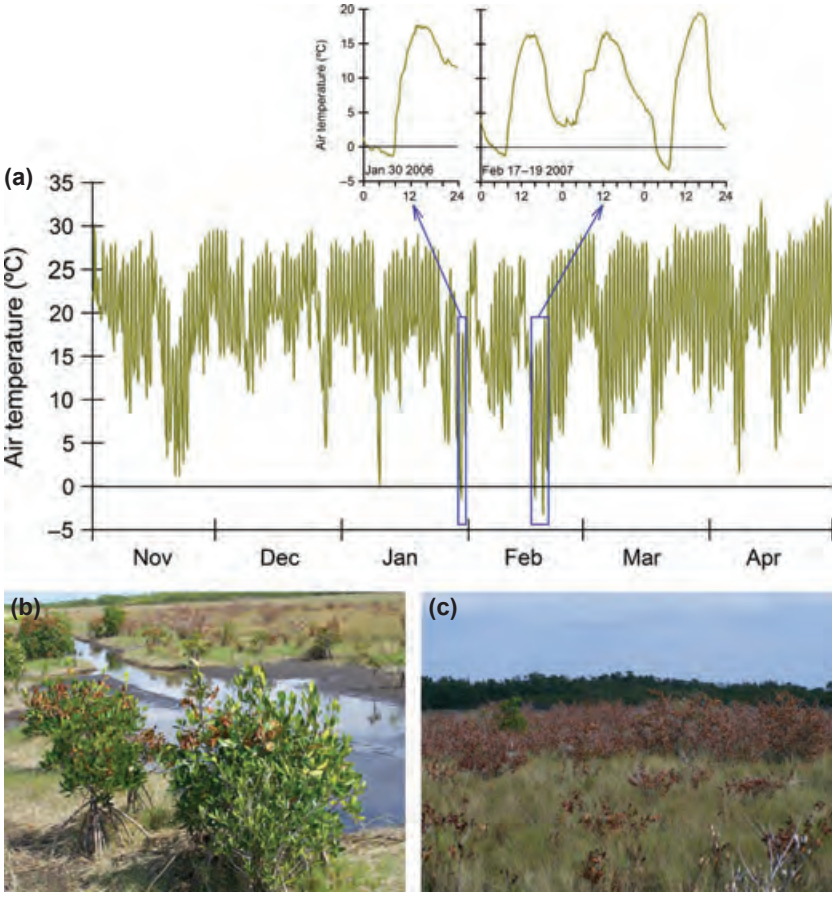


Fig. 2 (a) Air temperatures (°C) for the Ten Thousand Islands region of Florida, USA from November 2006 through April 2007, with days having subzero temperatures highlighted (inset graphs). These subzero temperatures were responsible for (b) branch tip mortality from vascular embolism in *Rhizophora mangle*, and (c) complete stem dieback in many *Laguncularia racemosa* trees growing in open environments. *Avicennia germinans* trees in the Ten Thousand Islands region were generally unaffected by this freeze. (*Temperature data source*: DBHYDRO Browser, South Florida Water Management District, www.sfwmd.gov/dbhydro, Station SGGEWX, accessed 11 April 2013).

Indeed, after extensive losses during the 1983 freeze, mangroves have extended in many Gulf study sites since 1984 (Giri *et al*., 2011) although have not reached pre-1983 extent (C. Giri, unpublished results). Mangrove trees have been documented visually in Louisiana as early as 1938 (Penfound & Hathaway, 1938) and in Texas as early as 1853 (cited in Sherrod & McMillan, 1981). Using an historical time-series of aerial photography extending back to 1956, Perry & Mendelssohn (2009) were able to demonstrate that mangroves first occupied their Louisiana site in 1995. Along with a reduced incidence of freeze-induced mortality, recent expansion of mangroves in Louisiana has been assisted by widespread dieback of *S. alterniflora* resulting from drought; *Avicennia germinans* was unaffected by drought and proliferated (McKee *et al*., 2004). Environmentally mediated competition between *S. alterniflora* and mangroves also occurs along latitudinal gradients in Florida (Kangas & Lugo, 1990) and was probably of importance during post-Pleistocene recolonization of mangroves toward northern latitudes. A recent analysis applied to the northern Gulf suggests that short-statured *A. germinans* vegetation has an overall lower requirement for water use in early growing season assessments than *S. alterniflora* (Krauss *et al*., 2013). This may help to explain the differential survival of *A. germinans* over *S. alterniflora* during drought, and suggests an interaction between climate variability in both temperature and rainfall (Krauss *et al*., 2013).

Much of what we are now documenting in the Southern USA is the northern boundary of the post-Pleistocene recolonization (sensu Sherrod & McMillan, 1985). Currently, mangroves (primarily *A. germinans*) have also extended north on the Florida Atlantic coast at least as far as St Augustine, occupying back-barrier intertidal flats as scattered clusters of individuals

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(29°57′59″N), and have expanded within this estuary since the early 1990s. In fact, *A. germinans* has expanded into salt marsh at several other sites on the Atlantic coast, including the Indian River lagoon (Harris & Cropper, 1992). To the south, *Rhizophora mangle* has expanded landward more than a kilometer into previously *Cladium* and *Eleocharis* marshlands in the Everglades (Ross *et al*., 2000), possibly in response to higher sea levels, changing water levels, and shifting fire regimes (Smith *et al*., 2013). Similar landward expansion has been noted on the Pacific coast of Mexico at Magdalena Bay, Baja California. Here, a 20% increase in mangrove extent through landward encroachment into sparse halophytic shrubland was attributed to sea-level rise, and was particularly pronounced during *El Nino* seasons (Lopez-Medellin *et al*., 2011).

On the Gulf Coast of Florida, mangroves increased coverage in the Ten Thousand Islands National Wildlife Refuge by 35% since 1927, principally at the expense of salt marsh (Krauss *et al*., 2011). Over a similar time period, oscillations between marsh and mangrove area have been documented in other Gulf coastal areas of Florida (Egler, 1952; Bischof, 1995; Smith *et al*., 2013); sometimes to the detriment of marsh and sometimes to the detriment of mangroves. In the absence of any discernable change in mean number of freeze days over the period, encroachment of mangroves onto marsh was attributed primarily to the increase in sea level over the period (2.24 mm yr^{-1} at the Key West station: Krauss *et al*., 2011). After comparing mangrove extent at three sites in Cedar Keys between 1995 and 1999, Stevens *et al*. (2006) predicted that all three sites would develop complete mangrove cover within 25–30 years, if not impacted by frost. Our assessment of the same sites using 2012 aerial photography (Google Earth imagery, 19 January 2012) suggests that this outcome has been realized in less than half the predicted time.

Asia. There are insufficient historic data on the southeast Japanese coast to unequivocally argue for an extension in natural range of *Kandelia obovata* (syn. *K. candel)*. The northern limit of *K. obovata* in Japan was reported by Wakushima *et al*. (1994) to be Kiire, Kagoshima Prefecture (31°30′N), although they note the long-term survival of a planted population in the estuary of the Aono River in the Shizuioka Prefecture at 34°38′N.

Determining changes in northern limits of mangroves in China and Taiwan is complicated by extensive clearance. A further complication in China is the introduction of mangroves north of their natural limits: *K. obovata* in Zheihang (Li & Lee, 1997); and *Sonneratia caseolaris* and *Bruguiera sexangula* in Guangdong (Li *et al*., 1998). One of the few locations where mangroves and salt marshes coexist in near natural state on the Chinese mainland coast is in the Zhanjiang Mangrove National Nature Reserve on the Leizhou Peninsula of Guangdong Province (21°34′N; 109°45′E). The reserve is a Ramsar-listed wetland of international significance and supports nearly one-third of China's mangroves. Regionally, mangroves have declined due to agricultural developments, and extensive dyking restricts landward encroachment (Leempoel *et al*., 2013). However, within the reserve mangroves, dominated by *A. marina, Aegiceras corniculatum* and *K. obovata*, have expanded fourfold, including encroachment on salt marsh (Durango-Cordero *et al*., 2013). Mangroves have also proliferated in the Zhuhai Qi'ao Provincial Nature Reserve (22°26′N; 113°37′E), established in 2000 to encourage the rehabilitation of mangroves (Peng *et al*., 2009). Spread in the extent of the native mangrove *K. obovata* as well as *Sonneratia apelata*, introduced from the Sunderban (Ren *et al*., 2009), has led to a decline in *Spartina alterniflora* saltmarsh (G. Lei, personal communication).

The northernmost mangrove community in Taiwan is located in the Danshui River estuary (21°09′N; 121°26′E) and is the largest *K. obovata* forest in the world (Lee & Yeh, 2009). The mangrove and associated *Phragmites communis* salt marsh community has been protected in the Danshui Mangrove Reserve since in mid-1980s. Mangroves have doubled in extent since the establishment of the reserve, and in detailed satellite imagery analysis Lee & Yeh (2009) were able to demonstrate landward encroachment of mangrove on non-mangrove vegetation, presumably *Phragmites* salt marsh.

Southern hemisphere

Australasia. The gray mangrove *A. marina* extends south on the Australian mainland to the southernmost intertidal flats within Corner Inlet, Victoria (38°54′25″S), and has occupied this range since the earliest historic records from the 19th century. These are the southernmost mangroves in the world, and the Bass Strait provides an effective barrier to further dispersal to the north coast of Tasmania. *A. marina* in southern Australia is exposed to more frequent but less extreme frosts than those encountered in the US Gulf Coast by *A. germinans*, and has developed a greater resistance to freeze-induced embolism (Stuart *et al*., 2007).

Mangrove expansion within estuaries is a near ubiquitous trend in southeastern Australia, (Saintilan & Williams, 1999), and New Zealand (Burns & Ogden, 1985; Morrisey *et al*., 2003; Lovelock *et al*., 2007; Stokes *et al*., 2010), and has been occurring since the time of earliest aerial photographic records (1950s), and perhaps earlier (McLoughlin, 1988, 2000). Temperature increases across

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the region over the past century are likely to be one of a suite of regional environmental changes promoting mangrove growth and a corresponding loss of salt marsh, including sea-level rise (Rogers *et al.*, 2006), increases in sedimentation following catchment development (emphasized in New Zealand studies: Lovelock *et al.*, 2007; Swales *et al.*, 2007; Morrisey *et al.*, 2010) and, in Queensland, higher rainfall (Eslami-Andargoli *et al.*, 2009). Mangroves in New Zealand have expanded across 29 locations by an average of 165% since the 1940s. There is less obvious salt marsh decline than in Australia (Morrisey *et al.*, 2010), possibly due to higher sedimentation rates and elevation gain (Stokes *et al.*, 2010), although some landward encroachment has been noted (Burns & Ogden, 1985). A median estimate of 30% of salt marsh has been lost to mangrove encroachment across SE Australia (Saintilan and Williams 2000; Straw & Saintilan, 2006), with some evidence that rates of loss are lower toward the southern limit in Victoria (5–10%) (Rogers *et al.*, 2005), although this may be due to competitive resilience of large saltbushes of the genus *Tecticornia*, as much as colder conditions slowing mangrove expansion in the south.

Mangrove floristic diversity declines with increasing latitude on the east and west coasts of the Australian continent. On the west coast, patterns in mangrove diversity at a regional scale are strongly influenced by aridity, confounding the assessment of temperature effects on mangrove species range expansion (Semeniuk, 1983; Wells, 1983). The humid subtropical-temperate east coast presents an ideal setting to explore changes in mangrove diversity, with a cline in temperature extending across more than 150 estuaries, linked by the south-flowing East Australia Current south of the Great Barrier Reef. Species of the tropical family Rhizophoraceae (*Rhizophora stylosa* and *Bruguiera gymnorrhiza*) were common in northern NSW during the early- to mid-Holocene, when temperatures and sea levels were likely to have been higher than present (Hashimoto *et al.*, 2006), although were rare in the earliest contemporary surveys (Wells, 1983; West *et al.*, 1985) with *R. stylosa* recorded in seven estuaries in northern NSW. Both *R. stylosa* and *B. gymnorrhiza* appear to have expanded their range in recent decades. *Bruguiera gymnorrhiza* has recently colonized at least three southerly estuaries, the Sandon, Wooli Wooli Rivers, and Moonee Creek (Wilson, 2009). *Rhizophora stylosa* has now been recorded within 16 estuaries (Wilson, 2009), and has shown strong population growth within a number of NSW estuaries (Wilson & Saintilan, 2012). Although it is highly probable that *R. stylosa* was missed in at least two estuaries in earlier surveys in NSW, the colonization of others is clearly very recent, based on demographics. The 100 km southward extension of *R. stylosa* from the Corindi estuary to South West Rocks Creek (30°53′16″S), corresponds to the southward shift in temperature zones in the region over the past few decades (Hennessy *et al.*, 2004). However, colonization of estuaries between these latitudes is sporadic rather than incremental, and leaf phenology does not suggest a temperature cline limiting growth (Wilson & Saintilan, 2012).

South Africa. The earliest comprehensive survey of South African mangroves now dates back 50 years, and represents aerial photographic and field surveys over a 14-year period to 1962 (Macnae, 1963). South of Port St Johns, Macnae (1963) reported stands of mangroves at the estuaries of the Mtata (29°11′E, 31°57′S) and Mngazana Rivers (29°25′E, 31°42′S), 'isolated clumps' of mangroves at the estuaries of the Mbashe (29°25′E, 31°42′S) and Nxaxo (28°31′E, 32°35′S) Rivers, and 'occasional trees' southward. Macnae (1963) reported temperature thresholds on the basis of his observations of distribution as being 19 °C mean air temperature or where the mean of the coldest monthly air temperature does not drop below 13 °C. This placed the Mbashe and Nxaxo estuaries at the southern limit (19.1 °C mean, 11.9 °C mean coldest monthly), with Bufallo River in East London outside of the range (17.7 °C mean, 10.2 C mean coldest monthly).

Mean temperature at the Buffalo River for the period 1973–2011 rose from 17.7 to 18.7 °C, and the mean coldest temperature rose from 10.2 to 14.4 °C (Tutiemp, 2012), a shift extending the possible range of mangrove in South Africa to East London based on the untested thresholds of Macnae (1963). Some dispersal challenges on the Transkei coast include the proportionately high number of temporarily open/closed estuaries (17 of the 76 estuaries are permanently open), and although the Agulhas current flows south 2–3 km offshore, a counter-current develops between the Agulhas and the shoreline creating a predominantly northward drift (Macnae, 1963). In spite of these challenges, and widespread clearing of mangroves, in the 20 years to 1982 mangroves formed extensive stands in the estuaries of the Kobonqaba (28°30′E, 32°36′S, to the south of the Nxaxo), Nqabara (28°47′E, 32°30′S), Xora (29°05′E, 32°05′S), and Bulungula (29°00′E, 32°08′S) Rivers (Ward & Steinke, 1982). It is unlikely these were missed by Macnae; mangroves cover a larger area on the Xora estuary (16 ha) than the Mbashe (12.5 ha) and Nxaxo (14 ha), and line the lower shore of the estuary. In 1969, mangroves were observed for the first time in the Kwelera River (32°54′S, 28°04′E), still the southernmost known natural stand. Natural seeding in the Kwelera River is strongly suggested by the results of a drift card dispersal experiment, in which one of the cards

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

dropped offshore of the Nxaxo River was retrieved within 100 m of the Kwelera mangrove stand (Steinke & Ward, 2003).

Mangrove area has increased by approximately 40% in South African estuaries since the 1970s, with most of the gains in the Umhlatuze estuary (increase from 197 to 489 ha: Bedin, 2001; Ward & Steinke, 1982) and the Mtata (increase from 34 to 42 ha 1982–1999: Adams *et al*., 2004). Small declines were observed in more than half of estuaries sampled by Adams *et al.* (2004), and mangroves have been lost entirely from many estuaries (Quisthoudt *et al*., 2013). This may be related to limited available habitat for colonization (Wright *et al*., 1997) and in some cases the removal of mangroves manually (the Mnyameni: Adams *et al*., 2004) but is principally attributed to prolonged inundation following long-term closure of the estuary mouths on temporarily open/closed estuaries (e.g., the Bulungula, Umzimvuba, Kosi and Kobonqaba rivers: Breen & Hill, 1966; Adams *et al*., 2004).

However, mangroves appear to have established naturally in the Kei River (28°21′42″E, 32°40′00″S,) to the north of the Kwelera, and the Gqunube River (28°02′E, 32°56′S) to the south, with the Kobonqaba River a possible source (Steinke, 1986; Steinke & Ward, 2003). It is uncertain whether the Gqunube River mangroves were naturally dispersed or planted.

Avicennia marina, *B. gymnorrhiza*, and *Rhizophora mucronata* have also survived in the Nahoon estuary in East London after being transplanted from Durban Bay (Steinke, 1999), suggesting that climate was or is no longer a factor limiting their southern natural extent. Of these three species, it is only *A. marina* that has expanded substantially within the estuary, and now covers 1.6 ha of previously salt marsh flat, and is expanding at 0.1 ha yr^{-1} (A. Rajkaran, personal observations 2012). Quisthoudt *et al*. (2013) were able to successfully predict current distribution of *A. marina*, *B. gymnorrhiza*, and *R. mucronata* based on current climate variables, with number of growing days above an 18 °C threshold being the most important. On this basis, they predict latitudinal expansion of mangroves with continued climatic warming.

South America. Mangroves grow south on the Atlantic coast to Santo Antonia Lagoon in the Municipality of Laguna (28°28′S; 48°50′W) (Soares *et al*., 2012). This southern limit has not changed in the two decades since the survey of Schaeffer-Novelli *et al.* (1990), although populations of the dominant species *Laguncularia recemosa* show evidence of recent recruitment (Soares *et al*., 2012). At this site *L. racemosa* is stunted, a trait in common with species globally at their southern limit, although *Avicennia schaueriana* grows to 10 m, suggesting a vigour characteristic of a species well within its range (Soares *et al*., 2012). Further southward expansion may be limited by a strong northerly current described by Siegle & Asp (2007) extending from Ararangua, an estuary 100 km south, to Laguna (Soares *et al*., 2012).

The southern limit of mangrove communities on the South American west coast was considered by Clüsener & Breckle (1987) to be the River Thumbes at 3°35′S; beyond which were found only a few small individuals of *Rhizophora* near the village of Bocapan (at 3°44′S), and a small stand of *Avicennia* at the mouth of the Piura River. Mangroves were successfully planted within this range in their experimental studies in 1984–1985.

South of Cerro Illescas (6°0′S), the cold Peruvian current precludes mangrove colonization (Clüsener & Breckle, 1987), and because of the aridity of the coast, only three estuaries between Cerro Illescas and Bocapan provide intertidal conditions suitable for the development of mangrove, these being the Virrila estuary (5°50′S); the Piura River (5°30′S) and the Vichayal estuary (4°53′S). The 'small stand' of *Avicennia* described by Clüsener & Breckle (1987) at Piura is now very extensive, lining 9.5 km of shoreline and covering at least 38 ha in the north arm and 9 ha in the south arm of the estuary at San Pedro, the southernmost confirmed mangroves on the west coast (imagery dated 10 February 2011, DigitalGlobe, sourced from Google Earth Pro). The Vichayal estuary has a new stand of *Avicennia* at 4°53′22.6″S; 81°08′56.4″W covering 1.87 ha (field photographs provided by Manuel Ravelo, imagery dated 19 January 2010, DigitalGlobe, sourced from Google Earth Pro). These are absent from aerial photographs taken in 1970 (Google Earth Pro) and reportedly established during the El Niño event in the first decade of this century (E. Gerardo, personal communication 2012).

Discussion

Dispersal may be problematic in spite of the abundance of buoyant propagules produced by *Avicennia* spp. (Clarke *et al*., 2001; Sousa *et al*., 2007), and restricted gene flow in marginal populations (Dodd & Afzal Rafii, 2002) also suggests dispersal may restrict the expansion of range. In many places, the latitudinal limit of mangroves appears to lag behind changes in temperature thresholds, as documented in New Zealand (de Lange & de Lange, 1994), east coast Australia (Wilson & Saintilan, 2012), South Africa (Steinke, 1999), and South America (Soares *et al*., 2012). The difference between fundamental and realized niche is relatively large for *Avicennia* and *Rhizophora* on the basis of global comparisons (Quisthoudt *et al*., 2012), and on some coastlines may reflect slow expansion from Pleistocene extents.

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Disequilibrium between tree species distribution and rapidly changing temperature regimes has been noted for terrestrial species also (Willner *et al.*, 2009). It is likely that a more complex response than a steady stepping poleward will be the case for many mangrove species, especially those on relatively high wave energy coasts with few permanently open estuaries or where dispersal is subject to unfavourable currents. This infers that there is no simple function relating range extension and warming temperatures, something also implied by the global temperature and range analysis of Quisthoudt *et al.* (2012).

Parmesan & Yohe (2003) found poleward range shifts in 75–81% of 1045 species of higher plants and animals with quantitative records, with an average shift of 6.1 km per decade. Notwithstanding limited opportunities for dispersal and the difficulties of 'threading the needle' of estuarine entrances, an increase in range has been documented for the mangroves *A. germinans* in the USA and Peru, *A. marina* in South Africa and *R. stylosa* and *B. gymnorrhiza* in eastern Australia; and expanding mangrove populations near poleward limits are obvious within estuaries in Australia, New Zealand, the Gulf and Atlantic coasts of the USA, the Pacific and South Atlantic coasts of South America, and the Leizhou Peninsula of China, one of the few locations in southern China where large areas of mangrove and salt marsh are protected and have been retained. Poleward expansion in the coming decades will be most evident on open coasts where temperature currently exerts a strong control on contemporary distributions and available habitat exists. Osland *et al.* (2013) used contemporary mangrove forest distribution data and 30-year climate records from the Gulf and Atlantic US coasts to identify winter-climate based thresholds and develop mangrove species distribution and relative abundance models. Their models and analyses of the potential effect of alternative future winter climate scenarios show that, in southeastern USA and especially in Louisiana, Texas, and Florida, relatively small changes in winter climate can result in relatively dramatic mangrove range expansion at the expense of salt marsh. Applying a 2–4 °C increase in annual mean minimum temperature would lead to a 95% reduction in salt marsh in Louisiana, 100% reduction in Texas and 60% reduction in Florida (Osland *et al.*, 2013).

The comprehensive replacement of salt marsh by mangrove (cf., Osland *et al.*, 2013; Guo *et al.*, 2013) is predicated on temperature as the key delimiting factor of mangrove range expansion. In addition to temperature, local patterns of mangrove expansion into salt marsh are likely to be influenced by interactions between hydroperiod, sedimentation, elevation and salinity, with nutrients playing a role in some settings (Patterson & Mendelssohn, 1991; Patterson *et al.*, 1997), all of which can be impacted locally by human agency, such as building walls and structures in estuaries, dredging, and development in the catchment. In coastal Louisiana, mangroves currently tend to dominate higher elevation settings such as the shorelines of tidal creeks, and exclusion from lower interior marshes has been attributed to higher predation, lower retention of propagules (Patterson *et al.*, 1997), plant competition, and greater flooding stress (Patterson *et al.*, 1993). By contrast, mangroves in eastern Australia show greater mortality in less frequently inundated higher salinity areas where propagules become desiccated (Clarke & Allaway, 1993; Clarke & Myerscough, 1993). That mangroves are invading salt marshes in contrasting settings along the northern Gulf of Mexico vs. Australia would suggest that different mechanisms are at work, or that global changes are contributing to an increased capacity of mangroves to survive in previously marginal intertidal environments.

Mangrove expansion into salt marsh mirrors a global trend of woody shrub invasion of grassland (Knapp *et al.*, 2008; Williamson *et al.*, 2010), which has been attributed variously to altered fire and grazing intensity (Scholes & Archer, 1997; Van Auken, 2009), and elevated atmospheric CO_2 (Polley *et al.*, 1997; Eamus & Palmer, 2008). On most coastlines, there is little evidence that altered fire and grazing regimes are dominant drivers of vegetation change in intertidal settings. The proliferation of mangroves in previously salt marsh-dominated environments is likely to be driven by a suite of environmental factors favoring mangrove and which are changing globally, including elevated sea level, elevated atmospheric CO_2, and higher temperatures (Williamson *et al.*, 2010; McKee *et al.*, 2012). Landward encroachment of mangrove into salt marsh and salt pan has been attributed to sea-level rise in environments as disparate as Baja California (Lopez-Medellin *et al.*, 2011), the US Gulf Coast (Krauss *et al.*, 2011; Smith *et al.*, 2013), and east coast Australia, where Rogers *et al.* (2006) demonstrated a lower capacity of salt marsh to respond to sea-level rise through vertical accretion. Salt marsh floristic diversity increases in inverse correlation with mangrove diversity on the Australian east coast (Saintilan, 2009) and mangrove encroachment may place further pressure on an ecological community already listed as endangered in New South Wales.

The replacement of salt marsh by mangrove in temperate settings has important implications for ecosystem organization and function. Experimental studies in the Gulf of Mexico (Comeaux *et al.*, 2012) and temperate Australia (Rogers *et al.*, 2006) show improved mineral trapping leading to a higher rate of surface

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

elevation gain in encroaching mangrove than surrounding salt marsh, suggesting mangrove has greater potential to respond to increasing sea levels, although some of these differences may relate to different topographic settings. Carbon sequestration may be enhanced in some settings as a result of mangrove encroachment (Howe *et al*., 2009; Bianchi *et al*., 2013) and reduced in others, if redox potential is enhanced by mangrove root formation (Comeaux *et al*., 2012). The conversion of salt marsh to mangrove in the Gulf of Mexico alone could sequester 129 ± 45 Tg C over 100 years (Bianchi *et al*., 2013), more than 1% of 'Blue Carbon' estimates globally (Bianchi *et al*., 2013; Hopkinson *et al*. 2012), and a proportion that may rise if the trend of tropical mangrove deforestation continues (Valiela *et al*., 2001).

Acknowledgements

The authors thank Edwin Gerardo, and Dr J. Manuel Charcape Ravelo, National University of Piura, for their comments and photographs of mangroves in Peru. Robert J. Williams is thanked for comments on an earlier version of this manuscript. The use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government. We thank the UNEP World Conservation Monitoring Centre (WCMC) for access to mangrove and salt marsh distribution data, and Professor Guangchun Lei of Beijing Forestry University for his observations and photographs of mangrove encroachment into salt marsh in Guangdong Province, China.

References

Adams JB, Colloty BM, Bate GC (2004) The distribution and state of mangroves along the coast of Transkei, Eastern Cape Province, South Africa. *Wetlands Ecology and Management*, **12**, 531–541.

Alleman LK, Hester MW (2011) Refinement of the fundamental niche of black mangrove (Avicennia germinans) seedlings in Louisiana: Applications for restoration. *Wetlands Ecology and Management*, **19**, 47–60.

Alongi DM (2008) Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science*, **76**, 1–13.

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390–407.

Bedin T (2001) The progression of a mangrove forest over a newly formed delta in the Umhlatuze Estuary, South Africa. *South African Journal of Botany*, **67**, 433–438.

Berry EW (1916) *The Lower Eocene Floras of Southeastern North America*. Professional Paper 91, US Geological Survey, Washington, DC, USA.

Berry EW (1924) *The Middle and Upper Eocene Floras of Southeastern North America*. Professional Paper 92, US Geological Survey, Washington, DC, USA.

Bianchi TS, Allison MA, Zhao J, Li X, Comeaux RS, Feagin RA, Kulawardhana RW (2013) Historical reconstruction of mangrove expansion in the Gulf of Mexico: linking climate change with carbon sequestration in coastal wetlands. *Estuarine, Coastal and Shelf Science*, **119**, 7–16.

Bischof BC (1995) Aerial photographic analysis of coastal and estuarine mangrove system dynamics of the Everglages National Park, Florida, in response to hurricanes: Implications of the continuing sea level rise. MS Thesis, University of Miami, Coral Gables, FL, USA.

Breen CM, Hill BJ (1966) A mass mortality of mangroves in the Kosi estuary. *Transactions of the Royal Society of South Africa*, **41**, 285–301.

Burns BR, Ogden J (1985) The demography of the temperate mangrove [*Avicennia marina* (Forsk.) Vierh.] at its southern limit in New Zealand. *Australian Journal of Ecology*, **10**, 125–133.

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles*, **17**, 1111.

Clarke PJ, Allaway W (1993) The regeneration niche of the grey mangrove *Avicennia marina* – effects of salinity, light and sediment factors on establishment, growth and survival in the field. *Oecologia*, **93**, 548–556.

Clarke PJ, Myerscough PJ (1993) The intertidal distribution of the grey mangrove (*Avicennia marina)* in southeastern Australia: the effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. *Australian Journal of Ecology*, **18**, 307–315.

Clarke PJ, Kerrigan RA, Wetphal CJ (2001) Dispersal potential and early growth in 14 tropical mangroves: do early life history traints correlate with patterns of adult distribution? *Journal of Ecology*, **89**, 648–659.

Clüsener M, Breckle SW (1987) Reasons for the limitation of mangrove along the west coast of northern Peru. *Vegetatio*, **68**, 173–177.

Comeaux RS, Allison MA, Bianchi TS (2012) Mangrove expansion in the Gulf of Mexico with climate change: implications for wetland health and resistance to rising sea levels. *Estuarine, Coastal and Shelf Science*, **96**, 81–95.

Dodd R, Afzal Rafii Z (2002) Evolutionary genetics of mangroves: continental drift to recent climate change. *Trees*, **16**, 80–86.

Donato DC, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, **4**, 293–297.

Duke NC, Ball MC, Ellison JC (1998) Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, **7**, 27–47.

Durango-Cordero JS, Satyanarayana B, Zhang J *et al.* (2013) Vegetation structure at Zhangiang Mangrove National Nature Reserve (ZMMNR), P.R. China: a comparison between original and non-original trees using ground-truthing, remote sensing and GIS techniques. Available at: www.vliz.be/imisdocs/publications/232700.pdf (accessed 8 July 2013).

Eamus D, Palmer AR (2008) Is climate change a possible explanation for woody thickening in arid and semi-arid regions? *International Journal of Ecology*, **2007**, 5.

Egler FE (1952) Southeast saline Everglades vegetation, Florida, and its management. *Vegetatio*, **3**, 213–265.

Ellison AM, Farnsworth EJ, Merkt RE (1999) Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography*, **8**, 95–115.

Eslami-Andargoli L, Dale P, Sipe N, Chaseling J (2009) Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science*, **85**, 292–298.

Everitt JH, Judd FW, Escobar DE, Davis MR (1996) Integration of remote sensing and spatial information technologies for mapping black mangrove on the Texas gulf coast. *Journal of Coastal Research*, **12**, 64–69.

Field CD (1995) Impact of expected climate change on mangroves. *Hydrobiologia*, **295**, 75–81.

Friess DA, Krauss KW, Horstman EM, Balke T, Bouma TJ, Galli D, Webb EL (2012) Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biological Reviews*, **87**, 346–366.

Gedan K, Kirwan M, Wolanski E, Barbier E, Silliman B (2011) The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. *Climatic Change*, **106**, 7–29.

Gee CT (2001) The mangrove palm *Nypa* in the geologic past of the New World. *Wetlands Ecology and Management*, **9**, 181–194.

Gilman EL, Ellison J, Duke NC, Field CD (2008) Threats to mangroves from climate change and adaptation options: a review. *Aquatic Botany*, **89**, 237–250.

Giri C, Long J, Tieszen L (2011) Mapping and monitoring Louisiana's mangroves in the aftermath of the 2010 Gulf of Mexico oil spill. *Journal of Coastal Research*, **27**, 1059–1064.

Graham A (1995) Diversification of Gulf/Caribbean mangrove communities through Cenozoic time. *Biotropica*, **27**, 20–27.

Grindrod J, Moss P, Kaars SVD (1999) Late Quaternary cycles of mangrove development and decline on the north Australian continental shelf. *Journal of Quaternary Science*, **14**, 465–470.

Guo H, Zhang Y, Lan Z, Pennings SC (2013) Biotic interactions mediate the expansion of black mangrove (*Avicennia germinans*) into salt marshes under climate change. *Global Change Biology*, **19**, 2765–2774.

Harris LD, Cropper WP Jr (1992) Between the devil and the deep blue sea: implications of climate change for Florida's fauna. In: *Global Warming and Biological Diversity* (eds Peters RL, Lovejoy TE), pp. 309–324. Yale University Press, New Haven, CT.

Hashimoto TR, Saintilan N, Haberle SG (2006) Mid-Holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the Richmond River Estuary, New South Wales, Australia. *Geographical Research*, **44**, 63–76.

Hennessy K, Page C, McInnes K, Jones R, Bathols J, Collins D, Jones D (2004) *Climate Change in New South Wales, Part 1: Past Climate Variability and Projected Changes in Average Climate*. CSIRO Atmospheric Research, Aspendale, Victoria.

Hoekstra JM, Molnar JL, Jennings M *et al.* (2010) *The Atlas of Global Conservation: Changes, Challenges, and Opportunities to Make a Difference*. University of California Press, Berkeley.

Hopkinson CS, Caiíguez WJ, Hu X (2012) Carbon sequestration in wetland dominated coastal systems–a global sink of rapidly diminishing magnitude. *Current Opinion in Environmental Sustainability*, **4**, 186–194.

Howe AJ, Rodríguez JF, Saco PM (2009) Surface evolution and carbon sequestration in disturbed and undisturbed wetland soils of the Hunter estuary, southeast Australia. *Estuarine, Coastal and Shelf Science*, **84**, 75–83.

Kangas PC, Lugo AE (1990) The distribution of mangroves and saltmarshes in Florida. *Tropical Ecology*, **31**, 32–39.

Knapp AK, Briggs JM, Collins SL, *et al.* (2008) Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*, **14**, 615–623.

Krauss KW, Lovelock CE, McKee KL, López-Hoffman L, Ewe SML, Sousa WP (2008) Environmental drivers in mangrove establishment and early development: a review. *Aquatic Botany*, **89**, 105–127.

Krauss KW, From AS, Doyle TW, Doyle TJ, Barry MJ (2011) Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Inslands region of Florida, USA. *Journal of Coastal Conservation*, **15**, 629–638.

Krauss KW, McKee KL, Hester MW (2013) Water use characteristics of black mangrove (*Avicennia germinans*) communities along an ecotone with marsh at a northern geographical limit. *Ecohydrology*, doi: 10.1002/eco.1353/abstract.

de Lange WP, de Lange PJ (1994) An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicennia marina* var. *resinifera*) in New Zealand. *Journal of Coastal Research*, **10**, 539–548.

Lee T-M, Yeh H-C (2009) Applying remote sensing techniques to monitor shifting wetland vegetation: a case study of Danshui River estuary mangrove communities Taiwan. *Ecological Engineering*, **35**, 487–496.

Leempoel K, Bourgeois C, Zhang J *et al.* (2013) Spatial heterogeneity in mangroves assessed by GeoEye-1 satellite data: a case-study in Zhanjiang Mangrove National Nature Reserve (ZMNNR), China. *Biogeosciences Discussions*, **10**, 2591–2615.

Li MS, Lee SY (1997) Mangroves of China: a brief review. *Forest Ecology and Management*, **96**, 241–259.

Li Y, Zheng D, Liao B, Zheng S, Wang Y (1998) Preliminary report on introduction of several superior mangroves. *Forest Research*, **11**, 652–655.

Loarie SR, Carter BE, Hayhoe K, McMahon S, Moe R, Knight CA, Ackerly DD (2008) Climate change and the future of California's endemic flora. *PLoS ONE*, **3**, e2502.

Lonard RI, Judd FW (1991) Comparison of the effects of the severe freezes of 1983 and 1989 on native woody plants in the Lower Rio Grande Valley, Texas. *The Southwestern Naturalist*, **36**, 213–217.

López-Medellín X, Ezcurra E, González-Abraham C, Hak J, Santiago LS, Sickman JO (2011) Oceanographic anomalies and sea-level rise drive mangroves inland in the Pacific coast of Mexico. *Journal of Vegetation Science*, **22**, 143–151.

Lovelock CE, Feller IC, Ellis J, Schwarz AM, Hancock N, Nichols P, Sorrell B (2007) Mangrove growth in New Zealand estuaries: The role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia*, **153**, 633–641.

Lugo AE, Patterson Zucca C (1977) The impact of low temperature stress on mangrove structure and growth. *Tropical Ecology*, **18**, 149–161.

Macnae W (1963) Mangroves swamps in South Africa. *Journal of Ecology*, **51**, 1–25.

Markley JL, McMillan C, Thompson GA Jr (1982) Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*, from the western tropical Atlantic and Pacific Panama. *Canadian Journal of Botany*, **60**, 2704–2715.

McKee KL, Rooth JE (2008) Where temperate meets tropical: multi-factorial effects of elevated CO_2, nitrogen enrichment, and competition on a mangrove-salt marsh community. *Global Change Biology*, **14**, 971–984.

McKee KL, Mendelssohn IA, Materne M (2004) Acute salt marsh dieback in the Mississippi River deltaic plain: a drought-induced phenomenon? *Global Ecology and Biogeography*, **13**, 65–73.

McKee KL, Cahoon DR, Feller IC (2007) Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, **16**, 545–556.

McKee KL, Rogers K, Saintilan N (2012) Responses of Salt Marsh and Mangrove Wetlands to changes in Atmospheric CO_2, Climate and Sea-Level. In: *Global Change and the Function and Distribution of Wetlands* (ed. Middleton BA), pp. 63–96, Springer, New York.

McLoughlin L (1988) Mangroves and grass swamps: changes in the shoreline vegetation of the Middle Lane Cover River, Sydney, 1780's-1880's. *Wetlands (Australia)*, **7**, 13–24.

McLoughlin L (2000) Estuarine wetlands distribution along the Parramatta River, Sydney, 1788-1940: Implications for planning and conservation. *Cunninghamia*, **6**, 579–610.

McMillan C (1971) Environmental factors affecting seedling establishment of the black mangrove on the central Texas coast. *Ecology*, **52**, 927–930.

McMillan C, Sherrod CL (1986) The chilling tolerance of black mangrove, *Avicennia germinans*, from the Gulf of Mexico coast of Texas, Louisiana and Florida. *Contributions in Marine Science*, **29**, 9–16.

Michot TC, Day RH, Wells CJ (2010) Increase in black mangrove abundance in coastal Louisiana. *Louisiana Natural Resources News, Newsletter of the Louisiana Association of Professional Biologists*, January, 4–5.

Mildenhall DC (1994) Early to Mid Holocene pollen samples containing mangrove pollen from Sponge Bay, East Coast, North Island, New Zealand. *Journal of the Royal Society of New Zealand*, **24**, 219–230.

Montague CL, Odum HT (1997) The intertidal marshes of Florida's Gulf Coast. In: *Ecology and Management of Tidal Marshes: A Model From the Gulf of Mexico* (eds Coultas CL, Hsieh Y), pp. 1–9. St Lucie Press, Delroy Beach, Florida, USA.

Morrisey DJ, Skilleter GA, Ellis JI, Burns BR, Kemp CE, Burt K (2003) Differences in benthic fauna and sediment among mangrove (Avicennia marina var. australasica) stands of different ages in New Zealand. *Estuarine, Coastal and Shelf Science*, **56**, 581–592.

Morrisey DJ, Swales A, Dittman S, Morrison MA, Lovelock CE, Beard CM (2010) The ecology and management of temperate mangroves. *Oceanography and Marine Biology: An Annual Review*, **48**, 43–160.

Nagelkerken I, Blaber SJM, Bouillon S *et al.* (2008) The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany*, **89**, 155–185.

NOAA (2013) Sea surface temperature (SST) contour charts. Prepared by National Oceanic and Atmospheric Administration (NOAA) satellites and Information. Available at: http://www.ospo.noaa.gov/data/sst/contour/global_small.c.gif (accessed 6 July 2013).

Osland MJ, Enwright N, Day RH, Doyle TW (2013) Winter climate change and coastal wetland foundation species: salt marshes versus mangrove forests in the southeastern United States. *Global Change Biology*, **19**, 1482–1494.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Parmesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Patterson CS, Mendelssohn IA (1991) A comparison of physicochemical variables across plant zones in a mangal/salt marsh community in Louisiana. *Wetlands*, **11**, 139–161.

Patterson CS, Mendelssohn IA, Swenson EM (1993) Growth and survival of Avicennia germinans seedlings in a mangal/salt marsh community in Louisiana, U.S.A. *Journal of Coastal Research*, **9**, 801–810.

Patterson CS, McKee KL, Mendelssohn IA (1997) Effects of tidal inundation and predation on Avicennia germinans seedling establishment and survival in a sub-tropical mangal/salt marsh community. *Mangroves and Salt Marshes*, **1**, 103–111.

Penfound WT, Hathaway ES (1938) Plant communities in the marshlands of southeastern Louisiana. *Ecological Monographs*, **8**, 1–56.

Peng Y, Chen G, Tian G, Yang X (2009) Niches of plant populations in mangrove reserve of Qu'ao Island, Pearl River Estuary. *Acta Ecologica Sinica*, **29**, 357–361.

Perry C, Mendelssohn I (2009) Ecosystem effects of expanding populations of Avicennia germinans in a Louisiana salt marsh. *Wetlands*, **29**, 396–406.

Pickens C, Hester M (2011) Temperature tolerance of early life history stages of black mangrove Avicennia germinans: implications for range expansion. *Estuaries and Coasts*, **34**, 824–830.

Polley HW, Mayeux HS, Johnson HB, Tischler CR (1997) Viewpoint: atmospheric CO_2, soil water and shrub/grass rations on rangelands. *Journal of Range Management*, **50**, 278–284.

Quisthoudt K, Schmitz N, Randin C, Dahdouh-Guebas F, Robert ER, Koedam N (2012) Temperature variation among mangrove latitudinal range limits worldwide. *Trees*, **26**, 1919–1931.

Quisthoudt K, Adams J, Rajkaran A, Dahdouh-Geubas F, Koedam N, Randin CF (2013) Disentangling the effects of global climate and regional land-use on the current and future distribution of mangroves in South Africa. *Biodiversity Conservation*, **22**, 1369–1390.

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Ren H, Lu H, Shen W, Huang C, Guo Q, Li ZA, Jian S (2009) *Sonneratia apetala* Buch. Ham in the mangrove ecosystems of China: An invasive species or restoration species? *Ecological Engineering*, **35**, 1243–1248.

Rogers K, Saintilan N, Heijnis H (2005) Mangrove encroachment of salt marsh in Western Port Bay, Victoria: The role of sedimentation, subsidence and sea level rise. *Estuaries*, **28**, 551–559.

Rogers K, Wilton KM, Saintilan N (2006) Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science*, **66**, 559–569.

Ross MS, Meeder JF, Sah JP, Ruiz PL, Telesnicki GL (2000) The southeast saline Everglades revisited: 50 years of coastal vegetation change. *Journal of Vegetation Science*, **11**, 101–112.

Saintilan N (2009) Biogeography of Australian saltmarsh plants. *Austral Ecology*, **34**, 929–937.

Saintilan N, Williams RJ (1999) Mangrove transgression into saltmarsh environments in South-East Australia. *Global Ecology and Biogeography*, **8**, 117–124.

Saintilan N, Williams RJ (2010) Short Note: The decline of saltmarsh in southeast Australia: Results of recent surveys. *Wetlands (Australia)*, **18**, 49–54.

Saintilan N, Rogers K, McKee K (2009) Saltmarsh-Mangrove interactions in Australasia and the Americas. Chapter 31. In: *Coastal Wetlands; an Integrated Ecosystems Approach* (eds Perillo GME, Wolanski E, Cahoon DR, Brinson MM), pp. 855–883. Elsevier, Atlanta.

Schaeffer-Novelli Y, Cintron-Molero G, Adaime RR, de Camargo TM (1990) Variability of mangrove ecosystems along the Brazilian Coast. *Estuaries*, **13**, 204–218.

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.

Semeniuk V (1983) Mangrove distribution in Northwestern Australia in relationship to regional and local freshwater seepage. *Vegetatio*, **53**, 11–31.

Semeniuk V (2013) Predicted response of coastal wetlands to climate changes: a Western Australian model. *Hydrobiologia*, **708**, 23–43.

Sherrod CL, McMillan C (1981) Black mangrove, *Avicennia germinans*, in Texas: Past and present distribution. *Contributions in Marine Science*, **24**, 115–131.

Sherrod CL, McMillan C (1985) The distributional history and ecology of mangrove vegetation along the northerm Gulf of Mexico coastal region. *Contributions in Marine Science*, **28**, 129–140.

Sherrod CL, Hockaday DL, McMillan C (1986) Survival of red mangrove, *Rhizophora mangle*, on the Gulf of Mexico coast of Texas. *Contributions in Marine Science*, **29**, 27–36.

Siegle E, Asp NE (2007) Wave refraction and longshore transport patterns along the southern Santa Catarina coast. *Brazilian Journal of Oceanography*, **55**, 109–120.

Smith TJ III, Foster AM, Tiling-Range G, Jones JW (2013) Dynamics of mangrove-marsh ecotones in subtropical coastal wetlands: Fire, sea-level rise, and water levels. *Fire Ecology*, **9**, 66–77.

Snedaker S (1995) Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. *Hydrobiologia*, **295**, 43–49.

Soares MLG, Estrada GCD, Fernandez V, Tognella MMP (2012) Southern limit of the Western South Atlantic mangroves: Assessment of the potential effects of global warming from a biogeographical perspective. *Estuarine, Coastal and Shelf Science*, **101**, 44–53.

Solomon S, Qin D, Manning M *et al*. (eds.) (2007) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Sousa WP, Kennedy PG, Mitchell BJ, Ordonez BM (2007) Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure? *Ecological Monographs*, **77**, 53–76.

Spalding M (2012). *World Atlas of Mangroves*. Earthscan, New York.

Steinke TD (1986) Mangroves of the East London area. *The Naturalist*, **30**, 50–53.

Steinke TD (1999) Mangroves in South African estuaries. In: *Estuaries of South Africa* (eds Allanson BR, Baird D), pp. 119–140. Cambridge University Press, Cambridge, UK.

Steinke TD, Ward CJ (2003) Use of plastic drift cards as indicators of possible dispersal of propagules of the mangrove Avicennia marina by ocean currents. *Africal Journal of Marine Science*, **25**, 169–176.

Stevens PW, Fox SL, Montague CL (2006) The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management*, **14**, 435–444.

Stokes DJ, Healy TR, Cooke PJ (2010) Expansion dynamics of monospecific, temperate mangroves and sedimentation in two embayments of a barrier-enclosed lagoon, Tauranga Harbour, New Zealand. *Journal of Coastal Research*, **26**, 113–122.

Straw P, Saintilan N (2006) Loss of shorebird habitat as a result of mangrove incursion due to sea-level rise and urbanization. In *Waterbirds Around the World (eds Boere GC, Galbraith CA, Stroud DA)*, 717–720. TSO Scotland, Edinburgh, UK.

Stuart SA, Choat B, Martin KC, Holbrook NM, Ball MC (2007) The role of freezing in setting the latitudinal limits of mangrove forests. *New Phytologist*, **173**, 576–583.

Sturm M, Racine C, Tape K (2001) Increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.

Swales A, Bentley SJ, Lovelock C, Bell RG (2007) Sediment processes and mangrove-habitat expansion on a replidly prograding muddy coast, New Zealand. In: *Coastal Sediments '07. Proceedings of the Sixth International Conference on Coastal Engineering and Science of Coastal Sedimetn Processes, New Orleans, May 2007* (ed. Krauss NC, Rosati JD), pp. 1441–1454. American Society of Civil Engineers, Reston, Virginia, USA.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, **399**, 213.

Tutiemp (2012) *Climate East London*. Available at: http://www.tutiempo.net/en/Climate/East_London/688580.htm (accessed 7 November 2012

Valiela E, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major tropical environments. *BioScience*, **51**, 807–815.

Van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management*, **90**, 2931–2942.

Van der Stocken T, DeRyck DJR, Balke T, Bouma TJ, Dahdouh-Guebas F, Koedam N (2013) The role of wind in hydrochorous mangrove propagule dispersal. *Biogeosciences*, **10**, 895–925.

Wakushima S, Kuraishi S, Sakurai N (1994) Soil salinity and pH in Japanese mangrove forests and growth of cultivated mangrove plants in different soil conditions. *Journal of Plant Research*, **107**, 39–46.

Walsh GE (1974) Mangroves: a review. *Ecology of Halophytes* (eds Reimold RJ, Queen WH), pp. 51–174. Academic Press, London.

Walther GR, Post E, Convey P *et al*. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Ward CJ, Steinke TD (1982) A note on the distribution and approximate areas of mangroves in South Africa. *South African Journal of Botany*, **3**, 51–53.

Wells AG (1983) Distribution of mangroves species in Australia. In: *Biology and Ecology of Mangroves* (ed.Teas HJ), pp. 57–76. Dr W. Junk, The Hague, the Netherlands.

West RJ, Thorogood C, Walford T, Williams RJ (1985) Mangrove distribution in New South Wales. *Wetlands (Australia)*, **4**, 2–6.

Westgate JW, Gee CT (1990) Paleoecology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **78**, 163–177.

Williamson GJ, Boggs GS, Bowman DMS (2010). Late 20th century mangrove encroachment in the coastal Australian monsoon tropics parallels the regional increase in woody biomass. *Regional Environmental Change*, **11**, 19–27.

Willner W, Di Pietro R, Bergmeier E (2009) Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography*, **32**, 1011–1018.

Wilson NC (2009) The distribution, growth, reproduction and population genetics of a mangrove species, *Rhizophora stylosa* Griff. near it southern limits in New South Wales, Australia. PhD Thesis, Australian Catholic University, North Sydney.

Wilson NC, Saintilan N (2012) Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. *Aquatic Botany*, **101**, 8–17.

Wilton K, Saintilan N (2000). *Protocols for Mangrove and Saltmarsh Habitat Mapping*. Estuaries Branch, NSW Department of Land and Water Conservation, Sydney.

Woodroffe CD (1990) *The Impact of sea-Level Rise on Mangrove Shorelines*. Turpin, Letchworth, ROYAUME-UNI.

Woodroffe CD, Grindrod J (1991) Mangrove biogeography: the role of quaternary environmental and sea-level change. *Journal of Biogeography*, **18**, 479–492.

Wright CI, Lindsay P, Cooper JAG (1997) The effect of sedimentary processes on the ecology of the mangrove-fringed Kosi estuary/lake system, South Africa. *Mangroves and Salt Marshes*, **1**, 79–94.

13652486, 2014, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.12341 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Research review

Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings

Author for correspondence:
Neil Saintilan
Tel: +612 9995 5631
Email:
neil.saintilan@environment.nsw.gov.au

Received: *14 September 2014*
Accepted: *19 September 2014*

Neil Saintilan[1,2] and Kerrylee Rogers[2]

[1]Department of Environmental Science, Macquarie University, Australia; [2]GeoQuest, University of Wollongong, Wollongong, New South Wales 2522, Australia

New Phytologist (2015) **205:** 1062–1070
doi: 10.1111/nph.13147

Key words: atmospheric CO_2, encroachment, fire, saltmarsh, shrub.

Summary

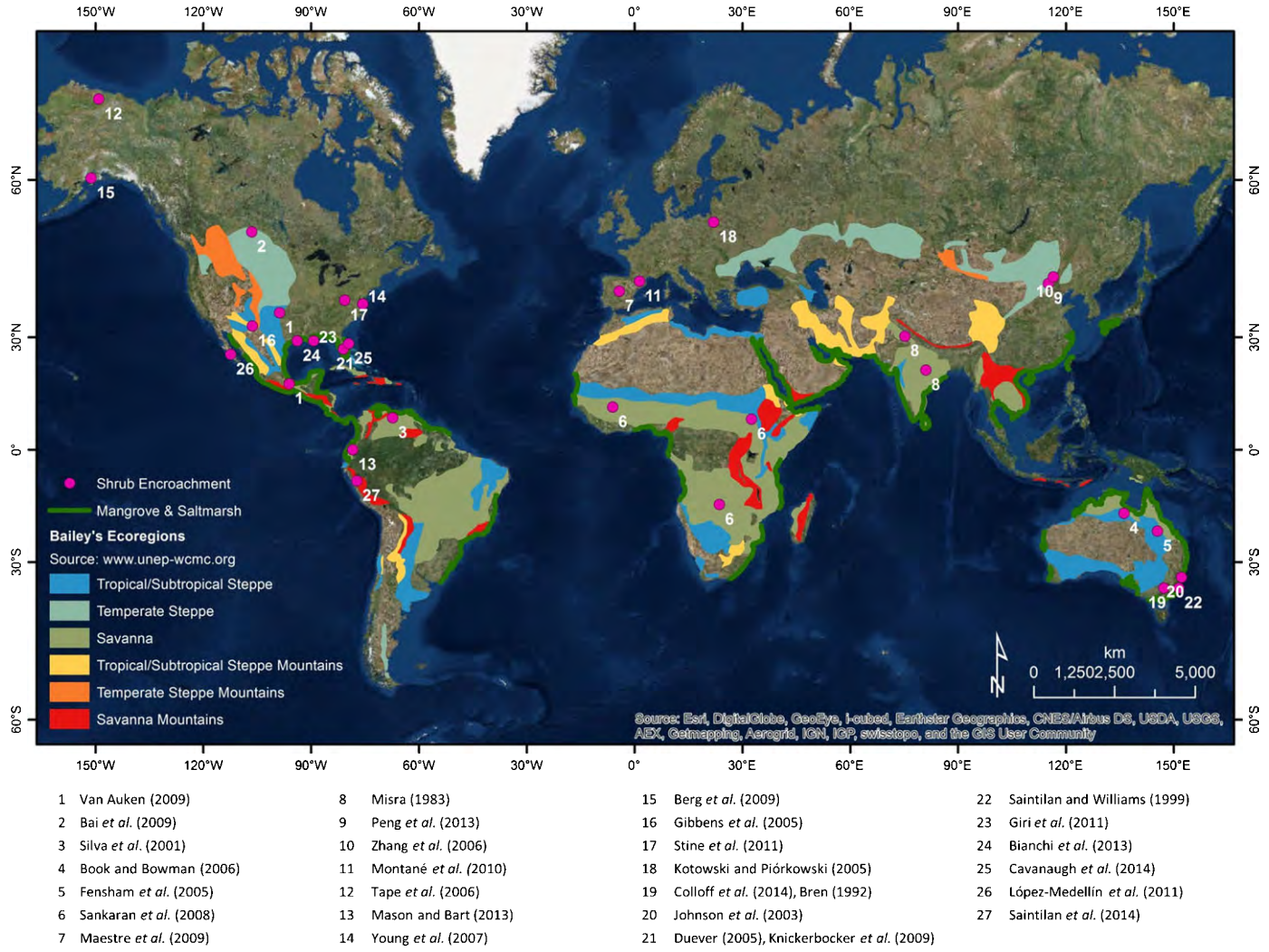
A global trend of woody plant encroachment of terrestrial grasslands is co-incident with woody plant encroachment of wetland in freshwater and saline intertidal settings. There are several arguments for considering tree encroachment of wetlands in the context of woody shrub encroachment of grassland biomes. In both cases, delimitation of woody shrubs at regional scales is set by temperature thresholds for poleward extent, and by aridity within temperature limits. Latitudinal expansion has been observed for terrestrial woody shrubs and mangroves, following recent warming, but most expansion and thickening has been due to the occupation of previously water-limited grassland/saltmarsh environments. Increases in atmospheric CO_2, may facilitate the recruitment of trees in terrestrial and wetland settings. Improved water relations, a mechanism that would predict higher soil moisture in grasslands and saltmarshes, and also an enhanced capacity to survive arid conditions, reinforces local mechanisms of change. The expansion of woody shrubs and mangroves provides a negative feedback on elevated atmospheric CO_2 by increasing carbon sequestration in grassland and saltmarsh, and is a significant carbon sink globally. These broad-scale vegetation shifts may represent a new stable state, reinforced by positive feedbacks between global change drivers and endogenic mechanisms of persistence in the landscape.

Introduction

A recent trend towards semi-arid and mesic grassland conversion to shrub dominance is global in scale and common to all vegetated continents (Fig. 1). Woody shrub encroachment and thickening has converted grassland to woodland in the savannahs and prairies of North America (Bai *et al.*, 2009; Van Auken, 2009), South America (Silva *et al.*, 2001), semi-arid and tropical Australia (Fensham *et al.*, 2005; Brook & Bowman, 2006), Africa (Sankaran *et al.*, 2008), Europe (Maestre *et al.*, 2009), India (Misra, 1983) and China (Peng *et al.*, 2013), where over 5 million hectares of the inner Mongolian grassland has been encroached by *Caragana microphylla* (Zhang *et al.*, 2006). In cold climates, alpine grasslands have been encroached by shrubs in the high Andes in South America (Matson & Bart, 2013), and the Iberian Peninsula and Pyrenees in Europe (Montané *et al.*, 2010), while Tape *et al.* (2006) make a case for pan-arctic shrub expansion into tundra on the basis of aerial photography dating to the 1940s. Shrub thickets are expanding into grass dominated swales on Atlantic US coast barrier islands (Young *et al.*, 2007).

Shrub encroachment of arid and semi-arid grasslands in the United States has been estimated to affect 220–330 million ha (Houghton *et al.*, 1999; Pacala *et al.*, 2001). In North America alone Knapp *et al.* (2008) describe a shift in graminoid to shrub dominance across eight sites spanning 5550 km, and climatic gradients extending from 200 to 1100 mm mean annual precipitation and −12.5 to 22.0°C mean annual temperature. For example, observations stretching back to 1858 in the latter case confirm a steady conversion of the prairie grass Black grama (*Bouteloua eriopoda*) to shrub dominance in the Jornada Basin in New Mexico (Gibbens *et al.*, 2005). Grasses covered 98% of the Jornada Experimental Range in 1858, and < 1% by the turn of the millennium. These changes were well advanced by 1928, and shrub eradication measures, including clearance and grazing regulation, have at best slowed the advance.

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust



1 Van Auken (2009)
2 Bai *et al.* (2009)
3 Silva *et al.* (2001)
4 Book and Bowman (2006)
5 Fensham *et al.* (2005)
6 Sankaran *et al.* (2008)
7 Maestre *et al.* (2009)
8 Misra (1983)
9 Peng *et al.* (2013)
10 Zhang *et al.* (2006)
11 Montané *et al.* (2010)
12 Tape *et al.* (2006)
13 Mason and Bart (2013)
14 Young *et al.* (2007)
15 Berg *et al.* (2009)
16 Gibbens *et al.* (2005)
17 Stine *et al.* (2011)
18 Kotowski and Piórkowski (2005)
19 Colloff *et al.* (2014), Bren (1992)
20 Johnson *et al.* (2003)
21 Duever (2005), Knickerbocker *et al.* (2009)
22 Saintilan and Williams (1999)
23 Giri *et al.* (2011)
24 Bianchi *et al.* (2013)
25 Cavanaugh *et al.* (2014)
26 López-Medellín *et al.* (2011)
27 Saintilan *et al.* (2014)

Fig. 1 Global distribution of grasslands, as sourced from Bailey's Ecoregions map of the World (Bailey, 1989a,b : provided by UNEP-WCMC). Pink points denote locations of cited shrub encroachment into grassland.

There are several published accounts of woody vegetation expansion into freshwater wetlands dominated by reeds and/or grasses. Wet Sphagnum–sedge fens have suffered an accelerating rate of loss to woody encroachment since the 1950s in locations as diverse as the Alaskan Kenai Peninsula (Berg *et al.*, 2009); small Appalachian mountain peatlands (Warren *et al.*, 2007; Stine *et al.*, 2011) and the Biebrza and Narew river valleys of Poland (Kotowski & Piórkowski, 2005). Trees had previously been excluded from the Alaskan fens for 18 000 yr (Berg *et al.*, 2009). Wetland grasslands dominated by the C4 graminoid *Pseudoraphis spinescens* have been replaced progressively by river red gum *Eucalyptus camaldulensis* in Australia's largest inland forested wetland, the Barmah-Millewa forest (Bren, 1992; Colloff *et al.*, 2014), and by *Melaleuca quinquenervia* on large coastal floodplains within SE Australia (Johnston *et al.*, 2003) over a period of at least 70 yr. Sawgrass (*Cladium jamaicense*) has been extensively colonised by Red Maple (*Acer rubrum*) in Florida (Duever, 2005; Knickerbocker *et al.*, 2009) since the 1940s. It is difficult to ascertain whether these are representative of broader trends across wetlands globally.

Contemporaneous with the expansion and thickening of woody shrubs in grassland biomes across the globe has been the expansion of mangrove into saltmarsh environments. Mangroves are woody trees and shrubs that occur exclusively in the marine environment, distributed by tides and colonising intertidal soft-sediment environments, primarily in tropical and subtropical latitudes. Along many of the world's coastlines, mangroves co-occur with saltmarshes, a floristically diverse group of low-stature plants tolerant of saline, periodically saturated conditions, though not exclusively intertidal in distribution. Interactions between mangroves and saltmarshes have been the subject of growing interest; with widespread reports of transitions in boundaries corresponding to regional and global environmental change (Saintilan *et al.*, 2014). On the US Gulf coast, mangrove advance into saltmarsh has been periodically arrested by frost in SE Louisiana (Giri *et al.*, 2011), but further south in Texas and Florida stratigraphic and photographic evidence suggests a consistent expansion and thickening of mangrove over the past century (Bianchi *et al.*, 2013; Smith *et al.*, 2013). Indeed, the mangrove area in Florida has doubled at the northern end of their distribution since 1984 (Cavanaugh *et al.*,

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust

14698137, 2015, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13147 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

New Phytologist

14698137, 2015, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13147 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2014). Similar expansion has been observed on the Pacific coast of Mexico (López-Medellín *et al.*, 2011) and Peru (Saintilan *et al.*, 2014).

Changes in the distribution of mangrove and saltmarsh on the Australian mainland further illustrate this trend. Mangrove encroachment of saltmarsh is near-ubiquitous in the estuaries of SE Australia, occurring within estuaries along 4000 km of coastline from central Queensland to South Australia, encompassing the range of geomorphic and climatic settings within which the two communities co-exist (Saintilan & Williams, 1999). Historical documents, including paintings, maps and plans of early Sydney suggest that the expansion of mangrove into saltmarsh environments may have commenced in the 19th century (McLoughlin, 1987, 2000) when saltmarsh dominated now mangrove-fringed shorelines. Mangroves are also encroaching saline and freshwater wetlands in the tropical north, prompting Williamson *et al.* (2011) to propose that mangrove encroachment of saltmarsh might be analogous to shrub encroachment of savannahs in the same region.

Interactions between woody vegetation and grasslands in terrestrial and wetland contexts have hitherto been considered in discrete bodies of literature reflecting the disciplinary boundaries of terrestrial, freshwater and marine ecology, with only two studies (Williamson *et al.*, 2011; D'Odorico *et al.*, 2012) drawing comparisons across the wetland–terrestrial divide. This might not be surprising given the obvious differences in the growth habits of the species and the characteristics of the environments being considered, and that a strong *prima facie* case might be made for fire and hydrology as drivers of change in these contrasting settings. However, there are several compelling similarities between the woody shrub encroachment that is common across these settings. For the most part, saltmarshes and floodplain wetlands are grasslands, and one of the few instances where C4 grasses extend into higher latitudes (Collatz *et al.*, 1998). Many of the dominant saltmarsh and floodplain wetland species across the globe are members of the family Poaceae (including species of saltmarsh genera *Spartina, Distichlis, Pragmites, Puccinellia* and *Sporobolus,* and in freshwater wetlands: *Pseudoraphis* and *Paspalum*). Though coastal wetlands are regularly inundated by tidal water, physiological water stress is imposed by the presence of salt, carried on tidal waters and concentrated through evaporation between inundation and rainfall events. Shrubs growing in saltmarsh environments therefore share many traits associated with plants in semi-arid climates, including succulence (Chenopodiaceae) and tightly regulated transpiration promoting high water use efficiency in mangroves (Ball, 1996; Krauss *et al.*, 2014), and stunted growth. On floodplain wetlands, hydrological drawdown can induce sharp competition over water between grasses and tree seedlings (Bren, 1992).

This review poses the question of whether tree expansion in freshwater and intertidal wetlands is best understood in the context of woody encroachment of grasslands observed to have occurred over the same period across nearly every other important grassland biome. If so, the case of wetlands may provide some important insights into global drivers of grassland loss, in that many of the putative drivers of change in coastal wetlands cannot apply to terrestrial grasslands and *vice versa.* For example, much of the debate over the drivers of tree encroachment in terrestrial grassland has focused on the role of fire (Higgins *et al.*, 2007; Wakeling *et al.*, 2012), and yet fire is absent from many wetland types subject to tree encroachment considered in this review. Our thesis is that global drivers (elevated CO_2 and temperature) modulate the response of woody plants to local drivers (such as fire and hydrology). Furthermore, similar feedbacks between encroachment, persistence and CO_2 sequestration may apply across the spectrum of terrestrial and wetland settings.

Tree range expansion and temperature

Kaufman *et al.* (2009) document a cooling trend over two millennia in the arctic abruptly terminated at the time of the industrial revolution. This cooling was most probably associated with decreases in summer insolation that commenced following the Holocene thermal maximum some 7500 yr ago. Over the latter Holocene, the tree line retreated and herbaceous tundra expanded in Eurasia (Fisher *et al.*, 1995; Seppä & Birks, 2002). This sequence provides the backdrop against which historical observations should be interpreted and it is reasonable to suppose that woody shrub encroachment in sub-polar regions following 1850 is related to climatic warming. Supporting evidence is found in the increase in radial and vertical growth of woody plants since 1860, and accelerating since 1970 coinciding with acceleration of warming in the region (Hallinger *et al.*, 2010).

The arctic is not the only region where temperature controls on shrub expansion may be important. D'Odorico *et al.* (2012) note that most of the shrubs encroaching on arid grasslands are limited by low temperatures. For example, cold sensitivity has been reported for *Prosopis glandulosa* in south-west Texas and New Mexico (Felker *et al.*, 1982), *Acacia mellifera* encroaching savannah in southern Africa (Sekhwela & Yates, 2007) and *Larrea tridentata* in the Sonoran Desert, the northern limit of which corresponds to the −18°C winter isotherm, the temperature at which freezing-induced cavitation and mortality occurs (Pockman & Sperry, 1996, 2000). Holocene climate variability over the region has influenced the relative extent of grassland and shrubland, with shrubs expanding during the Medieval Warm Period (Bradley *et al.*, 2003), then contracting during the 'Little Ice Age' (Neilson, 1986). The late 19th century would represent a minimum northern extent for the Holocene for terrestrial shrubs and mangroves, and some expansion may be due to range extension within new thermal limits.

Mangrove range expansion provides an interesting illustration of this trend. The tropical mangrove family Rhizophoraceae dominated the mangrove flora of the Richmond River, northern New South Wales, Australia, during the Holocene thermal maximum (Hashimoto *et al.*, 2006). At the time of the first historical surveys following European colonisation the species was rare in the region (West *et al.*, 1985), though has shown strong population growth and southward expansion over the past half-century (Wilson, 2009), corresponding to changing temperature clines (Hennessy *et al.*, 2004), and appears to be well within thermal limits on the basis of leaf phenology (Wilson & Saintilan, 2012). This observation concords with a noted global conservatism in mangrove range expansion in relation to temperature thresholds

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust

14698137, 2015, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13147 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(Quisthoudt *et al.*, 2012) suggesting that dispersal constraints limit latitudinal range extension, particularly on wave-dominated coastlines.

The mangrove genus *Avicennia* is able to withstand mild frosts and extends to higher latitudes than *Rhizophora. A. marina* contracted in latitudinal range during cooling that followed the mid-Holocene thermal maxima in New Zealand (Mildenhall, 1994) and, in spite of strong population growth over the past four decades, has not reclaimed former latitudes due probably to dispersal constraints (De Lange & De Lange, 1994). Geomorphic controls on dispersal are less of an issue on low-wave energy open coastlines, such as the US Gulf coast. Here, *A. germinans* is periodically subjected to intense freezing-induced mortality. The last major event occurred > 25 yr ago, and *A. germinans* populations have shown strong recovery since, expanding into and replacing *Spartina*-dominated saltmarsh (Giri *et al.*, 2011), particularly at poleward limits (Cavanaugh *et al.*, 2014). Thermal modelling based on IPCC projections suggests that in a medium–high gas emissions scenario (A2) with a 2–4°C increase in mean annual minimum temperature, nearly 10 000 km^2 of the herbaceous saltmarsh of the Gulf coast will be vulnerable to mangrove encroachment (Osland *et al.*, 2013). This represents, as a percentage of the state total for saltmarsh, 95% for Louisiana, 100% for Texas and 60% for Florida. *Avicennia* spp. expansion into herbaceous saltmarsh at poleward limits has also been observed in Australia, South Africa and South America (Saintilan *et al.*, 2014).

CO_2 and tree escape from disturbance

While temperature is an important control of the shrub/mangrove distribution at latitudinal and altitudinal limits, most expansion and thickening occurs well within the thermal limits of the species involved. Regional and sub-continental studies of shrub encroachment into grassland stress the importance of aridity gradients in determining shrub cover. For example, phases of woody shrub proliferation and contraction in semi-arid Australia correspond to phases of wet and dry, respectively (Fensham *et al.*, 2005). Similarly, woody cover in the African savannah is strongly associated with Mean Annual Precipitation to a threshold of 650 mm yr^{-1}, above which other factors appear to influence thickening (Sankaran *et al.*, 2008), and alternate states of tree cover may correspond to fire frequency (Staver *et al.*, 2011). Frequent fire may induce a recruitment bottleneck, preventing saplings from 'escaping' to a height immune from fire mortality (Kgope *et al.*, 2010). Fire suppression, often a consequence of grazing (and reduced fuel loads), is often cited as a driver of tree encroachment and thickening in savannahs (Scholes & Archer, 1997; Van Auken, 2000).

Experimental studies have suggested that elevated CO_2 may assist saplings in escaping the fire trap by increasing the growth rate to a height above the fire threat (Kgope *et al.*, 2010). Under elevated CO_2, most notably between sub-ambient and ambient concentrations, saplings accumulate greater belowground carbon stores, which, facilitated by post-fire nutrient release; stimulates faster re-sprouting; and increases the likelihood that the sapling will recruit to fire resistant height (Kgope *et al.*, 2010). Fire regimes that excluded trees from grasslands a century ago may no longer do so (Wigley *et al.*, 2010). Models of the relationship between CO_2 concentration, sapling growth to 'escape height' and fire frequency are consistent with paleo records in South Africa documenting a commencement of woody encroachment following the last glacial maximum and acceleration over the historical period (Bond *et al.*, 2003). It is also consistent with lower recruitment in cooler, upland settings (Wakeling *et al.*, 2012).

The 'escape height' model (Bond & Midgley, 2000; Wakeling *et al.*, 2012) developed to explain the interaction between altered fire regime, CO_2 fertilisation and tree recruitment for terrestrial grasslands can be adapted tree encroachment in some freshwater wetlands (Fig. 2a,b). In the absence of fire, the flood return period is an analogous disturbance. *E. camaldulensis* encroachment of *P. spinescens* grasslands has been attributed to alterations in flooding regime, as floods of 6-month duration above seedling foliage height have been sufficient historically to repress river red gum germination (Bren, 1992; Colloff *et al.*, 2014). River regulation for irrigation has reduced depth and duration of large floods while providing a more reliable base flow. We propose that both alterations to flooding regime, seedling survival and growth rate, may combine to alter fundamentally the recruitment success across the wetland. In this case, the race to achieve 'escape height' between successive flood peaks would be aided by CO_2 fertilisation, an effect facilitated by higher soil water nutrient loads resulting from agricultural developments in the catchment (Fig. 2a).

Studies across three continents have shown woody shrub encroachment in areas subject to a range of disturbance regimes from heavy fire and grazing to ungrazed and rarely burnt (Hastings & Turner, 1965; Lenzi-Grillini *et al.*, 1996; Silva *et al.*, 2001; Fensham *et al.*, 2005; Wigley *et al.*, 2010). Woody encroachment in semi-arid Australian savannah showed no relationship with fire, or the interaction of fire and grazing, over large spatial and temporal scales (Fensham *et al.*, 2005). Woody encroachment of tallgrass prairie has been noted to occur where fire intensities have increased (Knapp *et al.*, 1998; Briggs *et al.*, 2005). Shrub removal programs on the whole fail to stem the progression of shrub encroachment (Rango *et al.*, 2005; D'Odorico *et al.*, 2012), even when combined with changes in land-use aimed at ameliorating these threats (Gibbens *et al.*, 1992). Though fire is important on a local scale in many settings, the more pervasive effect of global drivers seem to override these effects at broader spatial and temporal scales.

CO_2, aridity and drought tolerance

Soil water has also been identified as a limiting factor regulating shrub encroachment of mesic grasslands. Although precipitation is sufficient to allow the development of a closed forest, grassland water use in the upper soil imposes water limitation on seedling establishment (Scholes & Archer, 1997). A similar mechanism has been invoked to explain the dieback of *E. camaldulensis* seedlings in competition with *Pseudoraphis spinescens* wet grassland during hydrological drawdown (Bren, 1992). However, with an increase in the ambient to intracellular CO_2 diffusion gradient comes a greater uptake of CO_2 with a minimal reduction in stomatal conductance (Polley *et al.*, 1997). Photosynthesis can thereby be maintained with lower water loss, and this mechanism has been proposed as a

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust

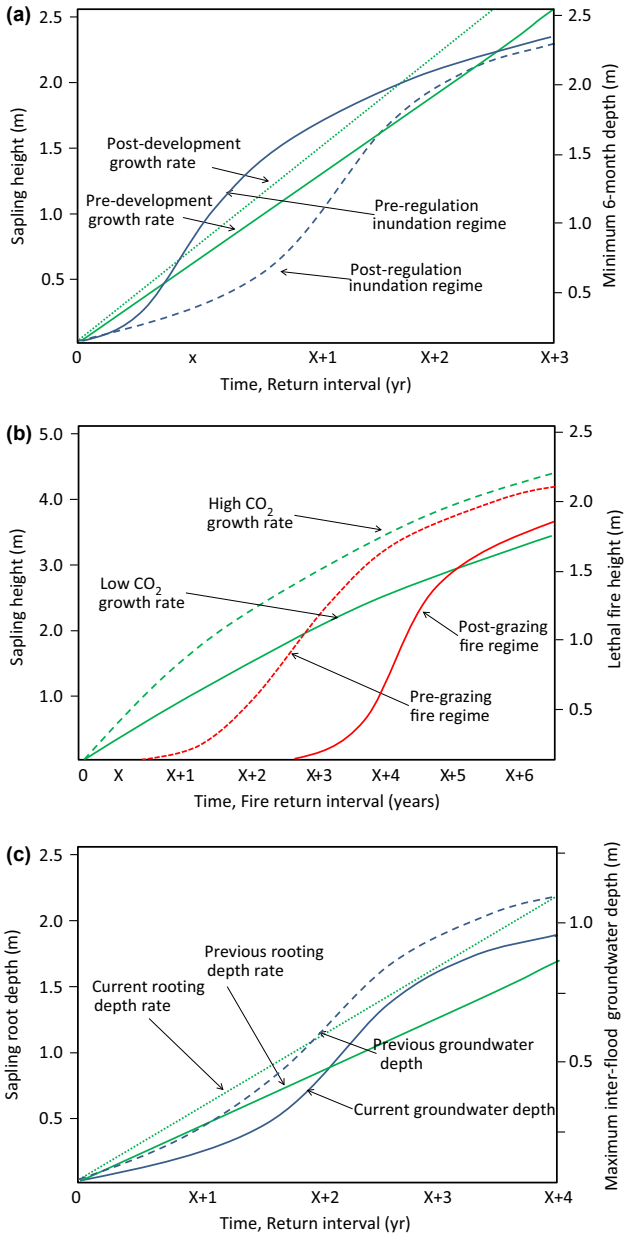


Fig. 2 (a) Conceptual model of the relationship between sapling growth rate and inundation regime on *Pseudoraphis spinescens* (Moira grass) plains. Inundation regime is represented as the return interval of 6-month continual inundation at depths 0–2.5 m, for natural (solid blue line) and post-regulation (dashed blue line) conditions. Growth rate is represented as pre-development (solid green line) and current (dotted line), following nutrient and CO_2 fertilisation. (b) Conceptual model of the relationship between sapling growth rate and fire regime in the African savannah. Fire regime is represented as the return interval of fires capable of killing saplings at a specified height, for natural conditions (dashed red line) and heavily grazed savannah (solid red line). Growth rate is represented as pre-industrial, low CO_2 (solid green line) and current (dotted line), adapted from Bond *et al.* (2003). (c) Conceptual model of the relationship between sapling rooting depth rate and groundwater depth regime for a groundwater dependent wetland. In this case, current groundwater levels (solid blue line) increase on historic norms (dashed blue line) because of sea-level rise in coastal wetlands, and/or reduced transpiration losses. The recruitment bottleneck is avoided when rooting depth exceeds saturated groundwater depth. Growth rate is represented as current (dotted green line), following nutrient and CO_2 fertilisation, and previous (solid green line).

driver of shrub encroachment into grassland along aridity gradients (Idso, 1992).

Elevated CO_2 reduces the leaf conductance of rangeland shrubs (Morgan *et al.*, 2004) and *Spartina* saltmarshes (Rozema *et al.*, 1991; Mateos-Naranjo *et al.*, 2010a,b), though this is offset to some extent by a negative feedback between transpiration rate, leaf temperature and ambient humidity (Morgan *et al.*, 2004). Nonetheless, evapotranspiration may be reduced by up to 20% in savannah ecosystems (Nelson *et al.*, 2004; Polley *et al.*, 2011) and saltmarsh sedgelands (Li *et al.*, 2010). That decreased evapotranspiration is occurring over broad regional scales is supported by evidence of increased soil moisture (Hungate *et al.*, 2002; Carol Adair *et al.*, 2011) and run-off (Labat *et al.*, 2004) in areas where woody thickening is occurring (Eamus & Palmer, 2008). These improved soil moisture conditions may improve percolation to the lower rooting zone of rangeland shrubs, and allow survival of seedlings in mesic settings in competition with shallow-rooting grasses. Elevated CO_2 tends to facilitate a higher growth rate and a higher proportional allocation of plant mass to roots (Nie *et al.*, 2013), providing for an increased rate of root growth to critical depths for drought resistance, or the maintenance of the high root: shoot ratios required of mangroves in saline and hypersaline environments (Saintilan, 1997). The 'escape height' model describing CO_2 effects on fire resistance therefore finds a parallel in 'escape depth' to drought resistance (Fig. 2c).

Improved mangrove seedling survival may also be promoted under improved soil moisture, especially following the depletion of cotyledon reserves (Farnsworth *et al.*, 1996), when elevated CO_2 has been shown to improve the growth of *Avicennia germinans* (Mckee & Rooth, 2008). The proportion of mangrove and saltmarsh can be predicted in northern Australia on the basis of rainfall (Bucher & Saenger, 1991), and field studies of seedling establishment suggest that mangroves are delimited by desiccation in the saltmarsh (Clarke & Myerscough, 1993). Mangrove encroachment of saltmarsh has been associated with higher water levels in Florida (Krauss *et al.*, 2011; Smith *et al.*, 2013), eastern Australia (Rogers *et al.*, 2006), Mexico (López-Medellín *et al.*, 2011) and tropical Australia (Williamson *et al.*, 2011). Phases of higher rainfall and sea-level are often coincident, associated with inter-annual and inter-decadal phases of atmosphere-oceanic cycles such as the El Nino Southern Oscillation and the Inter-decadal Pacific Oscillation (Zhang & Church, 2012). These phases often correspond to phases in vegetation transition (Kim *et al.*, 2010; Rogers *et al.*, 2014). However, while some die-back of shrubs during drought has been noted (Fensham *et al.*, 2005; Sankaran *et al.*, 2008), more commonly shrubs are retained and provide a platform for a successive phase of colonisation. This directional trend requires a press driver, and gives credence to the global effect of elevated CO_2 in sustaining the effect of drivers operating in pulses, such as rainfall and sea-level.

Feedbacks between shrub encroachment, local persistence and CO_2 sequestration

While exogenic factors operating at regional and global scales provide opportunities for woody shrub recruitment, several

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust

14698137, 2015, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13147 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

14698137, 2015, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13147 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

endogenic feedback mechanisms may promote persistence and further thickening (D'Odorico *et al.*, 2012) in an alternative stable state. For example, the shrub architecture promotes the concentration of rainfall to the base of the stem, and improved infiltration and soil moisture near the base of trees (Eldridge & Freudenberger, 2005), conferring a competitive advantage over surrounding grasses. Soil nitrogen and carbon is enhanced in most settings by the presence of shrubs (Maestre *et al.*, 2009; Eldridge *et al.*, 2011), providing opportunities for clonal expansion (Ratajczak *et al.*, 2011). In cold-limiting environments, woody encroachment provides an insulating microclimate in both savannah and saltmarsh (D'Odorico *et al.*, 2012), increasing winter nocturnal temperatures. The competitive replacement of grasslands reduces fuel loads, which improves the recruitment of adult bushes (D'Odorico *et al.*, 2006). Exogenic drivers interact with these feedbacks: CO_2 reducing evapo-transpiration and further enhancing soil moisture; warmer winters leading to greater snow coverage further insulating soils (Sturm *et al.*, 2005).

The triggering of endogenic feedback mechanisms by exogenic global change drivers may lead to more persistent ecosystem states in the long-term. For example, elevated CO_2 may help intertidal wetland plants respond to the pressure of sea-level rise by facilitating the production of belowground biomass, and through this, the building of marsh surface elevation. Experimental manipulation of CO_2 in a mixed *Schoenoplectus americanus* (C_3 sedge) and *Spartina alterniflora* (C_4 grass) saltmarsh field site demonstrated increased growth of *S. americanus*, in elevated ambient CO_2 with this species dominating surface elevation gain (Cherry *et al.*, 2009; Langley *et al.*, 2009). Experimental studies on CO_2 and nitrogen effects on root mass suggest similar responses might be expected in mangroves. *Avicennia germinans* root mass increases under elevated CO_2, and this effect was enhanced under enhanced levels of nitrogen (Mckee & Rooth, 2008). However, these responses may be mediated by environmental conditions including inter-specific competition (Mckee & Rooth, 2008) and salinity (Ball *et al.*, 1997).

The higher rate of soil carbon accumulation in mangrove, and improved sediment trapping observed in USA and Australian comparisons of sympatric mangrove and saltmarsh (Lovelock *et al.*, 2011; Comeaux *et al.*, 2012; Saintilan *et al.*, 2013), suggest that mangrove encroachment of saltmarsh may promote elevation-building and long-term persistence at higher rates of sea-level rise. Relatively higher mangrove soil strength might also improve marsh resistance to wave attack (Comeaux *et al.*, 2012). Increased drought resistance may also be conferred in the transition from saltmarsh to mangrove. In a comparison of water use efficiency of the invasive mangrove *Avicennia germinans* and the dominant Gulf Coast saltmarsh, *Spartina alterniflora*, Krauss *et al.* (2014) demonstrated a 53–65% greater transpiration from *Spartina,* concluding that mangrove encroachment would conserve water in the substrate, helping to explain the persistence of mangrove in areas of saltmarsh dieback in a recent Gulf Coast drought (Mckee *et al.*, 2004).

Additional carbon sequestration resulting from the conversion of grassland and saltmarsh to shrub-dominance represents a potentially significant negative feedback on increasing atmospheric CO_2. Eldridge *et al.* (2011) reviewed 51 studies reporting on soil carbon in the upper 15 cm of shrub and grassland communities, and found a highly significant increase in soil carbon with shrub encroachment, one of the most consistent ecosystem effects of shrub encroachment measured. The net sequestration benefit of mangrove encroachment on saltmarsh has seen less attention, though potentially represents an important carbon sink. The progressive removal of cold-temperature limitations on mangrove northern expansion in the Gulf of Mexico exposes over a million hectares of saltmarsh to mangrove encroachment over the coming century (Bianchi *et al.*, 2013). While posing many challenges to ecosystem services provided uniquely by saltmarsh (Osland *et al.*, 2013; Saintilan & Rogers, 2013), mangrove expansion may facilitate feedbacks promoting the long-term resilience of wetlands to climate change and their enhanced mitigation of radiative forcing. Bianchi *et al.* (2013) estimated that conversion of the coastal marshes of the Gulf of Mexico to mangrove dominance would represent a net increase in carbon sequestration of 1.29 ± 0.32 Tg C yr^{-1} (Bianchi *et al.*, 2013).

Conclusions and Further Research

The breadth of grassland settings subject to tree encroachment, from intertidal and freshwater wetland through semi-arid savannah, and the range of disturbance regimes associated with these, strongly implicates common global drivers. Recent poleward expansion has been observed in both terrestrial and intertidal settings in relation to warmer minimum temperatures. However, most woody shrub/mangrove encroachment and thickening occurs well within species thermal limits, and in these situations elevated CO_2 may act in concert with local drivers to facilitate woody encroachment (Higgins & Scheiter, 2012). The 'escape height' model is a good illustration of this: that elevated CO_2 promotes a higher growth rate and greater likelihood of escape (sapling recruitment) between successive fires. Fire is absent from most wetland systems, but the 'escape height' model works equally well in explaining woody recruitment into wetland grasslands between successive floods.

In other situations CO_2 may facilitate woody sapling persistence by conferring greater drought tolerance. A 5-yr experiment on the Colorado shortgrass steppe (Morgan *et al.*, 2007) in which CO_2 was doubled with respect to controls, led to an *c.* 40-fold increase in the aboveground biomass and a 20-fold increase in plant cover of the shrub *Artemisia frigida*, common to North American and Asian grasslands. For a variety of reasons tree species may be prevented from recruiting into grasslands by periodic drought, either because of competition for water by grasses (in both rangelands and wetlands) or by the combination of periodic aridity and high salinity ('physiologically dry' in the case of saltmarshes). A shift to tree dominance may occur when droughts are no longer sufficient to induce mortality. This may occur because of local hydrological changes (more consistent base flows in regulated rivers, higher eustatic sea-levels), but will be aided by the effects of elevated CO_2 on drought resistance, including the potentially higher water availability resulting in lower transpiration losses, or an improved rate of root growth to access more dependable groundwater at depth (Fig. 2c).

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust

There are, however, important information gaps and new hypotheses to be tested. We do not have global, consistent estimates of rates of grassland and wetland loss to woody encroachment. Few CO_2 enrichment studies have been of sufficient duration to properly consider CO_2 acclimation effects on photosynthesis and carbon partitioning (Smith & Dukes, 2013). Most experiments to date have tested the response of shrubs (mangrove and terrestrial shrubs) to anticipated levels of CO_2 (e.g. *c.* 700 ppm) rather than sub-ambient concentrations relevant to a consideration of historical responses (though see Polley *et al.*, 1997; Kgope *et al.*, 2010). Research on the response of mangroves to elevated and sub-ambient CO_2 is limited to a handful of laboratory studies. These are important questions in the context of adaptation and mitigation measures globally. The shift in vegetation dominance from grassland to shrub with the onset of elevated atmospheric CO_2 is consistent with a trend to higher carbon sequestration potential, a negative feedback that may have regulated atmospheric CO_2 concentrations in periods of less rapid increase than at present. The shift from grassland/saltmarsh to shrub/mangrove dominance also has implications for vegetation persistence in altered climatic and hydrological conditions associated with climate change.

References

Bai Y, Colberg T, Romo JT, Mcconkey B, Pennock D, Farrell R. 2009. Does expansion of western snowberry enhance ecosystem carbon sequestration and storage in Canadian Prairies? *Agriculture, Ecosystems & Environment* **134**: 269–276.

Bailey RG. 1989a. Explanatory supplement to ecoregions map of the continents. *Environmental Conservation* **16**: 307–309.

Bailey RG. 1989b. Bailey's ecoregions of the World. [WWW document] URL http://www.unep-wcmc.org/resources-and-data/baileys-ecoregions-of-the-world [accessed 26 August 2014].

Ball MC. 1996. Comparative ecophysiology of mangrove forest and tropical lowland moist rainforest. In: Mulkey SC, Chazdon RL, Smith AP, eds. *Tropical forest plant ecophysiology*. New York, NY, USA: Chapman and Hall, 461–496.

Ball MC, Cochrane MJ, Rawson HM. 1997. Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO_2. *Plant, Cell & Environment* **20**: 1158–1166.

Berg EE, Hillman KM, Dial R, Deruwe A. 2009. Recent woody invasion of wetlands on the Kenai Peninsula Lowlands, south-central Alaska: a major regime shift after 18 000 years of wet Sphagnum–sedge peat recruitment. *Canadian Journal of Forest Research* **39**: 2033–2046.

Bianchi TS, Allison MA, Zhao J, Li X, Comeaux RS, Feagin RA, Kulawardhana RW. 2013. Historical reconstruction of mangrove expansion in the Gulf of Mexico: linking climate change with carbon sequestration in coastal wetlands. *Estuarine, Coastal and Shelf Science* **119**: 7–16.

Bond WJ, Midgley GF. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**: 865–869.

Bond WJ, Midgley GF, Woodward FI. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973–982.

Bradley RS, Hughes MK, Diaz HF. 2003. Climate in Medieval Time. *Science* **302**: 404–405.

Bren LJ. 1992. Tree invasion of an intermittent wetland in relation to changes in the flooding frequency of the River Murray, Australia. *Australian Journal of Ecology* **17**: 395–408.

Briggs JM, Knapp AK, Blair JM, Heisler JL, Hoch GA, Lett MS, Mccarron JK. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* **55**: 243–254.

Brook B, Bowman DJS. 2006. Postcards from the past: charting the landscape-scale conversion of tropical Australian savanna to closed forest during the 20th century. *Landscape Ecology* **21**: 1253–1266.

Bucher D, Saenger P. 1991. An Inventory of Australian estuaries and enclosed marine waters: an overview of results. *Australian Geographical Studies* **29**: 370–381.

Carol Adair E, Reich PB, Trost JJ, Hobbie SE. 2011. Elevated CO_2 stimulates grassland soil respiration by increasing carbon inputs rather than by enhancing soil moisture. *Global Change Biology* **17**: 3546–3563.

Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W, Feller IC. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences, USA* **111**: 723–727.

Cherry JA, Mckee KL, Grace JB. 2009. Elevated CO_2 enhances biological contributions to elevation change in coastal wetlands by offsetting stressors associated with sea-level rise. *Journal of Ecology* **97**: 67–77.

Clarke PJ, Myerscough PJ. 1993. The intertidal distribution of the grey mangrove (*Avicennia marina*. in southeastern Australia: the effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. *Australian Journal of Ecology* **18**: 307–315.

Collatz GJ, Berry JA, Clark JS. 1998. Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and future. *Oecologia* **114**: 441–454.

Colloff MJ, Ward KA, Roberts J. 2014. Ecology and conservation of grassy wetlands dominated by spiny mud grass Pseudoraphis spinescens in the southern Murray-Darling Basin, Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**: 238–255.

Comeaux RS, Allison MA, Bianchi TS. 2012. Mangrove expansion in the Gulf of Mexico with climate change: implications for wetland health and resistance to rising sea levels. *Estuarine, Coastal and Shelf Science* **96**: 81–95.

De Lange WP, De Lange P. 1994. An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicannia marina* var. *resinifera*). in New Zealand. *Journal of Coastal Research* **10**: 539–548.

D'Odorico P, Laio F, Ridolfi L. 2006. A probabilistic analysis of fire-induced tree–grass coexistence in Savannas. *American Naturalist* **167**: E79–E87.

D'Odorico P, Okin GS, Bestelmeyer BT. 2012. A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecohydrology* **5**: 520–530.

Duever M. 2005. Big Cypress regional ecosystem conceptual ecological model. *Wetlands* **25**: 843–853.

Eamus D, Palmer AR. 2008. Is climate change a possible explanation for woody thickening in arid and semi-arid regions? *International Journal of Ecology* **2007**: 1–5.

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* **14**: 709–722.

Eldridge DJ, Freudenberger D. 2005. Ecosystem wicks: woodland trees enhance water infiltration in a fragmented agricultural landscape in eastern Australia. *Austral Ecology* **30**: 336–347.

Farnsworth EJ, Ellison AM, Gong WK. 1996. Elevated CO_2 alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.). *Oecologia* **108**: 599–609.

Felker P, Clark PR, Nash P, Osborn JF, Cannell GH. 1982. Screening Prosopis (Mesquite) for cold tolerance. *Forest Science* **28**: 556–562.

Fensham RJ, Fairfax RJ, Archer SR. 2005. Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* **93**: 596–606.

Fisher DA, Koerner RM, Reeh N. 1995. Holocene climatic records from Agassiz Ice Cap, Ellesmere Island, NWT, Canada. *The Holocene* **5**: 19–24.

Gibbens R, Beck R, Mcneely R, Herbel C. 1992. Recent rates of mesquite establishment in the northern Chihuahuan Desert. *Journal of Range Management* **45**: 585–588.

Gibbens RP, Mcneely RP, Havstad KM, Beck RF, Nolen B. 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. *Journal of Arid Environments* **61**: 651–668.

Giri C, Long J, Tieszen L. 2011. Mapping and monitoring Louisiana's Mangroves in the aftermath of the 2010 Gulf of Mexico oil spill. *Journal of Coastal Research* **27**: 1059–1064.

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust

14698137, 2015, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13147 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hallinger M, Manthey M, Wilmking M. 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* **186**: 890–899.

Hashimoto TR, Saintilan N, Haberle SG. 2006. Mid-Holocene development of mangrove communities featuring rhizophoraceae and geomorphic change in the Richmond River Estuary, New South Wales, Australia. *Geographical Research* **44**: 63–76.

Hastings J, Turner RM. 1965. *The changing mile: an ecological study of vegetation change with time in the lower mile of a semi-arid region*. Tucson, AZ, USA: University of Arizona Press.

Hennessy K, Page C, Mcinnes K, Jones R, Bathols J, Collins D, Jones D. 2004. *Climate change in New South Wales Part 1: past climate variability and projected changes in average climate. Technical Report*. Aspendale, Vic., Australia: CSIRO Atmospheric Research.

Higgins SI, Bond WJ, February EC, Bronn A, Euston-Brown DIW, Ensin B, Govender N, Rademan L, O'Regan S, Potgieter ALF *et al.* 2007. Effects of four decades of fire manipulation on woody vegetation structure in Savanna. *Ecology* **88**: 1119–1125.

Higgins SI, Scheiter S. 2012. Atmospheric CO_2 forces abrupt vegetation shifts locally, but not globally. *Nature* **488**: 209–212.

Houghton RA, Hackler JL, Lawrence KT. 1999. The U.S. carbon budget: contributions from land-use change. *Science* **285**: 574–578.

Hungate BA, Reichstein M, Dijkstra P, Johnson D, Hymus G, Tenhunen JD, Hinkle CR, Drake BG. 2002. Evapotranspiration and soil water content in a scrub-oak woodland under carbon dioxide enrichment. *Global Change Biology* **8**: 289–298.

Idso S. 1992. Shrubland expansion in the American Southwest. *Climatic Change* **22**: 85–86.

Johnston SG, Slavich PG, Hirst P. 2003. Alteration of groundwater and sediment geochemistry in a sulfidic backswamp due to *Melaleuca quinquenervia* encroachment. *Soil Research* **41**: 1343–1367.

Kaufman DS, Schneider DP, McKay NP, Ammann CM, Bradley RS, Biffa KR, Miller GH, Otto-Bliesner BL, Overpeck JT, Vinther BM *et al.* 2009. Recent warming reverses long-term Arctic cooling. *Science* **325**: 1236–1239.

Kgope BS, Bond WJ, Midgley GF. 2010. Growth responses of African savanna trees implicate atmospheric [CO_2] as a driver of past and current changes in savanna tree cover. *Austral Ecology* **35**: 451–463.

Kim D, Cairns DM, Bartholdy J. 2010. Environmental controls on multiscale spatial patterns of salt marsh vegetation. *Physical Geography* **31**: 58–78.

Knapp AK, Briggs JM, Collins SL, Archer SR, Bret-Harte MS, Ewers BE, Peters DP, Young DR, Shaver GR, Pendall E *et al.* 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology* **14**: 615–623.

Knapp AK, Briggs JM, Hartnett DC, Collins SL. 1998. *Grassland dynamics: long-term ecological research in tallgrass prairie*. New York, NY, USA: Oxford University Press.

Knickerbocker CM, Leitholf S, Stephens EL, Keellings DJ, Laird H, Anderson CJR, Fauth JE, Quintana-Ascencio PF. 2009. Tree encroachment of a sawgrass (*Cladium jamaicense*) marsh within an increasingly urbanized rcosystem. *Natural Areas Journal* **29**: 15–26.

Kotowski W, Piórkowski H. 2005. Competition and succession affecting vegetation structure in riparian environments: implications for nature management. *International Journal of Ecohydrology & Hydrobiology* **5**: 51–57.

Krauss K, From A, Doyle T, Doyle T, Barry M. 2011. Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Islands region of Florida, USA. *Journal of Coastal Conservation* **15**: 629–638.

Krauss KW, Mckee KL, Hester MW. 2014. Water use characteristics of black mangrove (*Avicennia germinans*) communities along an ecotone with marsh at a northern geographical limit. *Ecohydrology* **7**: 354–365.

Labat D, Goddéris Y, Probst JL, Guyot JL. 2004. Evidence for global runoff increase related to climate warming. *Advances in Water Resources* **27**: 631–642.

Langley JA, Mckee KL, Cahoon DR, Cherry JA, Megonigal JP. 2009. Elevated CO_2 stimulates marsh elevation gain, counterbalancing sea-level rise. *Proceedings of the National Academy of Sciences, USA* **106**: 6182–6186.

Lenzi-Grillini CR, Viskanic P, Mapesa M. 1996. Effects of 20 years of grazing exclusion in an area of the Queen Elizabeth National Park, Uganda. *African Journal of Ecology* **34**: 333–341.

Li J, Erickson JE, Peresta G, Drake BG. 2010. Evapotranspiration and water use efficiency in a Chesapeake Bay wetland under carbon dioxide enrichment. *Global Change Biology* **16**: 234–245.

López-Medellín X, Ezcurra E, González-Abraham C, Hak J, Santiago LS, Sickman JO. 2011. Oceanographic anomalies and sea-level rise drive mangroves inland in the Pacific coast of Mexico. *Journal of Vegetation Science* **22**: 143–151.

Lovelock C, Bennion V, Grinham A, Cahoon D. 2011. The role of surface and subsurface processes in keeping pace with sea level rise in intertidal wetlands of Moreton Bay, Queensland, Australia. *Ecosystems* **14**: 745–757.

Maestre FT, Bowker MA, Puche MD, Belén-Hinojosa M, Martínez I, García-Palacios P, Castillo AP, Soliveres S, Luzunaga AL, Sanchez AM *et al.* 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters* **12**: 930–941.

Mateos-Naranjo E, Redondo-Gómez S, Álvarez R, Cambrollé J, Gandullo J, Figueroa ME. 2010a. Synergic effect of salinity and CO_2 enrichment on growth and photosynthetic responses of the invasive cordgrass *Spartina densiflora*. *Journal of Experimental Botany* **61**: 1643–1654.

Mateos-Naranjo E, Redondo-Gómez S, Andrades-Moreno L, Davy AJ. 2010b. Growth and photosynthetic responses of the cordgrass *Spartina maritima* to CO_2 enrichment and salinity. *Chemosphere* **81**: 725–731.

Matson E, Bart D. 2013. Interactions among fire legacies, grazing and topography predict shrub encroachment in post-agricultural páramo. *Landscape Ecology* **28**: 1829–1840.

Mckee KL, Mendelssohn IA, Materne MD. 2004. Acute salt marsh dieback in the Mississippi River deltaic plain: a drought-induced phenomenon? *Global Ecology and Biogeography* **13**: 65–73.

Mckee KL, Rooth JE. 2008. Where temperate meets tropical: multi-factorial effects of elevated CO_2, nitrogen enrichment, and competition on a mangrove-salt marsh community. *Global Change Biology* **14**: 971–984.

McLoughlin L. 1987. Mangroves and Grass Swamps: changes in the shoreline vegetation of the Middle Lane Cove River, Sydney, 1780's–1880's. *Wetlands (Australia)* **7**: 13–24.

McLoughlin L. 2000. Estuarine wetlands distribution along the Parramatta River, Sydney, 1788–1940: implications for planning and conservation. *Cunninghamia* **6**: 579–610.

Mildenhall DC. 1994. Early to Mid Holocene pollen samples containing mangrove pollen from Sponge Bay, East Coast, North Island, New Zealand. *Journal of the Royal Society of New Zealand* **24**: 219–230.

Misra R. 1983. Indian savannas. In: Bourliere F, ed. *Ecosystems of the World*. New York, NY, USA: Elsevier, 151–166.

Montané F, Romanyà J, Rovira P, Casals P. 2010. Aboveground litter quality changes may drive soil organic carbon increase after shrub encroachment into mountain grasslands. *Plant and Soil* **337**: 151–165.

Morgan JA, Milchunas DG, LeCain DR, West M, Mosier AR. 2007. Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. *Proceedings of the National Academy of Sciences, USA* **104**: 14724–14728.

Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA *et al.* 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. *Oecologia* **140**: 11–25.

Neilson RP. 1986. High-resolution climatic analysis and southwest biogeography. *Science* **232**: 27–34.

Nelson J, Morgan J, Lecain D, Mosier A, Milchunas D, Parton B. 2004. Elevated CO_2 increases soil moisture and enhances plant water relations in a long-term field study in semi-arid shortgrass steppe of Colorado. *Plant and Soil* **259**: 169–179.

Nie M, Lu M, Bell J, Raut S, Pendall E. 2013. Altered root traits due to elevated CO_2: a meta-analysis. *Global Ecology and Biogeography* **22**: 1095–1105.

Osland MJ, Enwright N, Day RH, Doyle TW. 2013. Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology* **19**: 1482–1494.

Pacala SW, Hurtt GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath L, Sanquist ET, Stallard RF, Ciais P *et al.* 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science* **292**: 2316–2320.

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust

14698137, 2015, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13147 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Peng H-Y, Li X-Y, Li G-Y, Zhang Z-H, Zhang S-Y, Li L, Zhao G-Q, Jiang Z-Y. 2013. Shrub encroachment with increasing anthropogenic disturbance in the semiarid Inner Mongolian grasslands of China. *CATENA* **109**: 39–48.

Pockman WT, Sperry JS. 1996. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* **109**: 19–27.

Pockman WT, Sperry JS. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* **87**: 1287–1299.

Polley HW, Mayeux HS, Johnson HB, Tischler CR. 1997. Viewpoint: atmospheric CO_2, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management* **50**: 278–284.

Polley HW, Morgan JA, Fay PA. 2011. Application of a conceptual framework to interpret variability in rangeland responses to atmospheric CO_2 enrichment. *Journal of Agricultural Science* **149**: 1–14.

Quisthoudt K, Schmitz N, Randin C, Dahdouh-Guebas F, Robert ER, Koedam N. 2012. Temperature variation among mangrove latitudinal range limits worldwide. *Trees* **26**: 1919–1931.

Rango A, Huenneke L, Buonopane M, Herrick JE, Havstad KM. 2005. Using historic data to assess effectiveness of shrub removal in southern New Mexico. *Journal of Arid Environments* **62**: 75–91.

Ratajczak Z, Nippert JB, Hartman JC, Ocheltree TW. 2011. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. *Ecosphere* **2**: art121.

Rogers K, Saintilan N, Woodroffe CD. 2014. Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: implications for coastal wetland response to climate change. *Estuarine, Coastal and Shelf Science* **149**: 46–56.

Rogers K, Wilton KM, Saintilan N. 2006. Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science* **66**: 559–569.

Rozema J, Dorel F, Janissen R, Lenssen G, Broekman R, Arp W, Drake BG. 1991. Effect of elevated atmospheric CO_2 on growth, photosynthesis and water relations of salt marsh grass species. *Aquatic Botany* **39**: 45–55.

Saintilan N. 1997. Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Marine and Freshwater Research* **48**: 147–152.

Saintilan N, Rogers K. 2013. The significance and vulnerability of Australian saltmarshes: implications for management in a changing climate. *Marine and Freshwater Research* **64**: 66–79.

Saintilan N, Rogers K, Mazumder D, Woodroffe C. 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. *Estuarine, Coastal and Shelf Science* **128**: 84–92.

Saintilan N, Williams RJ. 1999. Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography* **8**: 117–124.

Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW. 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology* **20**: 147–157.

Sankaran M, Ratnam J, Hanan N. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* **17**: 236–245.

Scholes RJ, Archer SR. 1997. Tree–grass interactions in Savannas. *Annual Review of Ecology and Systematic* **28**: 517–544.

Sekhwela MBM, Yates DJ. 2007. A phenological study of dominant acacia tree species in areas with different rainfall regimes in the Kalahari of Botswana. *Journal of Arid Environments* **70**: 1–17.

Seppä H, Birks HJB. 2002. Holocene climate reconstructions from the Fennoscandian tree-line area based on pollen fata from Toskaljavri. *Quaternary Research* **57**: 191–199.

Silva JF, Zambrano A, Fariñas MR. 2001. Increase in the woody component of seasonal savannas under different fire regimes in Calabozo, Venezuela. *Journal of Biogeography* **28**: 977–983.

Smith NG, Dukes JS. 2013. Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO_2. *Global Change Biology* **19**: 45–63.

Smith TJ III, Foster AM, Tiling-Range G, Jones JW. 2013. Dynamics of mangrove–marsh ecotones in subtropical coastal wetlands: fire, sea-level rise, and water levels. *Fire Ecology* **9**: 66–77.

Staver AC, Archibald S, Levin S. 2011. Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. *Ecology* **92**: 1063–1072.

Stine MB, Resler LM, Campbell JB. 2011. Ecotone characteristics of a southern Appalachian Mountain wetland. *CATENA* **86**: 57–65.

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE. 2005. Winter biological processes could help convert Arctic tundra to shrubland. *BioScience* **55**: 17–26.

Tape KEN, Sturm M, Racine C. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* **12**: 686–702.

Van Auken OW. 2000. Shrub Invasions of North American Semiarid Grasslands. *Annual Review of Ecology and Systematics* **31**: 197–215.

Van Auken OW. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* **90**: 2931–2942.

Wakeling JL, Cramer MD, Bond WJ. 2012. The savanna-grassland 'treeline': why don't savanna trees occur in upland grasslands? *Journal of Ecology* **100**: 381–391.

Warren RJ, Rossell IM, Moorhead KK, Dan Pittillo J. 2007. The influence of woody encroachment upon herbaceous vegetation in a Southern Appalachian wetland complex. *American Midland Naturalist* **157**: 39–51.

West RJ, Thorogood CA, Walford TR, Williams RJ. 1985. *Estuarine inventory for New South Wales, Australia*. Sydney, NSW, Australia: Department of Agriculture and Fisheries Bulletin No. 2.

Wigley BJ, Bond WJ, Hoffman MT. 2010. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Global Change Biology* **16**: 964–976.

Williamson G, Boggs G, Bowman DJS. 2011. Late 20th century mangrove encroachment in the coastal Australian monsoon tropics parallels the regional increase in woody biomass. *Regional Environmental Change* **11**: 19–27.

Wilson NC. 2009. *The distribution, growth, reproduction and population genetics of a mangrove species,* Rhizophora stylosa *Griff. near it southern limits in New South Wales, Australia.* Unpublished PhD Australian Catholic University, North Sydney, Australia.

Wilson NC, Saintilan N. 2012. Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. *Aquatic Botany* **101**: 8–17.

Young DR, Porter JH, Bachmann CM, Shao G, Fusina RA, Bowles JH, Korwan D, Donato TF. 2007. Cross-scale patterns in shrub thicket dynamics in the Virginia Barrier Complex. *Ecosystems* **10**: 854–863.

Zhang X, Church JA. 2012. Sea level trends, interannual and decadal variability in the Pacific Ocean. *Geophysical Research Letters* **39**: L21701.

Zhang Z, Wang SP, Nyren P, Jiang GM. 2006. Morphological and reproductive response of *Caragana microphylla* to different stocking rates. *Journal of Arid Environments* **67**: 671–677.

© 2014 The Authors
New Phytologist © 2014 New Phytologist Trust

14698137, 2015, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13147 by Macquarie University, Wiley Online Library on [23/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Chapter 2: Trophic Dynamics in Mangrove and Saltmarsh Ecosystems

2.1 **Saintilan N.,** (2004). Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine Coastal and Shelf Science* 61: 591-601.

2.2 **Saintilan N**., and Wen L. (2012) Environmental predictors of estuarine fish landings along a temperate coastline *Estuarine Coastal and Shelf Science* 113 221-230

2.3 **Saintilan N**. and Mazumder D., (2010). Fine scale variability in the dietary sources of grazing invertebrates in a temperate Australian Saltmarsh. *Marine and Freshwater Research*.61 615-620 75.

2.4 Alderson, B., Mazumder, D., **Saintilan, N.,** Zimmerman, K., & Mulry, P. (2013). Application of isotope mixing models to discriminate dietary sources over small-scale patches in saltmarsh. *Marine Ecology Progress Series*, *487*, 113-122.

2.5 Mazumder D., **Saintilan N.** and Williams R. 2005. Temporal variation in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. *Wetlands Ecology and Management.* 13(4) 457-467

2.6 Mazumder, D., **Saintilan, N.,** Williams, R. J., & Szymczak, R. (2011). Trophic Importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. *Marine and Freshwater Research*, *62*(1), 11-19.

2.7 Mazumder, D., & **Saintilan, N.** (2010). Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. *Wetlands*, *30*, 375-380.

2.8 Mazumder D, **Neil Saintilan,** Yusoff, Fatimah M. & Kelleway, J. J. 2019, 'Equivalence of trophic structure between a tropical and temperate mangrove ecosystem in the Indo-Pacific', Marine and Freshwater Research, vol. 70, no. 10, pp. 1436–1444, doi:10.1071/MF18072

2.9 **Saintilan, N**., & Mazumder, D. (2017). Mass spawning of crabs: ecological implications in subtropical Australia. *Hydrobiologia*, *803*(1), 239-250.

2.10 **Saintilan N.** Hossain K., and Mazumder D. (2007). Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. *Wetlands Ecology and Management* 15 (4) 277-286.

2.11 Mazumder, D., **Saintilan, N.,** Alderson, B. & Hollins, S. 2015, 'Inputs of anthropogenic nitrogen influence isotopic composition and trophic structure in SE Australian estuaries', Marine Pollution Bulletin, vol. 100, no. 1, pp. 217-223

2.12 Kelleway, J.J., Cavanaugh, K., Rogers, K., Feller, I.C., Ens, E., Doughty, C. & **Saintilan, N.** 2017, 'Review of the ecosystem service implications of mangrove encroachment into salt marshes', Global Change Biology, vol. 23, no. 10, pp. 3967-3983

Available online at www.sciencedirect.com
SCIENCE DIRECT®
Estuarine, Coastal and Shelf Science 61 (2004) 591–601
ESTUARINE COASTAL AND SHELF SCIENCE
www.elsevier.com/locate/ECSS

Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries

Neil Saintilan

Australian Catholic University, PO Box 968, North Sydney NSW2059, Australia

Received 26 May 2003; accepted 5 July 2004

Abstract

Multivariate analyses of estuarine geomorphic variables and fish-catch data support the hypothesis that estuaries in New South Wales can be classified in terms of measurable geomorphic characteristics, and that these geomorphic characteristics exert an influence on estuarine biota. The clearest example of this association is the extent to which the area of seagrass, mangrove and central mud basin relates to geomorphic settings and the extent to which the area of these units in turn predict commercial landings of fish and crustaceans. Infilled estuaries with sand barrier entrances, with higher areas of mangrove and lower areas of seagrass and central mud basin yield a catch of fish different to estuaries which are not infilled, and contain relatively high areas of seagrass and central mud basin, and less mangrove. The species contributing most to these differences in assemblages are those which multiple regression analysis identifies to be consistently associated with seagrass area, and which ecological studies reveal to be dependant upon seagrass in their post-settlement phase.
© 2004 Elsevier Ltd. All rights reserved.

Keywords: geomorphology; mangrove; multidimensional scaling; seagrass; fish habitat; south-east Australian estuaries

1. Introduction

In a synthesis of recent research into the geomorphology, hydrology and ecology of NSW estuaries, Roy et al. (2001) suggested a geologically based model as a framework for understanding broad-scale variability in hydrological and ecological characteristics of estuaries in the region. This classification system is based on a suite of geomorphic variables, with the conditions of the estuary entrance dominating the classification of estuary type. Estuary maturity was assessed from the relative extent of four main geomorphic units, these being the marine tidal delta, the central mud basin, the fluvial delta and the riverine channel and associated alluvial plain. As the estuary infills, the riverine channel and associated alluvial plain progressively replace the central mud basin. It is a contention of Roy et al. (2001) that these geomorphic changes influence the floral and faunal characteristics of an estuary to the extent that a model might be developed predicting the influence of increasing estuarine maturity on the biological characteristics of the estuary (Roy et al., 2001).

This hypothesis is subject to experimental investigation using multivariate techniques. In an analysis of commercial fish landings in relation to estuary size, Pease (1999) found that catch per taxa and richness of taxa were lower in the smaller estuaries in New South Wales, with a 4 km^2 threshold being significant. Among larger estuaries, the average catch per taxa and richness of taxa were highest in the central region of the state and lowest in the southern region. Pease (1999) suggested that the high correlation between water area and the diversity of catch indicate that estuary size is the

E-mail address: n.saintilan@mackillop.acu.edu.au.

0272-7714/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2004.07.002

primary factor delineating the catch composition of estuarine fisheries. This relationship undoubtedly involves many abiotic and biotic variables, with Pease (1999) suggesting that extent of seagrass, heterogeneity of habitats and estuary entrance conditions (restricted or deep) may be contributing factors.

The Ozestuaries database (www.Ozestuaries.org), recently published by the Australian Geological Survey Organisation, provides sufficient data for the relationship between geomorphology, habitat and fish landings to be examined in more detail. Data are now available on the area of the primary geomorphic units within Australian estuaries, including the fluvial delta, central mud basin, and river channel, as well as the area of mangrove and saltmarsh. West et al. (1985) surveyed the areas of seagrass in the estuaries of New South Wales. Annual landings of each major species are also available for the commercial fishery in each estuary in New South Wales (Pease and Grinberg, 1995; Scribner and Kathuria, 1996; Tanner and Liggins, 2000).

Multivariate statistical techniques, including multiple regression analysis and non-metric multidimensional scaling and associated analytical techniques, allow for the determination of the extent to which the estuarine classification of Roy et al. (2001), and the associated geomorphic units predict the floral and faunal characteristics of an estuary. The empirical testing of this conceptual framework is of importance given the stated aim of the original model in assisting managers to assign relative ecological value to estuaries or parts of estuaries.

Specifically, the aims of this paper are threefold. Firstly, the analysis will determine whether the classification of estuaries by Roy et al. (2001) is confirmed by clustering and ordination techniques involving geomorphic and geometric variables referred to in their paper. Secondly, the paper examines the extent to which geomorphic and geometric variables, and estuary types (defined below), influence the area of mangrove, saltmarsh and seagrass. Finally, the analysis seeks to determine which geomorphic and wetland variables best predict the landings of commercially important fish, and whether the infilling of estuaries predictably impacts upon fish assemblages as predicted by Roy et al. (2001).

2. Methods

Estuaries in New South Wales have been classified by Roy et al. (2001) into the following four categories:

Type I Ocean embayments,
Type II Tide dominated estuaries (funnel-shaped macrotidal estuaries and drowned river valleys),
Type III Wave-dominated estuaries, including barrier (Type III5) and interbarrier (Type III7) estuaries,
Type IV Intermittent estuaries, including saline coastal lagoons, which become isolated from the sea for extended periods of time.

Roy et al. (2001) further sub-classified these estuaries by stages of infilling (Fig. 1), from Stage A (0–25% filled, youthful), Stage B (25–50% filled, intermediate), Stage C (50–75% filled, semi-mature) to Stage D (75–100% filled, mature).

A data set was assembled for 55 estuaries (Fig. 2), which were classified on the basis of estuary type and stage of maturity as they appear in Roy et al. (2001). Geomorphic variables and their sources are described in Table 1. The area of seagrass in the estuaries of New South Wales was extracted from the survey of West et al. (1985). Annual commercial landings for each of the fish species listed in Table 2 were extracted from Tanner and Liggins (2000). Landings were recorded by weight rather than numbers. After filtering the data set to remove exclusively oceanic species, a total of 81 species were included in the data set, encompassing fish, molluscs and crustaceans. Tanner and Liggins (2000) also provide estimates of the number of days fished in each estuary, allowing the standardisation of data for fishing effort.

3. Statistical analyses

3.1. Classification of estuaries on the basis of environmental variables

The value of each environmental variable listed in Table 1 was fourth-root transformed and a triangular similarity matrix between pairs of estuaries constructed using normalised Euclidean distance. Non-metric multidimensional scaling (nMDS; Clarke and Warrick, 2001) was then used to represent the similarity of estuaries on the basis of geomorphic units, with estuary type of Roy et al. (2001) represented as a factor on the nMDS plot. The nMDS plot provides representation in two dimensions of the relative similarity of sites in their multivariate characteristics. The stress value is a measure of the accuracy of this representation, with a figure below 0.1 indicating a reliable representation (Clarke and Warrick, 2001). A clustering ordination was performed to confirm groupings of estuaries in the nMDS.

There were sufficient numbers of Type III estuaries ($n = 29$) and Type IV estuaries ($n = 17$) to determine whether the estuary maturity classifications of Roy et al. (2001) were consistent with differences in the environmental variables in Table 1. The procedures described

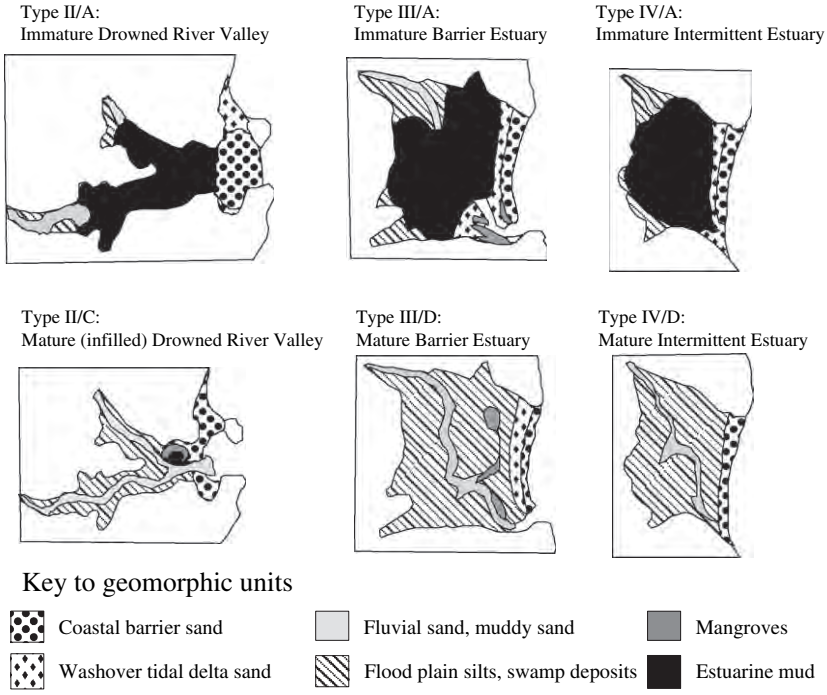


Fig. 1. Plan view of the distribution of geomorphic units in Type II, III and IV estuaries at the immature and mature phases of infill (after Roy et al., 2001).

above were therefore repeated for Type III (barrier) estuaries only, and Type IV (intermittent) estuaries only, with estuary maturity represented as a factor. The significance of differences between estuary types on the basis of environmental variables was tested using one-way analysis of similarities (ANOSIM; Clarke and Warrick, 2001). The procedure was repeated using proportions of the same geomorphic units, after the percentage data were square root transformed.

3.2. Factors correlating with extent of vegetated habitats

A two-way ANOSIM procedure was used to determine whether estuary types and levels of maturity could be differentiated on the basis of the area of mangrove, saltmarsh and seagrass. The hypothesis that the area or proportion of mangrove, saltmarsh and seagrass is related to particular geomorphic or

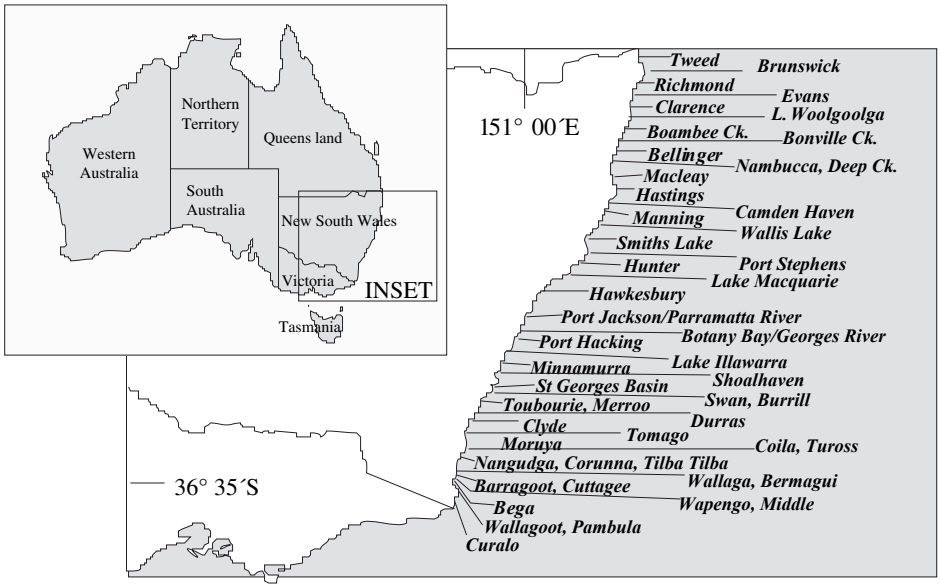


Fig. 2. Location of estuaries included in the analysis.

Table 1
Environmental variables included in the analysis

Variables	Source
(a) Geomorphic variables (area)	
Tidal sand banks	Ozestuaries database
Central Mud Basin	Ozestuaries database
Barrier/backbarrier sands	Ozestuaries database
Fluvial bayhead delta	Ozestuaries database
Channel	Ozestuaries database
Intertidal flats (unvegetated)	Ozestuaries database
(b) Geometric variables	
Estuary greatest width	Ozestuaries database
Estuary length	Ozestuaries database
Estuary perimeter	Ozestuaries database
Water area	Ozestuaries database
Entrance width	Ozestuaries database
Entrance cross-sectional area	Pease 1999
Catchment area	Roy et al. 2001
(c) Vegetation variables	
Mangrove area	Ozestuaries database
Saltmarsh area	Ozestuaries database
Seagrass area	West et al. 1985

climatic conditions was tested using linear regression analyses.

3.3. Analysis of fish catch by geomorphic context

Data on annual commercial fish landings by biomass for each species were treated as an assemblage and Bray–Curtis similarity matrices generated using fourth-root transformed fish-catch (weight) data. This formed the basis of an nMDS representation of fish landings with estuary type represented as a factor. Separate nMDS plots were generated for Type III and Type IV estuaries with their geomorphic maturity represented as a factor. The ANOSIM procedure was then performed according to the manner described in the previous section for environmental variables. Where ANOSIM tests identified significant differences in assemblages between estuary types, a similarities percentage test (SIMPER; Clarke and Warrick, 2001) was used to identify species contributing most to these dissimilarities.

Fish landing data were standardised for fishing effort by dividing the catch of each species by the number of days fished in each estuary, as reported by Tanner and Liggins (2000). An additional problem posed by differences in fishing effort in multivariate analyses is the increased number of species encountered with greater effort. To compensate for this in standardizing for effort, catches of less than 0.1 kg were assigned a zero value.

The extent to which geomorphic variables explained the variability in fish catch was determined using the BIOENV procedure (Clarke and Ainsworth, 1993). A draftsman's plot was used to select non-correlating geomorphic, geometric and vegetation variables to maximise the Spearman rank correlation with the fish-catch similarity matrix. All cluster and ordination analyses were performed using Primer Version 5 statistical software.

The relationship between the commercial landings of species and geomorphic, geometric and vegetation variables was determined using multiple regression analysis in the SPSS program. The primary purpose of this analysis was to determine the extent to which vegetated habitats (mangrove, saltmarsh and seagrass) were important predictors of individual fish species landings, both for all estuaries examined and within estuary types.

4. Results

4.1. Classification of estuaries on the basis of environmental variables

The classification of estuaries into Types I–IV by Roy et al. (2001) appears to strongly supported by the nMDS plot (Fig. 3) when variables included the geomorphic variables listed in Table 1(a), along with mangrove and entrance cross-sectional area. Of 55 estuaries studied, 49 are grouped in the ordination in a way corresponding to their classification in Roy et al. (2001). Of the exceptions, four estuaries classified as Type III (barrier) by Roy et al. (2001) clustered with Type IV estuaries (intermittent) in terms of overall geomorphic characteristics (St Georges Basin, Burrill Lake, Bega River and Wallaga Lake). The Hunter River clustered with the Type II (Drowned River Valley) estuaries rather than Type III, and Botany Bay clustered with Type II estuaries rather than Type I (coastal embayments), sensu Roy et al. (2001).

ANOSIM results show a high degree of statistically significant discrimination between estuary types on the basis of geomorphic variables, with Type III different to Type IV ($P = 0.001$), Type III different to Type II ($P = 0.002$) and Type IV different to Type II ($P = 0.002$). No significant difference was found between the Type I estuary and other estuary types, though only one Type I estuary was represented (Botany Bay). Clearly, a greater number of Type I estuaries would be required to avoid a type II experimental error.

Discrimination between estuaries on the basis of maturity produced less equivocal results, though the analysis was weakened by the absence of data on the area of the alluvial plain. A two-way crossed ANOSIM using estuary type and estuary maturity as factors failed to show statistically significant differences between estuaries on the basis of maturity. This may not be surprising, as different types of estuaries move through different phases of infilling (Roy, 1984). For this reason, the analysis was repeated for individual estuary types

Table 2
Faunal species used in the fish-catch assemblage data for each estuary

Crustaceans
Crab Blue Swimmer *Portunus pelagicus*
Crab Mud *Scylla serrata*
Prawn king *Penaeus plebejus*
Prawn Greasyback *Metapenaeus bennettae*
Prawn, School *Metapenaeus macleayi*
Prawn, Tiger *Penaeus esculentus*, *P. semisulcatus*
Prawn, Unspecified Estuary
Teleost
Anchovy *Engraulis australis*
Australian salmon *Arripis trutta*
Bream, Black and Yellowfin *Acanthopagrus butcheri*, *A. australis*
Catfish, Estuary *Cnidoglanis macrocephalus*
Catfish, Forktailed *Arius graeffei*
Cod, Unspecified *Scorpaena* sp.
Dart *Trachinotus* spp.
Dory *Zeus faber*, *Zenopsis nebulosus*
Drummer *Girella elevata*
Eel, Conger *Conger verreauxi*
Eel, Longfin River *Anguilla reinhardtii*
Eel, Pike *Muraenesox bagio*
Eel, Shortfin River *Anguilla australis*
Eel, Unspecified
Flathead, Dusky *Platycephalus fuscus*
Flathead, Sand *P. caeruleopunctatus*
Flathead, Unspecified
Flounder, Unspecified Families Bothidae and Pleuronectidae
Garfish, River *Hyporhamphus regularis*
Garfish, Shortbill *Arrhamphus sclerolepsis*
Garfish, Sea *Hyporhamphus australis*
Gunard *Chelidonichthys kuma*
Hairtail *Trichiurus coxii*
Kingfish *Seriola lalandi*
Leatherjacket, Family Monacanthidae
Longtom Family Belonidae
Luderick *Girella tricuspidata*
Mackerel *Scomber australasicus*
Morwong, Rubberlip, Red: *Cheilodactylus fuscus*, *Nemadactylus douglasii*
Mullet, Fantail *Liza argentea*
Mullet, Pink-eye *Myxus petardi*
Mullet, Red Family Mullidae
Mullet, Sand *Myxus elongatus*
Mullet, Sea *Mugil cephalus*
Mullet, Unspecified
Mulloway *Argyrosomus hololepidotus*
Pike *Dinolestes lewini*
Perch, Unspecified Genus *Helicolenus*, *Anthias*, *Glaucosoma*.
Pilchard *Sardinops neopilchardus*
Samson Fish *Seriola hippos*
Sandy sprat (whitebait) *Hyperlophus vittatus*
Silver biddy *Gerres subfasciatus*
Snapper *Pagrus auratus*
Sole, Black *Achlyopa nigra*
Sole, Lemon *Pelotretis flavilatus*
Sole, Mixed
Tailor *Pomatomus saltatrix*
Tarwhine *Rhabdosargus sarba*
Trevally, Silver *Pseudocaranx dentex*
Trumpeter *Latridopsis forsteri*
Whiting, Sand, school *Sillago ciliata*, *S. flindersi*
Whiting, Trumpeter *Sillago maculata*
Whiting, Unspecified
Yellowtail *Trachurus novaezelandiae*
Sharks and rays
Shark, Black Tip *Carcharhinus* spp.
Shark, Carpet *Orectolobus ornatus*, *O. maculatus*
Shark, Fiddler *Trygonorrhina* spp.
Shark, Hammerhead *Sphyrna* spp.
Shark, Port Jackson
Shark, Unspecified
Stingray Subfamily Dasyatididae
Molluscs
Calamari, Southern *Sepioteuthis australis*
Pipi *Plebidonax deltoides*
Cockle *Anadara trapexia*
Cuttlefish *Sepia* spp.
Octopus *Octopus* spp.
Mussel, Blue *Mytilus edulis*
Scallop *Pecten fumatus*
Squid Family Loliginidae & Ommastrephidae

for which there was an acceptable level of replication, these being Type III and Type IV estuaries.

Type III estuaries displayed some differences on the basis of maturity. Significant differences exist between Types 5B and 5C ($P = 0.024$) and between Types 5B and 5D ($P = 0.019$, Fig. 4). Type 5B estuaries had higher areas of central mud basin, water area and maximum width than 5C and 5D estuaries, but lower areas of fluvial delta and channel. No other statistically significant differences were evident.

Type IV estuaries displayed no consistent differences on the basis of maturity when the area of geomorphic units are measured. Entrance area was not included in this analysis, as Type IV estuaries are usually closed. When a similarity matrix is generated using the proportions of geomorphic units, Type IV/8/C estuaries may be distinguished from Type IV/8/A estuaries (ANOSIM $P = 0.012$). This is primarily on the basis of a higher area of central mud basin and barrier/backbarrier sands in Type IV/8/A estuaries and lower areas of water.

4.2. Wetland vegetation in geomorphic and climatic context

A two-way ANOSIM was performed using the area of mangrove, saltmarsh and seagrass as variables and estuary type and estuary maturity as factors. The results

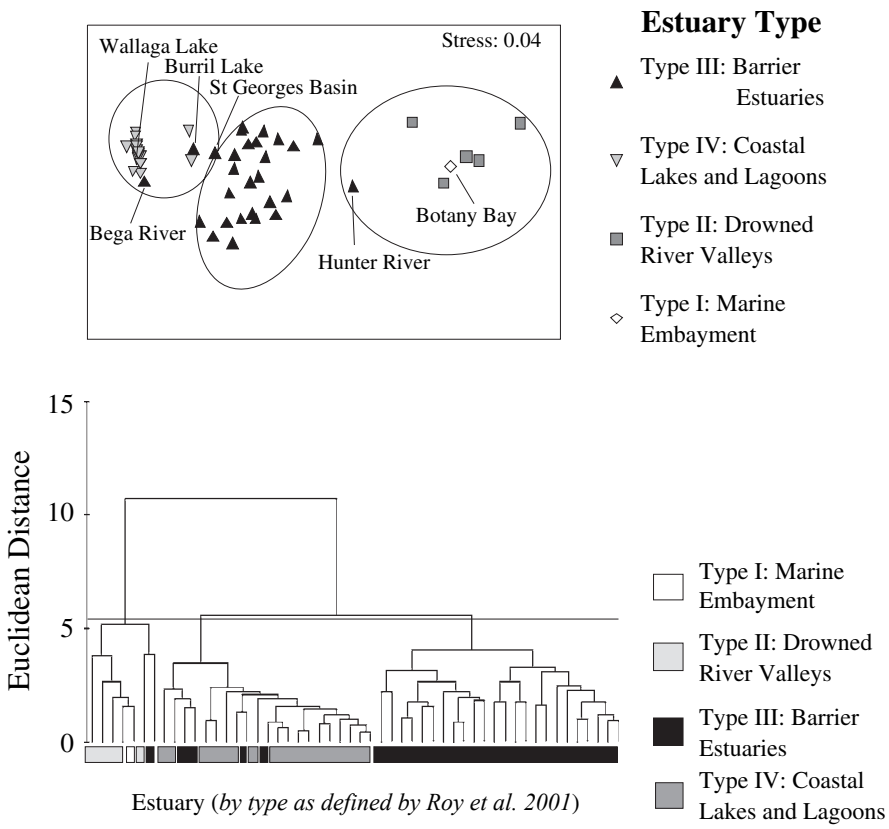


Fig. 3. Results of nMDS (top) and Cluster (bottom) ordinations of estuaries on the basis of environmental variables. The groups outlined on the nMDS plot correspond to the clusters identified at a Euclidean distance of 5.5, represented by a dotted line on the cluster dendogram. A stress value of 0.04 indicates that the position of the estuaries in the two-dimensional plot accurately represents their relative similarity in environmental (geomorphic) conditions.

show that estuary Types II, III and IV may be distinguished on the basis of these variables. Type II estuaries have a higher proportion of mangrove and saltmarsh than Type III estuaries, but similar proportions of seagrass. Type II and III estuaries have higher amounts of all three vegetated habitats than Type IV estuaries.

Significant differences could also be found in vegetated habitats between estuaries on the basis of maturity. In particular, stage D estuaries (infilled) had proportionally more mangrove, but less seagrass and saltmarsh than "immature" stage A estuaries ($P = 0.008$, Fig. 5). Compared to stage B estuaries, stage D had proportionally more mangrove and saltmarsh but less seagrass ($P = 0.004$).

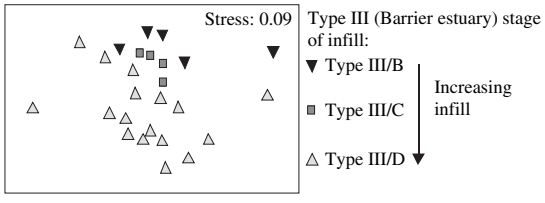


Fig. 4. nMDS plot showing similarities between Type III/5/B, III/5/C and III/5/D estuaries on the basis of environmental variables. The nMDS plot represents the similarity of estuaries in relation to these variables as distances in two-dimensional space. The stress value of 0.09 indicates that this two dimensional representation is a reliable indication of actual similarity as expressed in the similarity matrix.

The area of mangrove and saltmarsh in estuaries is highly correlated (correlation coefficient 0.794), though only two of the Type IV estuaries have mangrove. Linear multiple regression analyses found that of the variables which showed significant correlations with saltmarsh area (tidal sand banks, central mud basin, intertidal flat, mangrove area and water area), only mangrove area was included in a step-wise multiple regression, yielding an r^2 value of 0.617.

Mangrove area showed no significant correlation with the entrance area. Of correlating variables entered into a step-wise multiple regression analysis (tidal sand banks, central mud basin, intertidal flat, maximum length, and water area), only the area of tidal sand banks was significant ($r^2 = 0.432$, $P < 0.001$).

No significant relationship was found between the proportion of mangrove and saltmarsh and rainfall ($r^2 = 0.024$, $P = 0.375$), in estuaries supporting both communities. Channel area was selected as the primary factor predicting the proportion of saltmarsh ($r^2 = 0.149$, $P = 0.005$), with rainfall added to a second model

($r^2 = 0.185$, $P = 0.003$). Variables excluded are central mud basin, fluvial delta, intertidal flats, and water area.

Seagrass and mangrove area were not significantly correlated. Variables positively correlating with seagrass area included maximum width, and the size of the tidal sand banks and central mud basin. Step-wise multiple regression analysis included maximum width in an initial model ($r^2 = 0.357$, $P < 0.001$), adding tidal sand banks in a subsequent model ($r^2 = 0.592$, $P < 0.001$).

4.3. Analysis of fish landings by geomorphic context

The results of the nMDS analysis on annual fish landings confirm the finding of Pease (1999) that Type IV (intermittent) estuaries have a comparably low abundance and diversity of catch. Type III (barrier) estuary catch assemblages differ significantly from Type IV assemblages ($P = 0.01$) with higher catches of *Mugil cephalus*, *Girella tricuspidata*, *Anguilla* sp. and *Scylla serrata* all contributing more than 4% to dissimilarities. Type II (drowned river valley) estuaries again have significantly greater diversity and abundance of fish catch compared to Type IV estuaries ($P = 0.05$), again with *M. cephalus* and *G. tricuspidata* contributing most toward dissimilarities. *Rhabdosargus sarba* was the only species more commonly caught in Type IV estuaries. No significant difference was found in catch between Type III and Type II estuaries.

When fish catch is standardised for fishing effort, the only distinction in fish landings on the basis of estuary type is between Type III and Type IV estuaries ($P = 0.025$). Most species had higher catch rates in Type III estuaries, particularly *Metapenaeus macleayi*, *Mugil cephalus*, *Girella tricuspidata* and *Scylla serrata*. Exceptions to this trend were catch rates for *Rhabdosargus sarba* and *Penaeus plebejus*, which were higher in Type IV estuaries.

No differences in fish-catch assemblage could be detected between levels of maturity for Type III or for Type IV estuaries using absolute catch data. However, when fish catch is standardised for fishing effort, differences emerge between Type III estuaries on the basis of estuarine maturity. In particular, fish catch in Type IIID (infilled) estuaries may be distinguished from Type IIIB (less infilled; $P = 0.025$, Fig. 6) and Type IIIA (least infilled; $P = 0.036$) estuaries. SIMPER analysis revealed that Type IIID estuaries had higher catches of *Metapenaeus macleayi*, and lower catches of (predominantly) *Hemiramphus robustus*, *Hyporhamphus dussmieri*, *Gerres subfasciatus*, *Portunus pelagicus* and *Meuschenia* sp., than Type IIIB and Type IIIA estuaries when catch is standardised for effort (Table 3). *Anguilla reinhardtii*, *Myxus elongates* and *Scylla serrata* catches were higher in Type IIID estuaries, though these contributed less to dissimilarity between catch than species associated with seagrass. Type IIIB had higher

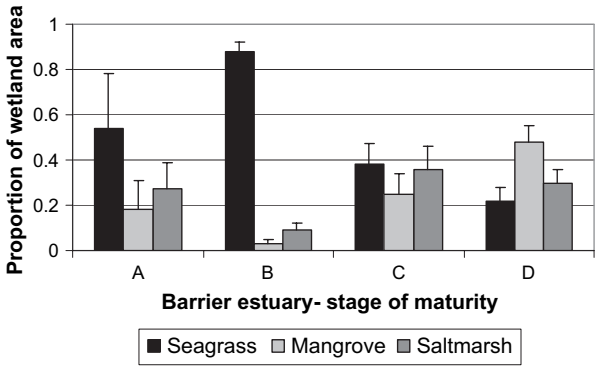


Fig. 5. The proportional area of mangrove, seagrass and saltmarsh in Type III (barrier) estuaries by stage of maturity.

catches of *Hyporhamphys* sp., *G. subfasciatus*, *Mugil cephalus* and *Penaeus plebejus* than Type IIIA estuaries, and lower catches in *Pseudocaranx* sp. and *Girella tricuspidata*, when standardised for fishing effort, though these results are only marginally significant ($P = 0.05$).

A draftsman's plot was used to generate a subset of 10 variables for the matching of environmental and biotic data using BIOENV. The variables selected were tidal sand bank, barrier/backbarrier sand, central mud basin, fluvial bayhead delta, channel area, intertidal flats (unvegetated), mangrove, water area, saltmarsh, seagrass and entrance area. Of these, a combination of tidal sand bank, central mud basin, channel, water area and saltmarsh produced the best correlation (Spearman correlation coefficient: 0.54) between the fish-catch Bray–Curtis matrix and the environmental variable matrix.

When the analysis was performed on Type III estuaries only, the variables producing the best correlation were barrier/backbarrier sands, central mud basin, channel and water area and saltmarsh, with a correlation coefficient of 0.67. For Type IV estuaries, the variables giving the highest correlation were mangrove, saltmarsh and seagrass, with a Spearman correlation coefficient of 0.490.

The capacity of selected environmental variables to predict individual species catch was assessed using a step-wise linear multiple regression analysis. Seventeen estuarine fish species were chosen for this analysis, a list comprising of species commonly found in coastal

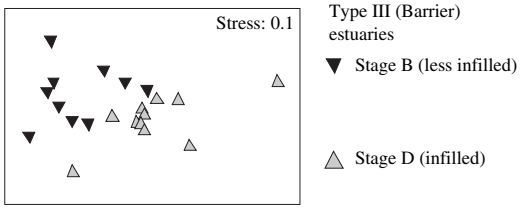


Fig. 6. nMDS plot showing extent of similarity between Type IIIB and Type IIID estuaries on the basis of fish landings, standardised for days fished (ANOSIM $P = 0.025$).

Table 3
Contribution of fish species to differentiation between Type III B, D, and A estuaries on the basis of fish landings

	Av. abundance	Av. abundance	% Contribution to dissimilarity	Cumulative % contribution to dissimilarity
	Type IIID	Type IIIB		
Hyporhamphus regularis	1.27	158.33	4.25	4.25
Metapenaeus macleayi	753.94	92.88	3.88	8.13
Gerres subfasciatus	31.01	423.35	3.73	11.85
Portunis pelagicus	2.34	256.22	3.35	15.20
Monacanthidae	0.29	73.50	3.20	18.40
Penaeus plebejus	17.88	195.18	3.17	21.57
	Type IIID	Type IIIA		
Hyporhamphus regularis	1.27	488.08	4.23	4.23
Gerres subfasciatus	31.01	725.54	3.82	8.05
Portunis pelagicus	2.34	286.48	3.60	11.65
Metapanaeus macleayi	753.94	77.58	3.60	15.25
Mugil cephalus	1276.02	1843.17	3.27	18.52
Monacanthidae	0.29	54.92	2.85	21.37

wetland and shallow estuarine environments. The 11 geomorphic and wetland variables used in the BIOENV analysis were used in the multiple regression analysis, on the basis that correlations were low between these variables (with the exception of mangrove and saltmarsh).

Regression analysis revealed that many species were consistently associated with seagrass across all estuaries (*Portunus pelagicus*, $r = 0.80$; *Platycephalus fuscus*, $r = 0.78$; *Hyporhamphus* sp., $r = 0.56$; *Sillago ciliata*, *Sillago flindersi*, $r = 0.66$; *Penaeus plebejus*, $r = 0.44$ and Monacanthidae, $r = 0.76$; and *Rhabdosargus sarba*, $r = 0.51$ across Type IV estuaries only). A second group of species were positively correlated with the area of central mud basin (*Acanthapagrus* sp., $r = 0.87$; *Girella tricuspidata*, $r = 0.83$; *Mugil cephalus*, $r = 0.80$ and *Gerres subfasciatus*, $r = 0.74$), while a third group is associated with the area of tidal sand bank (*Scylla serrata*, *Metapenaeus macleayi*, *Cnidoglanis macrocephalus*, and *Platycephalus caeruleopunctatus*). *Anguilla reinhardtii* and *Myxus elongatus* were consistently associated with mangrove ($r = 0.719$ and $r = 0.416$, respectively).

5. Discussion

A central task for estuarine ecology is to develop models of the relationship between estuary form and function, and to test these models empirically. The model of Roy et al. (2001), which provides a geomorphologic framework for understanding estuary types and their biotic variability, is used as a working model by estuary managers in New South Wales. The wish of the authors at the conclusion of their paper was that their preliminary findings would stimulate testing of their concepts, and the exploring in greater depth of the relationships between estuary form and function. The publication of data on the area of geomorphic units in New South Wales estuaries, and the development of multivariate statistical procedures capable of exploring relationships between numerous geomorphic and biotic variables, have allowed this model to be subject to rigorous examination.

5.1. Geomorphic variables and estuary classification

Multidimensional scaling and associated analytical techniques (cluster analysis, ANOSIM) using a broad range of geomorphic and geometric variables confirm the utility of Roy et al.'s (2001) classification of NSW estuaries into types. With few exceptions, estuaries grouped on an nMDS plot as predicted by the Roy et al. (2001), and ANOSIM results confirmed significant differences between estuaries, determined mainly by the cross-sectional area of the entrance. Classification of estuaries on the basis of maturity was less successful. Though insufficient data were available on the size of the alluvial plain, an important variable in their model, the remaining geomorphic units (tidal sand banks, central mud basin, barrier/backbarrier sands, fluvial bayhead deltas, channel, and intertidal flats) showed little consistency in absolute or proportional change between estuary stages of infill, with one exception. Less infilled barrier estuaries supported consistently higher areas of central mud basin, water area and width, and lower areas of fluvial delta and channel than estuaries classified as more infilled of this type.

5.2. Vegetated habitats and geomorphology

The suggestion of Roy et al. (2001) that the area of seagrass declines as estuaries infill and mature was confirmed in the two-way ANOSIM results, showing a significant decrease in seagrass extent with increasing estuary maturity, as well as correlation between seagrass

area and the width of the estuary. The analysis did not support the contention of Roy et al. (2001) that barrier estuaries support higher proportions of seagrass than drowned river valleys.

Mangrove proportion was found to increase with increasing estuary maturity as predicted by the Roy model. However, although saltmarsh area correlated with mangrove area, saltmarsh did not increase consistently through estuary stages of infill. The proportion of mangrove and saltmarsh showed no correlation with rainfall. This result contrasts to the findings of Bucher and Saenger (1994) for tropical and subtropical estuaries in Australia, where average annual rainfall showed a strong relationship with the relative proportion of mangrove and saltmarsh. The recent increase in the proportion of mangroves in NSW estuaries (Saintilan and Williams, 1999) is unlikely therefore to be solely a response to increases in rainfall.

5.3. Fish landings in relation to geomorphology and habitat

Fish assemblages of most commercially important species show little association with latitude in New South Wales. Gray et al. (1996) suggest this to be an effect of the east Australia current that flows parallel to the coast and supplies many of the recruits into estuaries. This degree of mixing makes possible statewide comparisons of fish catches on the basis of varying geomorphic settings. The influence of entrance cross-sectional area on fish landings appears limited to the differentiation of Type IV (intermittently open) estuaries from permanently open estuaries. Analysis of the fish-catch assemblage confirmed the finding of Pease (1999) that Type IV estuaries are relatively poor in species diversity and abundance. The closure of estuaries decreases opportunities for recruitment, and allows salinity fluctuations detrimental to survivorship of many species (Hannan and Williams, 1998; Griffiths and West, 1999; Pease, 1999). Entrance cross-sectional area did not correlate with the catch of any species within permanently open estuaries, nor was cross-sectional area utilised in the BIOENV analysis to define those estuarine variables best predicting the assemblage of fish caught. Once an estuary is open, variables other than entrance cross-sectional area appear to determine fish assemblages.

Entrance modification works are therefore unlikely to impact on fish abundance unless the status of the estuary is altered between closed and open. The lowering of tidal range caused by restriction of the entrance did not provide evidence of any major impact on fish assemblages within an estuary. The 50% of estuaries in NSW kept permanently open either by training walls or dredging works are likely to have higher diversity and abundance as a result, as predicted by Roy et al. (2001).

5.4. Estuary infill, habitat change and fish abundance

When data are standardised for fishing effort, differences emerge between Type III (barrier) estuaries on the basis of estuary maturity, with catch of (primarily) *Hemiramphus robustus*, *Hyporhamphus dussmieri*, *Penaeus plebejus*, *Meuschenia* sp., *Gerres subfasciatus*, *Portunus pelagicus* and *Mugil cephalus* declining with increased estuary infilling and maturity. By contrast, catch of *Metapenaeus macleayi* increased in the more infilled Type III estuaries. The differences in fish landings between immature barrier estuaries and mature, infilled barrier estuaries are explicable in terms of differences in habitats available to fish in these estuary types. All of the species declining in catch between immature and mature barrier estuaries were species which showed a correlation between catch and the extent of seagrass or central mud basin. Regression analysis demonstrated a link between seagrass extent and the catch of *P. pelagicus*, *H. robustus*, *H. dussmieri*, *Meuschenia* sp., *P. plebejus*, *Rhabdosargus sarba*, *Sillago ciliata* and *Platycephalus fuscus*, and between the area of mud basin and the catch of *M. cephalus* and *G. subfasciatus*. As estuaries infill and the area of seagrass and mud basin declines, so too does the catch of species dependant upon these habitats.

Ecological studies underscore the relationship between seagrass habitat and abundance of the above species. While post-settlement *Portunus pelagicus* make use of a range of habitats (Brown, 1997), larger individuals are more commonly found in seagrass beds (Edgar, 1990), where they feed on bivalves and ophiuroids (Williams, 1982). Half of the commercial catch in NSW is taken from Wallis Lake, a site of extensive seagrass beds (Kennelly, 1997).

Penaeus plebejus differ from *Metapenaeus macleayi* in their migration and habitat preferences. *Penaeus plebejus* spend up to 12 months in NSW estuaries before making a northern migration to spawning grounds in southern Queensland (Ruello, 1975; Montgomery, 1990). Larvae are swept south by the east Australia Current where they are recruited into estuaries, settling in inverse proportion to distance from the mouth of the estuary (Young and Carpenter, 1977). Numbers are lower in areas of lower salinity and higher in shallower areas of the estuary (Young and Carpenter, 1977). *Metapenaeus macleayi* have a less extensive northern migration (Glaister, 1978). Adult prawns congregate in the organically rich turbid areas produced by pronounced river discharges (Ruello, 1973). This behavior may explain the higher in catch of *M. macleayi* in relation to infilled, channelised estuaries.

Several studies have identified greater numbers of juvenile *Girella tricuspidata* over seagrass beds than bare estuarine areas (Middleton et al., 1984; Ferrell and Bell,

1991; McNeill et al., 1992; Gray et al., 1996), where they are thought to seek shelter and feed on algae. Similar associations have been observed for *Meuschenia* sp., in Botany Bay (Middleton et al., 1984; McNeill et al., 1992) and Western Port Bay (Edgar and Shaw, 1995) and *Sillago* sp. in Western Port Bay (Edgar and Shaw, 1995). *Acanthopagus australis* and *Rhabdosargus sarba* recruit into seagrass before moving into deeper habitat after 3–4 months (Middleton et al., 1984), explaining the absence of these species in surveys of post-recruitment fishes (eg. Ferrell and Bell, 1991), though Middleton et al. (1984) found *R. sarba* in *Posidonia* beds, a higher growing species with greater ephiphytic load, and more frequented by larger fish.

Garfish (*Hemiramphus robustus*, *Hyporhamphus dussmieri*) are known to produce eggs with an adhesive filament, which allows the eggs to attach to seagrass (Kuiter, 2000). Blaber and Blaber (1980) found higher concentrations of the same species in shallow waters of Morton Bay covered with extensive seagrass beds, though mature individuals moved to deeper estuarine and oceanic water.

The ecological literature cited above identifies direct links between juveniles and seagrass habitat for a small group of commercially important species. The present study has demonstrated that commercial catches of these same species (*Girella tricuspidata*, *Hyporhamphys* sp., *Portunis pelagicus*, Monacanthidae, *Sillago* sp., and *Rhabdosargus sarba*), are consistently associated with the extent of seagrass within the estuaries examined and it is these species which discriminate the fish catch between immature and infilled estuaries.

Other environmental variables appeared to be of lesser importance. Mangrove and saltmarsh area was consistently associated with the catch of *Scylla serrata*, *Anquilla reinhardtii*, and *Myxus elongatus*. *Scylla serrata* is a common occupant of mangrove and saltmarsh flats (Harty, 1997). Juvenile *M. elongatus* have been caught in the vicinity of mangroves (Clynick and Chapman, 2002; Mazumder et al., in press), while *A. reinhardtii* was one of three species dominating the biomass of a mangrove tidal creek community in Botany Bay (Bell et al., 1984). All three species show higher catches in mature (Type IIID) estuaries than less mature barrier estuaries supporting lower areas of mangrove. However, the contribution of these species to discrimination between Type III estuaries is less than that for the seagrass-dependant species.

6. Conclusions

The classification system proposed by Roy et al. (2001) is an effective means of distinguishing between estuaries on the basis of geomorphic units, and to a lesser extent their biological characteristics. Though differences could not be demonstrated between Type II (drowned river valley) and Type III (barrier) estuaries in commercial fish landings, the predominantly closed entrances of Type IV (intermittently open) estuaries are associated with lower catches of commercial fish and lesser areas of vegetated habitats. This would indicate that the artificial opening of estuaries in New South Wales is likely to have significant impacts on fish assemblages, in general increasing species diversity and abundance.

The view of Roy et al. (2001) that estuaries of intermediate infill (stage B) would show maximum diversity and abundance is confirmed for barrier estuaries, though some species (eg. *Metapenaeus macleayi*) appear benefited by estuarine infill. The higher diversity and abundance in stage B estuaries appears primarily related to seagrass extent rather than the maximum habitat diversity as suggested by Roy et al. (2001). The evidence for this lies in the high correlation between seagrass extent and the catch of species which were more abundant in stage B estuaries, species which have well-documented links with the seagrass habitat.

The infilling of barrier estuaries is associated with an increase in mangrove area and a decrease in the area of seagrass and central mud basin, which can be directly related to variation in the commercial catch of fish and crustaceans which utilize these habitats in their post-larval phase. The results strongly suggest that seagrass is a critically important habitat for a range of commercially important species, and that declines in seagrass area resulting from natural or anthropogenic disturbance should lead directly to decreases in stocks of these species.

Acknowledgements

Helpful comments on the manuscript were provided by Rob Williams, Riko Hashimoto, Bruce Pease and Eric Baran. Bruce Pease also provided data on the area of estuary entrances. ACU provided research leave, which allowed the development of this paper.

References

Bell, J.D., Pollard, D.A., Burchmore, J.J., Pease, B.C., Middleton, M.J., 1984. Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, NSW. Australian Journal of Marine and Freshwater Research 35, 33–46.

Blaber, S.J.M., Blaber, T.G., 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17, 143–162.

Brown, I., 1997. The fishery for Blue Swimmer Crab in South Queensland. In: Kumar, M. (Ed.), The First National Workshop on Blue Swimmer Crab. Australian Aquatic Science Centre, pp. 107–115.

Bucher, D., Saenger, P., 1994. A classification of tropical and subtropical Australian estuaries. Aquatic Conservation: Marine and Freshwater Ecosystems 4, 1–19.

Clarke, K., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92, 205–219.

Clarke, K., Warrick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, second ed. Primer-E, Plymouth.

Clynick, B., Chapman, M.G., 2002. Assemblages of small fish in patchy mangrove forests in Sydney Harbor. Marine and Freshwater Research 53, 669–677.

Edgar, G.J., 1990. Predator–prey interactions in seagrass beds. II. Distribution and diet of the blue manna crab *P. pelagicus* Linnaeus at Cliff Head, Western Australia. Journal of Experimental Marine Biology and Ecology 139, 23–32.

Edgar, G.J., Shaw, C., 1995. The production, trophic ecology of shallow-water fish assemblages of southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. Journal of Experimental Marine Biology and Ecology 194, 107–131.

Ferrell, D.J., Bell, J.D., 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. Marine Ecology Progress Series 72, 15–24.

Glaister, J.P., 1978. Movement and growth of tagged school prawns *Metapenaeus macleayi* (Haswell) (Crustacea: Penaeidae) in the Clarence River region of northern New South Wales. Australian Journal of Marine and Freshwater Research 29, 645–657.

Gray, C.A., McElligott, D.J., Chick, R.C., 1996. Intra and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. Marine and Freshwater Research 47, 723–735.

Griffiths, S.P., West, R.J., 1999. Preliminary assessment of shallow water fishes in three small intermittently open estuaries in south eastern Australia. Fisheries Management and Ecology 6, 311–321.

Hannan, J.C., Williams, R.J., 1998. Recruitment of juvenile marine fishes to seagrass habitat in a temperate Australian estuary. Estuaries 21, 29–51.

Harty, C., 1997. Mangroves in New South Wales and Victoria. Vista Publications, Melbourne.

Kuiter, R.H., 2000. Coastal Fishes of South-eastern Australia. Gary Allen, 437 pp.

Kennelly, S., 1997. The fishery for Blue Swimmer Crabs in NSW. In: Kumar, M. (Ed.), The First National Workshop on Blue Swimmer Crab. Australian Aquatic Science Centre, pp. 117–126.

Mazumder, D., Saintilan, N., Williams, R. Temporal variations in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. Wetlands Ecology and Management, in press.

McNeill, S.E., Worthington, D.G., Ferrell, D.J., Bell, J.D., 1992. Consistently outstanding recruitment of five species of fish to a seagrass habitat in Botany Bay, New South Wales. Australian Journal of Ecology 127, 359–365.

Middleton, M.J., Bell, J.D., Burchmore, J.J., Pollard, D.A., Pease, B.C., 1984. Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. Aquatic Botany 18, 89–108.

Montgomery, S., 1990. Movements of juvenile eastern king prawns, *Penaeus plebejus*, and identification of stocks along the east coast of Australia. Fisheries Research 9, 189–208.

Pease, B.C., 1999. A spatially oriented analysis of estuaries and their associated commercial fisheries in New South Wales, Australia. Fisheries Research 42, 67–86.

Pease, B.C., Grinberg, A., 1995. New South Wales Commercial Fisheries Statistics 1940 to 1992. Fisheries Research Institute, Cronulla, 351 pp.

Ruello, N.V., 1973. Burrowing, feeding and spatial distribution of the school prawn *Metapenaeus macleayi* (Haswell) in the Hunter River region, Australia. Journal of Experimental Marine Biology and Ecology 13, 189–206.

Ruello, N.V., 1975. Geographical distribution, growth and breeding migration of the eastern Australian King Prawn *Penaeus plebejus*. Australian Journal of Marine and Freshwater Research 26, 343–354.

Roy, P.S., 1984. New South Wales estuaries- their origin and evolution. In: Thom, B.G. (Ed.), Developments in Coastal Geomorphology in Australia. Academic Press, San Diego, CA, pp. 99–121.

Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of South-east Australian estuaries. Estuarine Coastal and Shelf Science 53, 351–384.

Saintilan, N., Williams, R.J., 1999. Mangrove transgression into saltmarsh environments in southeast Australia. Global Ecology and Biogeography Letters 8, 117–124.

Scribner, E.A., Kathuria, A., 1996. New South Wales Commercial Fisheries Statistics 1992/93. NSW Fisheries, Cronulla, 103 pp.

Tanner, M., Liggins, G.W., 2000. New South Wales Commercial Fisheries Statistics 1993/94 to 1997/98. NSW Fisheries Research Institute, Cronulla.

West, R.J., Thorogood, C.A., Walford, T.R., Williams, R.J., 1985. An estuarine inventory for New South Wales, Australia. Fisheries Bulletin No. 2, Department of Agriculture, New South Wales, 140 pp.

Williams, M.J., 1982. Natural food and feeding in the commercial sand crab *P. pelagicus* Linnaeus 1766 (Crustacea: Decapoda Portunidae) in Morton Bay, Queensland. Journal of Experimental Marine Biology and Ecology 59, 165–176.

Young, P.C., Carpenter, S.M., 1977. Recruitment of postlarval Penaeid prawns to nursery areas in Moreton Bay, Qld. Australian Journal of Marine and Freshwater Research 28, 745–773.

Estuarine, Coastal and Shelf Science 113 (2012) 221–230

Contents lists available at SciVerse ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Environmental predictors of estuarine fish landings along a temperate coastline

Neil Saintilan*, Li Wen

Rivers and Wetlands Unit, Office of Environment and Heritage, NSW Department of Premier and Cabinet, PO Box A290, Sydney South, NSW 1232, Australia

ARTICLE INFO

Article history:
Received 31 January 2012
Accepted 2 August 2012
Available online 14 August 2012

Keywords:
estuary
fish
river flow
environmental flow
multi-level modelling habitat
productivity

ABSTRACT

The regulation of freshwater flow into estuaries has been identified as a potential threat to estuarine ecosystem structure and function, and the productivity of fisheries in particular. Correlative studies are one means by which associations between freshwater inputs and commercial landings have been identified. The study compared monthly landings of five species of finfish and two species of crustacean with monthly and 6-month running means of river discharge, climatic variables (temperature and rainfall) and the area of vegetated habitat (saltmarsh, mangrove and seagrass) for 11 temperate estuaries on the NSW coast. The monthly climatic and discharge record covered a 10-year period (1997–2007). High river discharge and rainfall were associated with higher catches of flathead (*Platycephalus* spp.) and Mullet (*Mugil* spp.), a result consistent with subtropical estuaries to the north. We found no relationships between landings and river discharge for any of the other species, which included school prawns (*Metapenaeus macleayi*). Temporal variability at a monthly time-step was more consistently associated with variation in temperature, reflecting seasonal variation in activity, and possibly fishing effort. Landings of several species showed strong habitat relationships, with greater seagrass area consistently associated with higher catches of blue swimmer crab (*Portunis pelagicus*), and intertidal wetlands (mangrove and saltmarsh) with mud crab (*Scylla serrata*), school prawns, flathead, and mullet (*Mugil* spp.), a result consistent with habitat-scale surveys. The results draw into question the efficacy of dam releases as stimulants of fisheries productivity in the region, although the effects of flow on juvenile populations and catadromous species were not studied.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Over two-thirds of water flowing in the world's rivers is intercepted by an estimated 45,000 dams constructed to regulate flow (Nilsson and Berggren, 2000). The damming of rivers and diversion of water for agricultural use represents the most significant impact on aquatic ecosystems world-wide (Nilsson et al., 2005). The detrimental impact on freshwater rivers and wetlands is obvious and direct, and includes impacts on flood dependent vegetation (Shafroth et al., 2002), waterbird populations (Kingsford, 2000) fish migration (Gehrke et al., 2002), as well as system-wide declines in ecological integrity and function (Arthington and Pusey, 2003). The influence of freshwater in the estuarine section of rivers is more equivocal, given the significant marine tidal influence in many estuaries, and a biota that is adapted to higher salinity and in some cases higher variability in salinity.

There are several reasons to suggest *a priori* that the flow of freshwater into estuaries might be important in maintaining the productivity of estuarine fisheries. River waters carry nutrients that stimulate phytoplankton and benthic microalgae production which are important autotrophic sources of production for estuarine consumers (Drinkwater and Frank, 1994; Newell et al., 1995; Loneragan et al., 1997). River flow may also trigger recruitment into estuaries, the stimulation of breeding by catadromous fishes, or the relocation of fish into regions of the estuary where they are more likely to be caught (Staples and Vance, 1986; Loneragan and Bunn, 1999; Gillanders and Kingsford, 2002). Where river discharges maintain hydrological connectivity to the ocean in semi-arid environments, a failure of river flow may lead to hyper-salinity and declines in the diversity of benthic infauna. This may have detrimental impacts on waterbird habitat, as has been demonstrated in the Coorong wetland at the mouth of the Murray, Australia's largest river (Paton et al., 2009).

For this reason many authors have challenged the paradigm that water entering the sea is 'wasted', pointing to the important ecological functions of freshwater flows in estuarine and near shore environments (Rosenburg et al., 1995; Loneragan and Bunn, 1999). One test of the hypothesised link between freshwater flow and fisheries productivity is the strength of association between the variability of river discharge and the landing of commercial fish in estuaries where both are monitored. Ideally, linkages between flow and commercial fish harvest would be tested by experimental manipulation, however, in most circumstances such experiments would be precluded by

* Corresponding author.
E-mail address: Neil.Saintilan@environment.nsw.gov.au (N. Saintilan).

0272-7714/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.ecss.2012.08.007

limited opportunities for the control of inflows in impact and control settings (Robins et al., 2005). As a consequence, correlation and regression analysis is often used to explore relationships between commercial catch and environmental variables, most commonly rainfall and freshwater flow (Tyler, 1992; Robins et al., 2005).

Relationships between commercial fish landings and freshwater flow (and rainfall) have been demonstrated along many tropical and subtropical coastlines in Australia (Vance et al., 1998; Loneragan and Bunn, 1999; Robins et al., 2005), the USA (Browder et al., 2002; Powell et al., 2002), Mexico (Galindo-Bect et al., 2000) and Mozambique (Gammelsrod, 1992). For example, Loneragan and Bunn (1999) found a correlation between flow of the Logan River (South East Queensland) and the catch of several species, including the school prawn (*Metapenaeus macleayi*), and dusky flathead (*Platycephalus* spp.) over an eight year period. They concluded that the reduction of the flow of coastal rivers caused by river regulation might substantially reduce commercial and recreational fish catches in estuaries. However, other effects of flow on biological populations can also occur, including the washout of nekton or the imposition of freshwater osmotic effects on marine organisms (Deegan, 1990; Kaartvedt and Aksenes, 1992; Howarth et al., 2000). Broad-scale generalisations about the influence of freshwater flow on fishery productivity have been hindered by inconsistent outcomes, with contrasting results found between geographic settings in close proximity (Staples et al., 1995) and between time periods in the same location (Ardisson and Bourget, 1997).

This study extends an analysis of the links between freshwater flows and estuarine fishery productivity to a temperate coastline, and over a greater temporal and spatial range than previously attempted, and at a greater temporal resolution. The estuaries of New South Wales (NSW), Australia, are situated along a high wave energy coastline from the sub-tropical north where Pleistocene sand barriers form the predominant geological setting, to the temperate south dominated by Triassic and Permian sandstones. More than 90 estuaries are named along this 1500 km stretch of coast (Roy et al., 2001), and more than 50 support commercial fishing operations (Saintilan, 2004). The virtual absence of latitudinal gradients in the availability of important fish species has been attributed to the east Australia current (Gray et al., 1996), and facilitates comparisons of catch between estuaries on the basis of estuarine morphological and hydrological characteristics.

Broad-scale patterns in the variability of geomorphological, hydrological and ecological characteristics of estuaries in NSW have been schematized by Roy et al. (2001) who classified estuaries as either ocean embayments, tide dominated estuaries, wave dominated estuaries, and intermittent estuaries in varying stages of infill with terrigenous sediment. Saintilan (2004) tested the assumption that estuary type predicted fish assemblages by comparing commercial catch statistics with estuarine morphological and habitat characteristics at a state-wide scale. The analysis suggested that estuary entrance conditions exerted an important control on species assemblage, with the closure of the estuary mouth corresponding to a decline in recruitment opportunities and, in time, a decline in diversity and abundance. Further, the catch of individual species could be accurately predicted on the basis of estuarine habitat variables, such as the area of seagrass, mangrove, central mud basin or tidal sandbank.

The strong habitat dependencies suggested by Saintilan (2004) were estimated from a single year of commercial catch data, and do not incorporate the possible effects of hydrological and climatic variability. The link between climate, hydrology and commercial landings may be mediated by changes to the suitability of the estuary for recruitment, growth, survival and abundance, or by changes to the distribution of fish and their catchability (Drinkwater and Frank, 1994; Robins et al., 2005), resulting from the introduction of freshwater. Some of these responses will be immediate, such as the congregation of fish at the estuary mouth following freshwater flows (Vance et al., 1998). Some mechanisms will involve a time lag, particularly those associated with recruitment success. For this reason Robins et al. (2005) recommend that attention be given to life history characteristics relevant to flow regime, and that lagged correlations be conducted where appropriate.

This paper therefore aims to test the effect of hydrological variability on commercial fish landings using multi-level modelling techniques. Multi-level models, also known either as mixed linear models or, in a Bayesian context, as hierarchical linear models, have gained wide acceptance over the past two decades in many fields, particularly in educational (e.g. Raudenbush, 2005), public health (e.g. Bingenheimer and Raudenbush, 2004) and ecological studies (reviewed by Ogle, 2009), as an important methodology for dealing appropriately with nested or clustered data, i.e. data with hierarchical structure. In this study, we applied multi-level modelling techniques to 10 years of the monthly fish landing data (1997–2007) for each of seven common commercially important species to test the hypothesis that inclusion of river-flow inputs will improve the capacity to predict fish catch between estuaries, and between years within estuaries.

2. Material and methods

2.1. Data collection and preparation

The OzCoasts database (www.OzCoasts.org.au) published by Geosciences Australia provides the best available assessment of the area of geomorphic and habitat variables, and the geometric properties of estuaries around the Australian coastline. This database was the primary source of the estuary-level habitat quality variables used in the models (Table 1), which were used together with hydrological and climatic variables in the multi-level modelling procedures (detailed in the next section) to predict fish catch for 11 estuaries in NSW (Fig. 1). The area of seagrass, mangrove and saltmarsh extracted from OzCoasts were divided by the area of estuary (percentage) for further analysis.

Monthly river discharge and climatic variables (rainfall and maximum temperature) were downloaded from NSW Office of Water (http://www.waterinfo.nsw.gov.au/river-provisional-sites.shtml) and Australia Bureau of Meteorology (http://www.bom.gov.au/climate/averages/tables/cw_049002.shtml), respectively for the period 1997–2007. To avoid co-linearity and to allow the comparisons of the contribution of variables to the variability of respondent, we normalised the hydrological and climatic variables for each estuary according to:

$$\tilde{y}_i = \frac{y_i - \overline{y}}{\sigma} \quad (1)$$

where $\tilde{y}_i$ is the normalized variable y_i and $\overline{y}$ and σ and mean and standard deviation of y_i, respectively.

In addition, the normalised river flow data were further smoothed using a six-month moving average to represent a broader range of antecedent flow conditions. Two sets of models were fitted and compared: one with the 6-month averaged data and one with the original monthly data.

Monthly landings for selected fish and crustacean species were obtained from NSW Department of Primary Industries for the period 1997–2007 inclusive. These species include those that previous studies have identified as responding to freshwater flows (school prawn, *Metapenaeus macleayi*; flathead, *Platycephalus* spp.; Loneragan and Bunn, 1999, mud crab *Scylla serrata*; Robins et al., 2005), together with blue swimmer crab *Portunis pelagicus*, luderick (*Girella tricuspidata*), mullet (*Mugil* spp.), and mulloway (*Argyrosomus*

Table 1
Summary of the candidate variables for multi-level model.

Estuary	Level-1 predictors			Level-2 predictors		
	River flow range (ML)	Monthly rainfall (mm)	Maximum monthly temperature	Mangrove (km^2)	Saltmarsh (km^2)	Seagrass (km^2)
Tweed	0.8–3360.3	2.0–318.4	19.9–32.1	4.37	0.19	0.331
Richmond	3.3–11805.1	3.4–467.4	18.4–29.6	7.6	0	0.189
Clarence	0–26418.4	0.4–486.4	18.3–28.5	15.31	1.38	19.072
Macleay	150.9–19474.9	0.0–401.2	18.6–29.2	5.94	4.22	1.097
Manning	41.0–51457.2	2.2–416.0	18.6–31.8	4.83	0.13	0.329
Pt-Stephens	1.5–3843.7	3.4–498.6	16.4–33.4	27.44	37.46	7.453
Hunter River	28.8–17354.8	0.8–414.2	16.7–27.7	16.67	6.69	0.153
Hawkesbury	0.2–1046.6	6.0–389.4	16.2–28.6	2.24	4.88	0.47
Shoalhaven	2.7–1325.5	2.6–490.8	14.1–29.0	3.22	2.62	0.34
Illawarra	6.3–620.3	3.2–585.4	16.4–28.7	0	0.2	5.12
Tuggerah	0.3–1619.5	0.8–574.6	15.9–28.2	0.18	0.13	11.62

hololepidotus). Total landings for each estuary was divided by the area to obtain catch per unit of area (i.e. kg ha^{-1}), and was further log transformed to ensure variables were normally distributed. The transformed unit catch was the respondent variable in the model.

There are caveats which must be placed on the use of commercial catch data as a surrogate of abundance, given variation in fishing effort, gear type and reporting rigour between years. Loneragan and Bunn (1999) argued that the value of the fishery would tend to equilibrate catch with abundance (see also Potter et al., 1991) in the absence of catch per unit effort data. Ideally, independent data would be used to test this assumption, although in the present case the research question relates to commercial catch directly as a key ecosystem service of estuaries.

2.2. Multi-level models

2.2.1. Model specification

To justify the application of the multi-level model, we started by fitting a null model (i.e. no predictor) for each species to find the percentage of observed variance in the dependent variable (unit fish catch) attributable to estuary-level characters. In the empty models, only the levels (in the study, estuary) are defined, and the first level (fish landings) was not specified. The model assumed that the dependent variable is on the first level:

$$\text{Level 1}: \quad Y_{ij} = \beta_{0j} + r_{ij} \tag{2}$$

Y_{ij} is the ith record of fish catch at jth estuary. The fish catch was modelled to be the average value (β_{0j}) in a specific estuary plus an individual-level error γ_{ij}, which was assumed to have a normal distribution in the form of $N(0, \sigma^2)$. The estuary-level model is:

$$\text{Level 2}: \quad \beta_{0j} = \gamma_{00} + \mu_{0j} \tag{3}$$

Where γ_{00} is the estuary-specified mean and μ_{0j} is the error term, which is assumed to be normal distribution in the form of $N(0, \tau_{00})$.

Combining Equations (2) and (3) yields the null model:

$$Y_{ij} = \gamma_{00} + \mu_{01} + r_{ij} \tag{4}$$

The intra-class correlation coefficient (ICC), which can be referred to as percentage of observed variance attributable to the estuary-level is calculated as:

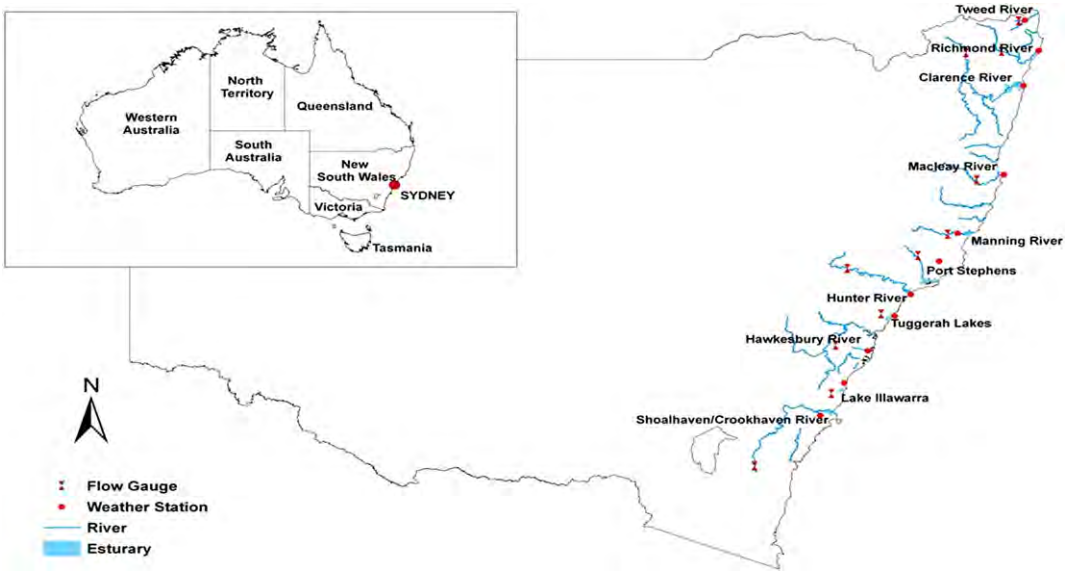


Fig. 1. Location of the 11 NSW estuaries included in analysis and the position of flow gauges and weather stations.

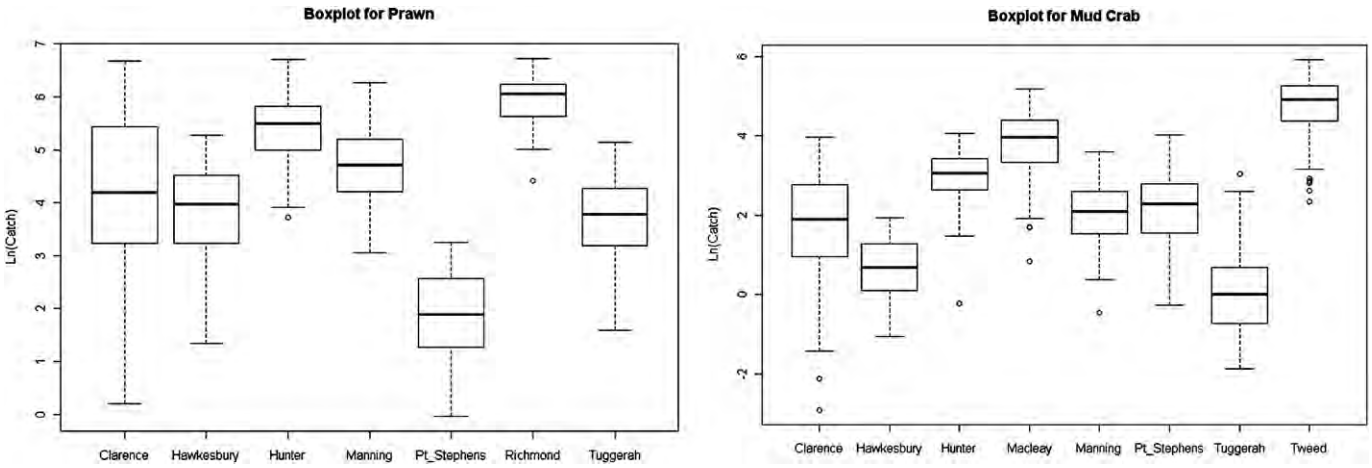


Fig. 2. Box and whisker plots for prawn and mud crab catch data show the variability at estuary level.

$$\mathrm{ICC} = \frac{\tau_{00}}{\tau_{00} + \sigma^2} \tag{5}$$

When we were satisfied that a large portion of observed variation was, in fact, due to the estuary level features, all six candidate predictors (Table 1) were added to the model. In the model, the slope of the random effect was assumed to be constant across the estuary (i.e. a random intercept model). Instead of introducing the predictors stepwise, all six predictors were included at once as the relative importance of level-1 and level-2 predictors were not of interest in the present study.

$$Y_{ij} = \gamma_{00} + \beta_{1j}X_{ij} + \mu_{01} + r_{ij} \tag{6}$$

In the random intercept model, X_{ij} are the individual-level covariate or predictor, and β_{1j} is the model estimate for jth predictor. The Pseudo-R^2 can be used to imply the improvement due to the introduction of level-1 predictors (also for the importance of these predictors):

$$\text{Pseudo} - R^2 = \frac{\sigma^2(\text{model1}) - \sigma^2(\text{model2})}{\sigma^2(\text{model1})} \tag{7}$$

2.2.2. Estimation of the highest posterior density (HPD) intervals for model parameters

To find the prediction intervals and p-values from the estimated multi-level model parameters, we used the Markov Chain Monte Carlo (MCMC) technique to draw samples (n = 10,000) from the joint posterior distributions of the unknown parameters. If the calculated p-value for a predictor was >0.05, the predictor was considered to be non-significant for fish catch.

The modelling was performed in R 2.10.1 (R Development Core Team, 2010). Multi-level model building and simulation for posterior distributions were carried out using the lme4 package by Bates and Naeche (2010).

3. Results

3.1. Between and within estuary variation

Unit catch for all species varied considerably between estuaries (Fig. 2). As the τ_{00} values >0 for all species in the null models (Table 2), there is evidence of a correlation structure. Furthermore, as between-estuary variability is much larger than the within estuary variability for luderick, blue swimmer crab, mud crab and flathead (Table 2), level-2 modelling which includes covariates to explain the different features between estuaries is likely to be valuable.

The intra-class coefficients ranged from 0.397 (mullet) to 0.820 (flathead) (Table 2), corresponding roughly to 39.7% to 82.0% of the variations in fish catch being explained by the site effects (i.e. the differences in estuary features such as the relative area of geomorphic and vegetated habitat units). The sizable variations attributable to estuary-level effects justified the use of the multi-level model.

The parameter estimate for random interception (τ_{00}) is less than its standard deviation for the mullet and blue swimmer crab models suggesting that the remaining unexplained variance is very small and, therefore, the addition of covariates is unlikely to improve the prediction significantly. On the other hand, the random intercept for the mud crab and flathead models is large relative to its standard deviation (3.478 and 2.259 to 1.865 and 1.503 for flathead and mud crab, respectively, Table 2). Thus, including predictors in these models could reduce the model residuals and improve the model performance.

3.2. The contribution of predictors to model performance

In general, the contribution of candidate variables was not high; and the effects of predictors on model performance varied widely (Psuedo-R^2 ranged from 0.02 to 0.21). For luderick, prawn and mud crab, moderate improvement was noticeable. However, the inclusion of predictors only improves the null-model marginally for blue swimmer crab and mullet (pseudo-R^2 = 0.02) suggesting that the

Table 2
Variance explained by site difference.

Species	Grand mean (γ_{00})	Residual (σ^2)	S.D.	Intercept (τ_{00})	S.D.	ICC	AIC
Prawn	4.23 (0.50)	0.961	0.981	1.733	1.317	0.643	1637
Mullet	4.85 (0.22)	0.828	0.910	0.545	0.738	0.397	3391
Flathead	3.22 (0.56)	0.763	0.874	3.478	1.865	0.820	3019
Mulloway	1.71 (0.46)	0.850	0.922	1.056	1.028	0.554	1027
Back Swimmer	2.22 (0.48)	0.861	0.928	0.925	0.962	0.518	1085
Luderick	3.30 (0.33)	0.643	0.802	1.081	1.040	0.627	2625
Mud Crab	2.25 (0.53)	1.055	1.027	2.259	1.503	0.682	1999

S.D. = Standard deviation; ICC = Intraclass coefficient; AIC = Akaike information criterion.

fish catch for these species were insensitive to any of the candidate predictors. The results were consistent with the ICC calculated from the null-model (Table 2); the models with higher ICC improved remarkably but the improvement was not realized for models with lower ICC.

The posterior density for fitted model parameters produced by MCMC sampling was reasonably symmetric and close to normal distribution (Fig. 3 is an example for the prawn model). Not surprisingly, significant variables based on MCMC *p*-value picked up all the important factors selected by *t*-value for all species.

3.2.1. Level-1 predictors

The effects of temperature on commercial fish catch were significant for six of the seven modelled species with blue swimmer as exception (Tables 3 and 4). However, the effects were not all the same for the species; while the relationship was significantly positive for prawn, mud crab and mullet, it was negative for luderick, flathead and mulloway.

The river discharge was positively related to fish catch for the luderick and mullet model (Tables 3 and 4) although the relationship was weak ($p = 0.032$, 0.026 for mullet and luderick, respectively, Table 3). For other species, the relationship was non-significant.

Rainfall was positively related to the unit catch for all species. However the relationship was significant for only two species: mullet and mulloway ($p = 0.005$ and 0.009 for mullet and mulloway, respectively, Table 4).

3.2.2. Level-2 predictors

The effects of habitat quality variables on fish catch were inconsistent, and varied from species to species (Table 3A). Prawn and mullet catches were positively related to mangrove area although negatively related to saltmarsh area. The catch of blue swimmer crab was negatively related to mangrove area but positively related to seagrass area and saltmarsh area. However, the relationship became negative in the case of mulloway.

Fig. 4 presents an example (the mud crab model) showing the partial effects of the predictors. It was clear that temperature was the most important level-1 factor, and mangrove area was the most important level-2 factor for fish landing prediction.

3.3. Random effects

The intercepts of the random effects were quite different from each other and from zero for all species models except the blue swimmer crab model (Fig. 5), indicating that the mean fish catch for each estuary is likely to be significantly different.

Differences in the expected mean fish production among estuaries was evident for each of the modelled species (Fig. 5). For

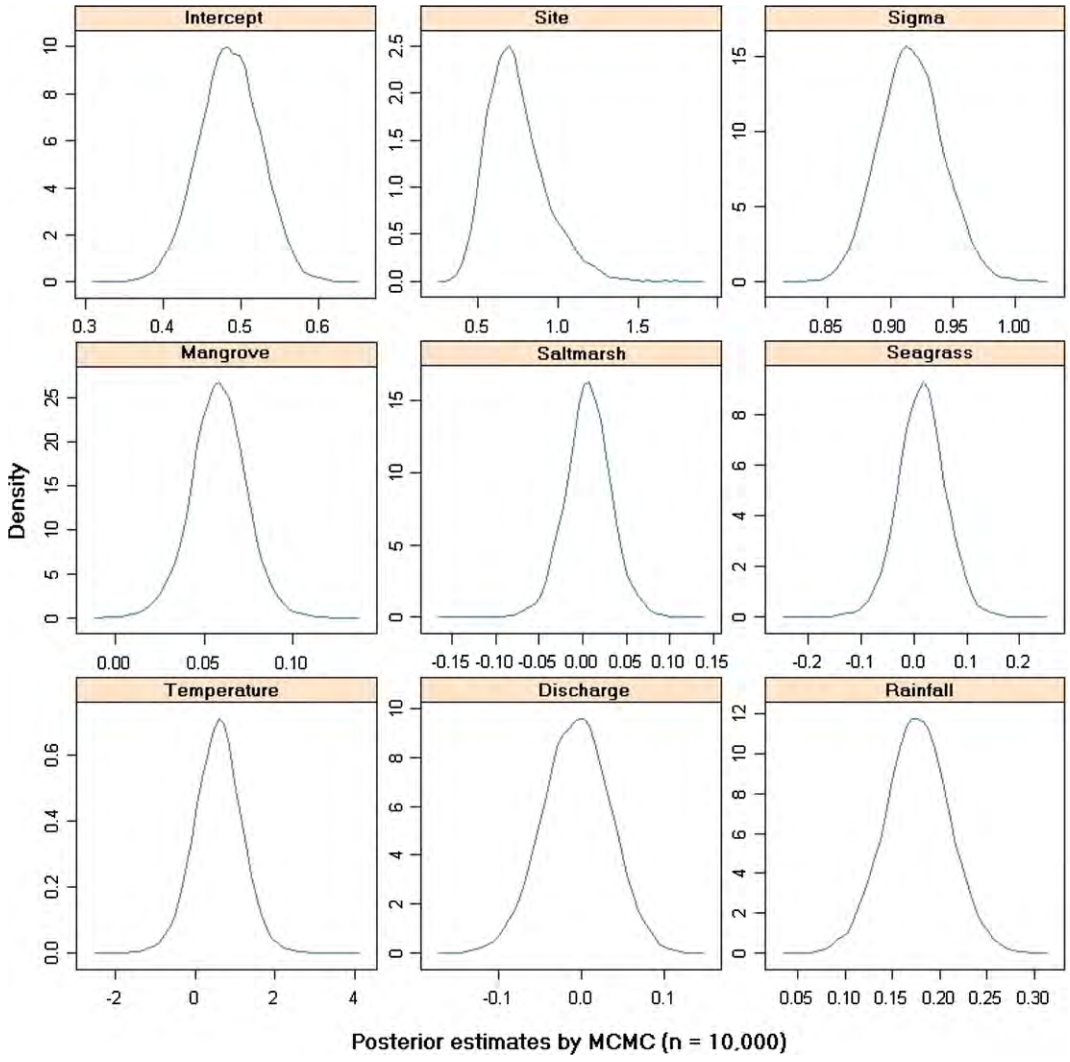


Fig. 3. Empirical density estimates for the MCMC samples ($n = 10{,}000$) for the posterior distribution of the parameters in the two-level model for mud crab.

Table 3
Summary of first-level covariates (standard error in brackets) for multi-level fish models (significant variables are in bold) A) with 6-month smoothed discharge and B) with raw discharge. A variable is considered as significant if the $|t| > 2$.

Species	Intercept	Discharge	Rainfall	Temperature	Mangrove	Saltmarsh	Seagrass	Pseudo-R^2	AIC
A. With 6-month smoothed discharge									
Prawn	**3.683 (0.473)**	0.015 (0.041)	0.079 (0.041)	**0.379 (0.051)**	**0.061 (0.0144)**	**−0.100 (0.024)**	−0.024 (0.036)	0.09	1611
Mullet	**4.172 (0.326)**	**0.057 (0.027)**	**0.072 (0.026)**	**0.092 (0.028)**	**0.036 (0.009)**	**−0.031 (0.015)**	0.027 (0.025)	0.02	3364
Flathead	2.283 (1.388)	0.034 (0.021)	0.037 (0.027)	**−0.196 (0.024)**	0.054 (0.037)	−0.059 (0.064)	0.038 (0.108)	0.06	2982
Mulloway	**2.617 (0.726)**	−0.018 (0.046)	**0.114 (0.043)**	**−0.178 (0.048)**	0.027 (0.023)	−0.069 (0.049)	**−0.132 (0.056)**	0.05	1021
Blue Swimmer	**−2.495 (0.693)**	0.088 (0.047)	0.075 (0.046)	**−0.104 (0.043)**	**−2.522 (0.508)**	**1.978 (0.388)**	**0.319 (0.044)**	0.02	1099
Luderick	**3.192 (0.944)**	**0.053 (0.024)**	0.014 (0.022)	**−0.232 (0.024)**	0.011 (0.026)	−0.008 (0.048)	−0.007 (0.073)	0.09	2564
Mud Crab	0.583 (0.810)	−0.006 (0.040)	**0.175 (0.033)**	**0.483 (0.040)**	**0.058 (0.021)**	0.006 (0.036)	0.015 (0.006)	0.21	1869
B. With raw discharge									
Prawn	**3.741 (0.320)**	0.039 (0.043)	0.071 (0.043)	**0.416 (0.051)**	**0.061 (0.010)**	**−0.106 (0.016)**	−0.027 (0.016)	0.11	1599
Mullet	**4.137 (0.331)**	**−0.004 (0.002)**	**0.075 (0.025)**	**0.092 (0.026)**	**0.038 (0.009)**	**−0.033 (0.015)**	0.028 (0.026)	0.02	3410
Flathead	**5.838 (1.907)**	**0.010 (0.005)**	0.048 (0.026)	**−0.161 (0.026)**	−0.009 (0.052)	−0.073 (0.088)	0.072 (0.155)	0.09	2740
Mulloway	**2.620 (0.742)**	−0.073 (0.043)	**0.144 (0.047)**	**−0.180 (0.047)**	0.027 (0.024)	−0.068 (0.048)	**−0.132 (0.058)**	0.05	1038
Blue Swimmer	**−2.525 (0.670)**	−0.074 (0.061)	0.103 (0.052)	**−0.083 (0.041)**	**−2.525 (0.510)**	**1.980 (0.390)**	**0.322 (0.045)**	0.02	1101
Luderick	**3.150 (0.940)**	0.016 (0.027)	0.009 (0.027)	**−0.251 (0.024)**	0.008 (0.026)	0.003 (0.047)	−0.007 (0.073)	0.09	2560

example, in the case of prawn, the rank of productivity, as indicated by commercial fish landings, is the Hawkesbury River, followed by the Hunter, Clarence, Tuggerah, Richmond, Port Stephens and Manning Rivers (from highest to lowest). Furthermore, the model suggested that in the most productive estuary, the Hawkesbury River, the unit fish catch could be more than 2.7 times higher than the least productive, the Manning River (1 in natural logarithm scale, Fig. 5).

Table 4
HPD prediction intervals for fixed effects calculated using Markov chain Monte Carlo sampling technique ($n = 10{,}000$), significant variables are in bold. A) With 6-month smoothed discharge and B) with raw discharge.

Species		Intercept	Discharge	Rainfall	Temperature	Mangrove	Saltmarsh	Seagrass
A. With 6-month smoothed discharge								
Prawn	HPD 95% lower	2.720	−0.066	0.000	0.269	0.031	−0.151	−0.100
	HPD 95% upper	4.681	0.099	0.158	0.473	0.092	−0.053	0.054
	P	**0.000**	0.719	**0.050**	**0.000**	**0.002**	**0.003**	0.457
Mullet	HPD 95% lower	3.524	0.006	0.022	0.044	0.018	−0.062	−0.023
	HPD 95% upper	4.851	0.110	0.122	0.141	0.054	−0.001	0.080
	P	**0.000**	**0.032**	**0.007**	**0.000**	**0.001**	**0.045**	0.263
Flathead	HPD 95% lower	1.184	−0.007	−0.014	−0.244	0.022	−0.111	−0.049
	HPD 95% upper	3.454	0.076	0.094	−0.148	0.083	−0.007	0.127
	P	**0.000**	0.114	0.152	**0.000**	**0.002**	**0.031**	0.383
Mulloway	HPD 95% lower	1.284	−0.109	0.030	−0.271	−0.018	−0.155	−0.236
	HPD 95% upper	3.966	0.073	0.199	−0.084	0.070	0.018	−0.023
	P	**0.002**	0.665	**0.010**	**0.000**	0.169	0.097	**0.021**
Blue Swimmer	HPD 95% lower	−7.540	−0.175	−0.013	−0.185	−6.362	−0.771	−0.015
	HPD 95% upper	2.988	0.007	0.163	−0.020	1.270	5.097	0.634
	P	0.190	0.064	0.100	**0.013**	0.119	0.114	0.053
Luderick	HPD 95% lower	2.286	0.008	−0.032	−0.279	−0.014	−0.057	−0.077
	HPD 95% upper	4.168	0.101	0.056	−0.185	0.039	0.039	0.071
	P	**0.000**	**0.027**	0.544	**0.000**	0.396	0.733	0.839
Mud crab	HPD 95% lower	−0.527	−0.086	0.113	0.408	0.027	−0.044	−0.076
	HPD 95% upper	1.784	0.070	0.244	0.563	0.088	0.058	0.101
	P	0.281	0.881	**0.000**	**0.000**	**0.003**	0.799	0.723
B. With raw discharge data								
Prawn	HPD 95% lower	2.984	−0.048	−0.013	0.319	0.037	−0.144	−0.089
	HPD 95% upper	4.568	0.122	0.156	0.517	0.085	−0.068	0.033
	P	**0.000**	0.381	0.099	**0.000**	**0.000**	**0.001**	0.293
Mullet	HPD 95% lower	3.465	−0.008	0.027	0.042	0.020	−0.065	−0.023
	HPD 95% upper	4.821	0.000	0.124	0.145	0.056	−0.003	0.081
	P	**0.000**	**0.043**	**0.002**	**0.000**	**0.001**	**0.041**	0.244
Flathead	HPD 95% lower	4.663	0.000	−0.003	−0.215	−0.040	−0.126	−0.020
	HPD 95% upper	7.002	0.019	0.103	−0.112	0.024	−0.019	0.174
	P	**0.000**	**0.045**	0.071	**0.000**	0.558	**0.011**	0.136
Mulloway	HPD 95% lower	1.237	−0.155	0.051	−0.274	−0.018	−0.160	−0.243
	HPD 95% upper	4.127	0.016	0.236	−0.087	0.074	0.026	−0.018
	P	**0.004**	0.099	**0.003**	**0.000**	0.183	0.118	**0.029**
Blue Swimmer	HPD 95% lower	−7.384	−0.198	0.007	−0.166	−5.995	−0.696	0.001
	HPD 95% upper	2.352	0.042	0.210	−0.002	0.925	4.584	0.605
	P	0.168	0.225	0.050	**0.044**	0.102	0.098	**0.044**
Luderick	HPD 95% lower	2.179	−0.038	−0.046	−0.296	−0.018	−0.047	−0.079
	HPD 95% upper	4.092	0.070	0.061	−0.203	0.035	0.050	0.069
	P	**0.000**	0.567	0.739	**0.000**	0.538	0.902	0.844
Mud crab	HPD 95% lower	−0.524	−0.002	0.097	0.408	0.030	−0.047	−0.076
	HPD 95% upper	1.741	0.012	0.232	0.558	0.088	0.053	0.099
	P	0.283	0.181	**0.000**	**0.000**	**0.002**	0.771	0.747

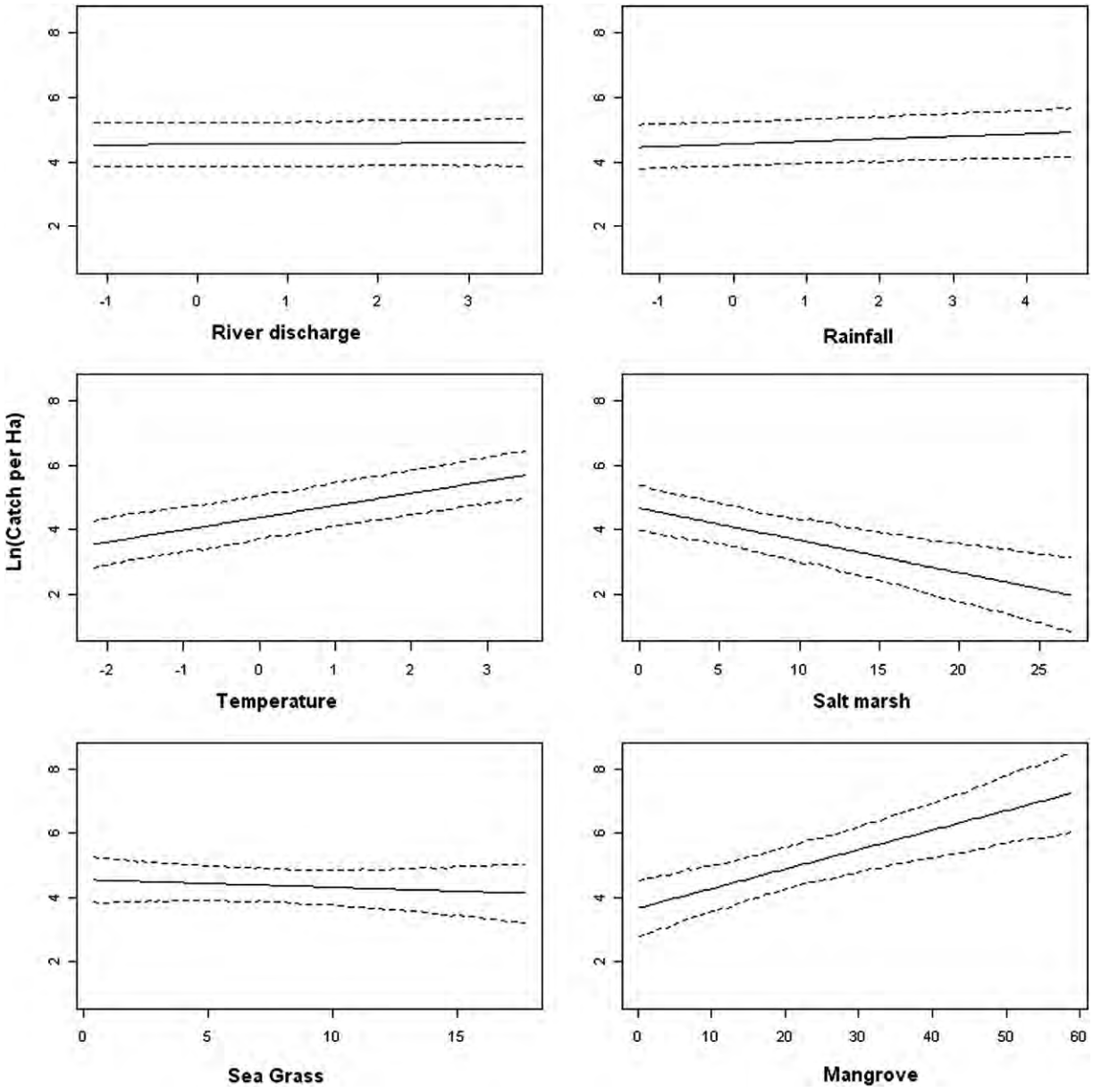


Fig. 4. Plot of partial effects of the level-1 and level-2 factors of the mud crab model. Dashed lines are the upper and lower 95% intervals (simulated using MCMC sampling technique, $n = 10{,}000$).

The biggest difference among estuaries exists for flathead. On the basis of catch per unit area, Port Stephens could produce more than 50 times more flathead than the Clarence (4 in natural logarithm scale, Fig. 5). For mud crab, the Macleay River tends to have a much higher catch per hectare and the Hunter River tends to have lower catches (the difference could be as much as 20 times, Fig. 5), while the others are close to the overall mean. For luderick, the Tweed and Shoalhaven Rivers are the most productive, the Manning River is close to the average, and the Hawkesbury, Clarence and Hunter Rivers are the least productive. Mulloway exhibits the smallest difference – less than 1 in the natural logarithm scale. The relatively few estuaries for which mulloway catch data are available (5), may partly contribute to the smaller difference in the estimated parameter value.

3.4. The effects of antecedent flow conditions

The smoothing of river flows (through the use of 6-month running means) improved the models for mullet, mulloway, blue swimmer and mud crab (a smaller AIC value, Table 3). However, for prawn and flathead, the model with the original (monthly) data was superior (Tables 3 and 4). Using smoothed river flow instead of the original had little effect on the contribution and importance of other covariates (Table 4). However, the antecedent flow conditions did have impacts on the consideration of effects of river flow on fish catch for some species. While the models with the original river discharge suggested a positive relationship for flathead and a negative relationship for mullet (Tables 3 and 4), the unit catch for luderick and mullet was positively related to the antecedent river flow conditions (Table 3).

4. Discussion

Studies of macroinvertebrates show penaeids present the most consistent relationship between rainfall, river flow and catch volumes, with positive correlations between rainfall, river flow and catches observed for the Clarence River, NSW (Glaister, 1978), the

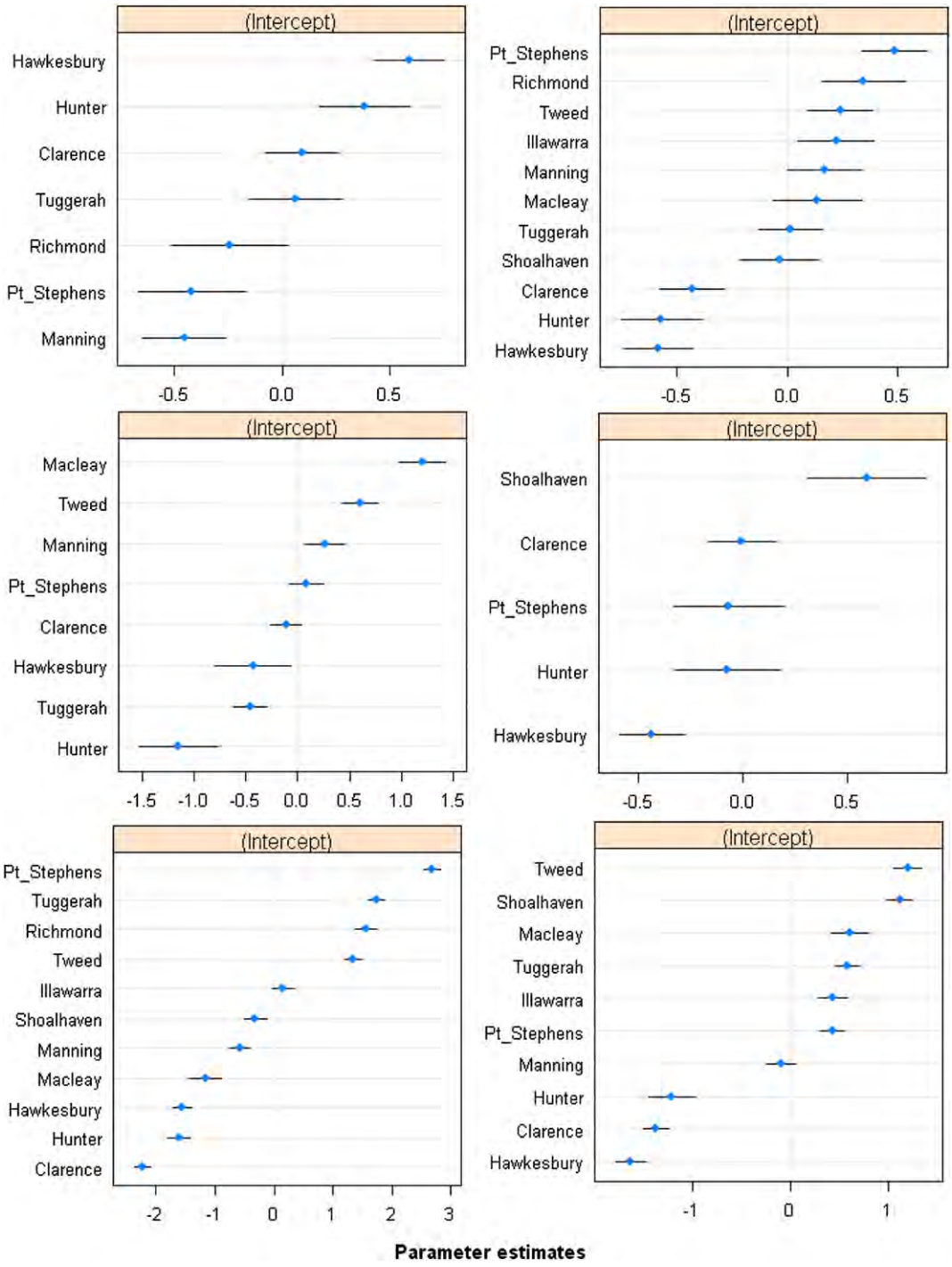


Fig. 5. Estimated random effects (site) of the multi-level models, from top left to bottom right: prawn, mullet, mud crab, mulloway, flathead and luderick. Solid lines represent the 95% posterior credible intervals for the estimated effects, dots are the estimated means. Note that the random effect for back swimmer crab was not significant probably due to the small sample size (only four estuaries have data).

Hunter River, NSW (Ruello, 1973), the Logan River, Queensland (Loneragan and Bunn, 1999), the Gulf of Carpentaria, northern Australia (Vance et al., 1998), the Florida Everglades (Browder, 1985), the US Gulf Coast (Gunter and Edwards, 1969) and Columbia (Díaz-Ochoa and Quiñones, 2008). However, regional differences in the efficacy of the relationship between river flow and prawn yields are evident in Australian waters, with a positive correlation reported for the eastern Gulf of Carpentaria, but not the north-eastern Gulf of Carpentaria or the Gulf of Papua (Vance et al., 1985; Staples et al., 1995; Loneragan and Bunn, 1999). Our study suggests that while some associations may hold for individual estuaries, relationships between prawn landings and monthly or immediately antecedent flow conditions, or rainfall, are not consistent between estuaries across the region. Individual estuary characteristics, such as the nature of estuarine entrance conditions, may confound these associations in many estuaries.

It is difficult, from correlative studies, to distinguish the possible effects of river discharge on productivity and ease of capture. Flow

may increase nutrients stimulating primary and secondary production, and hence the carrying capacity of a fishery (Gillanders and Kingsford, 2002). However, Kimmerer (2002) demonstrated that for the San Francisco estuary, the relationship between flow and the abundance of organisms at higher trophic levels could not have been forced by upward trophic transfer, given the lack of such an association at lower trophic levels. An alternative explanation is that a reduction in salinity induced by rainfall and higher freshwater flows may cause nekton to congregate in the deeper waters of the estuary mouth, where the risk of long-term exposure to freshwater is reduced. Nekton may also be flushed there by stronger river flows. In either case, higher catches may be an indication of ease of capture, given a concentration of fishing effort in these waters (Loneragan and Bunn, 1999). Our finding of higher catches of mud crab following rainfall is consistent with observations of rainfall stimulating the downstream migration of this species (Hill et al., 1982).

Our comparison of monthly and 6-month moving means attempted to distinguish the effects of immediate and antecedent flow conditions, but found little difference in effect for most finfish catches which, with the exception of mullet and flathead, were largely unresponsive to antecedent flow and rainfall conditions. We did not, however, consider the lag time that might be involved between spawning and recruitment to the commercially-targeted cohort. An improved ease of capture was proposed by Loneragan and Bunn (1999) to explain the higher catches of flathead in their analysis of Logan River commercial landings. The Logan River is located 40 km to the north of the northernmost estuary in our analysis, and the trend of rainfall and discharge influencing mullet and flathead landings is consistent with our observations from NSW.

The most important driver of temporal variability in fish catch in the estuaries of NSW appears to be temperature. However, this response was divided between those species with an increased catch in warmer months (school prawns, flathead and mud crab) and those with an increased catch in cooler months (mullet, mulloway, blue swimmer crab and luderick). The increased feeding activity of mud crabs in warmer temperatures has been demonstrated (Hill, 1980; Hill et al., 1982), and catches in subtropical Queensland have been positively correlated with daily water temperature and not salinity (Williams and Hill, 1982). School prawns show strong seasonality in catch, peaking in warmer months across the region (Ives et al., 2009). Less is known of the temperature response of those species showing declines in catch with increasing temperature in our study. Of these, mullet and luderick are found primarily in the cooler waters of southern NSW. Temperature may inhibit the growth of mullet in these waters: the closely related *Mugil curema* showed decreased juvenile growth and condition in higher temperatures, prompting Muhlia-Almazn et al. (2003) to suggest higher temperatures as a contributing cause of the decline of this species in Baja California.

Physical habitat variables strongly correlated to commercial catch for most species and this relationship, first identified in Pease (1999) and Saintilan (2004) held across years of contrasting climatic and hydrological conditions. There are valid reasons to suggest that many of the relationships between commercial catch and habitat variables are not auto-correlates but habitat dependencies. For example, blue swimmer crab was consistently associated with seagrass and corresponds to known habitat preferences of the species (Edgar, 1990) and the availability of preferred food items (Williams, 1982). Those species showing a relationship between catch and the area of mangrove and saltmarsh (prawns, flathead, mullet, mud crab) are those which utilise these habitats as a nursery or feeding ground (Mazumder et al., 2005, 2011).

Some caveats should be placed on the conclusion that flow is a poor predictor of commercial landings. Catadromous species were not sampled and at least one species, the Australian Bass (*Macquaria novemaculeata*) has shown a correlation between initial year class strength and river flow in the Hawkesbury River (Harris, 1988). Flow parameters may be more important predictors of juvenile populations than the mature fish sampled by commercial fishers. For example, although eggs of the black bream *Acanthopagrus butcheri* were found ubiquitously through the Gippsland Lakes and associated rivers (Williams et al., 2012), larvae were only found in association with the halocline within rivers. This highly specific location of larvae explains the relationship between stratification and recruitment success identified for the Gippsland Lakes by Jenkins et al. (2010). These studies suggest that the prediction of recruitment success may not simply be related to antecedent rainfall conditions, but several factors influencing the halocline, such as the co-incidence of flood and drought sequences in associated with estuary entrance conditions (Jenkins et al., 2010).

The problem of predicting fish catch on the basis of flow is not confined to estuarine systems in NSW. Growns (2008) found only weak relationships between fish assemblage and flow modification in the regulated freshwater rivers of the Murray Darling Basin, Australia. Growns (2008) suggested that a more appropriate focus might be the response of fish recruitment or behaviour to specific flow attributes, and that generalisations of response over broad scales could not be made. However, modelling and detecting responses between fish productivity and flow at the broad scale at which resources are often managed, appears elusive at present for both freshwater and estuarine systems in New South Wales.

Acknowledgements

Leroy Gonzalves is thanked for assisting with the compilation of Commercial Fisheries data. Tahir Hameed is thanked for providing access to the Pineena database.

References

Ardisson, P.L., Bourget, E., 1997. A study of the relationship between freshwater runoff and benthos abundance: a scale-oriented approach. Estuarine Coastal and Shelf Science 45, 535–545.

Arthington, A.H., Pusey, B.J., 2003. Flow restoration and protection in Australian rivers. River Research and Applications 19, 377–395.

Bates, D., Naeche, M., 2010. Package "lme4". http://CRAN.Rproject.org/package=lme4.

Bingenheimer, J., Raudenbush, S.W., 2004. Statistical and substantive inferences in public health: issues in the application of multi-level models. Annual Review of Public Health 25, 53–77.

Browder, J.A., 1985. Relationships between pink shrimp production on the Tortugas grounds and water flow patterns in the Florida everglades. Bulletin of Marine Science 37, 839–856.

Browder, J.A., Zein-Eldin, Z.P., Crailes, M., Robblee, M.B., Wong, S., Jackson, T.L., Sohnson, D., 2002. Dynamics of pink shrimp (*Farfantepenaeus duorarum*) recruitment potential in relation to salinity and temperature in Florida Bay. Estuaries 25, 1355–1371.

Deegan, L.A., 1990. Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. Marine Ecology Progress Series 68, 195–205.

Díaz-Ochoa, J.A., Quiñones, R.A., 2008. Relationship of precipitation, freshwater input, and sea level height with the abundance of the white shrimp (*Litopenaeus occidentalis*; Street, 1871) off Buenaventura, eastern tropical Pacific. Fisheries Research 92, 148–161.

Drinkwater, K.F., Frank, K.T., 1994. Effects of river regulation and diversion on marine fish and invertebrates. Aquatic Conservation: Marine and Freshwater Ecosystems 4, 135–151.

Edgar, G.J., 1990. Predator-prey interactions in seagrass beds. II: distribution and diet of the blue manna crab *P. pelagicus* Linnaeus at Cliff Head, Western Australia. Journal of Experimental Marine Biology and Ecology 139, 23–32.

Galindo-Bect, M.S., Glenn, E.P., Page, H.M., Fitzsimmons, K., Galindo-Bect, L.A., Hernandex-Ayon, J.M., Petter, R.L., Garcia-Hernandez, J., Moore, D., 2000. Penaeid Shrimp Landings in the Upper Gulf of California in Relation to Colorado River Freshwater Discharge, vol. 98. Fishery Bulletin, Washington, D.C, pp. 222–225.

Gammelsrod, T., 1992. Variation in shrimp abundance on the Sofala Bank, Mozambique and its relation to the Zambezi River runoff. Estuarine, Coastal and Shelf Science 35, 91–103.
Gehrke, P.C., Gilligan, D.M., Barwick, M., 2002. Changes in fish communities of the Shoalhaven River 20 years after construction of the Tallowa Dam, Australia. River Research and Applications 18, 265–286.
Gillanders, B.M., Kingsford, M.J., 2002. Impact of change sin flow of freshwater on estuarine and open coastal habitats and the associated organisms. Oceanography and Marine Biology: An Annual Review 40, 233–309.
Glaister, J.P., 1978. The impact of river discharge on distribution and production of the school prawn *Metapenaeus macleayi* (Haswell) (Crustacea: Penaeidae) in the Clarence River region, northern New South Wales. Australian Journal of Marine and Freshwater Research 29, 311–323.
Gray, C.A., McElligott, D.J., Chick, R.C., 1996. Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. Marine and Freshwater Research 47, 723–735.
Growns, I., 2008. The influence of changes to river hydrology on freshwater fish in regulated rivers of the Murray-Darling Basin. Hydrobiologia 596, 203–211.
Gunter, G., Edwards, J.C., 1969. The relation of rainfall and freshwater drainage to the production of penaeid shrimps (*Penaeus fluviatilis* Say and *Penaeus aztecus* Ives) in Texas and Louisiana waters. FAO Fisheries Report 57, 875–892.
Harris, J.H., 1988. Demography of Australian bass, *Macquaria novemaculteata* (Perciformes, Percichthyidae), in the Sydney Basin. Australian Journal of Marine and Freshwater Research 39, 355–369.
Hill, B.J., 1980. Effects of temperature on feeding activity in *Scylla serrata*. Marine Biology 59, 189–192.
Hill, B.J., Williams, M.J., Dutton, P., 1982. Distribution of juvenile, subadult and adult *Scylla serrata* (Crustacea:Portunidae) on tidal flats in Australia. Marine Biology 69, 117–120.
Howarth, R.W., Swaney, D.P., Butler, T.J., Marino, R., 2000. Climatic control on eutrophication of the Hudson River estuary. Ecosystems 3, 210–215.
Ives, M.C., Scandol, J.P., Montgomery, S.S., Suthers, I.M., 2009. Modelling the possible effects of climate change on an Australian multi-fleet prawn fishery. Marine and Freshwater Research 60, 1211–1222.
Jenkins, G.P., Conron, S.D., Morison, A.K., 2010. Highly variable recruitment in an estuarine fish is determined by salinity stratification and freshwater flow: implications of a changing climate. Marine Ecology Progress Series 417, 249–261.
Kaartvedt, S., Aksenes, D.L., 1992. Does freshwater discharge cause mortality of fjord-living zooplankton. Estuarine Coastal and Shelf Science 34, 305–313.
Kimmerer, W.J., 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Marine Ecology Progress Series 243, 39–55.
Kingsford, R., 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. Austral Ecology 25 (2), 109–127.
Loneragan, N.R., Bunn, S.E., 1999. River flows and estuarine ecosystems: implications for coastal fisheries from a review and a case study of the Logan River, southeast Queensland. Australian Journal of Ecology 24, 431–440.
Loneragan, N.R., Bunn, S.E., Kellaway, D.M., 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable isotope study. Marine Biology 130, 289–300.
Mazumder, D., Saintilan, N., Williams, R., 2005. Temporal variation in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. Wetlands Ecology and Management 13, 457–467.
Mazumder, D., Saintilan, N., Williams, R., Szymczak, R., 2011. Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. Marine and Freshwater Research 62, 11–19.
Muhlia-Almaz, A., Arturo Muhlia-Melo, A., Guillermina Alcaraz, G., 2003. Responses to temperature and salinity by White Mullet *Mugil curema*: possible explanation for the population decrease in Baja California Sur. Marine and Freshwater Behaviour and Physiology 36, 177–185.
Newell, R.I.E., Marshall, N., Sasekumar, A., Chong, V.C., 1995. Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. Marine Biology 123, 595–606.
Nilsson, C., Berggren, K., 2000. Alterations of riparian ecosystems caused by river regulation. BioScience 50, 783–792.
Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science 308, 405–408.
Ogle, K., 2009. Hierarchical Bayesian statistics: merging experimental and modelling approaches in ecology. Ecological Applications 19, 577–581.
Paton, D.C., Rogers, D.J., Hill, B.M., Bailey, C.P., Ziembicki, M., 2009. Temporal changes to spatially stratified waterbird communities of the Coorong, South Australia: implications for the management of heterogenous wetlands. Animal Conservation 12, 408–417.
Pease, B.C., 1999. A spatially oriented analysis of estuaries and their associated commercial fisheries in New South Wales, Australia. Fisheries Research 42, 67–86.
Potter, I.C., Manning, R.J.G., Longeragan, N.R., 1991. Size, movements, distribution and gonadal stage of the western king prawn (*Penaeus latisulcatus*) in a temperate estuary and local marine waters. Journal of Zoology 223, 419–445.
Powell, G.L., Matsumoto, J., Brock, D.A., 2002. Methods for determining minimum freshwater inflow needs of Texas bays and estuaries. Estuaries 2, 1262–1274.
R Development Core Team, 2010. R: A Language and Environment for Statistical Computing, Reference Index Version 2.10.1. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. URL: http://www.R-project.org.
Raudenbush, S.W., 2005. Learning from attempts to improve schooling: the contribution of methodological diversity. Educational Researcher 34 (5), 25–31.
Robins, J.B., Halliday, I.A., Staunton-Smith, J., Mayer, D.G., Sellin, M.J., 2005. Freshwater-flow requirements of estuarine fisheries in tropical Australia: a review of the state of knowledge and application of a suggested approach. Marine and Freshwater Research 56, 343–360.
Rosenberg, D.M., Bodaly, R.A., Usher, P.J., 1995. Environmental and social impacts of large scale hydroelectric development: who is listening? Global Environmental Change 5, 127–148.
Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of South-east Australian estuaries. Estuarine Coastal and Shelf Science 53, 351–384.
Ruello, N.V., 1973. The influence of rainfall on the distribution and abundance of the school prawn (*Metapenaeus macleayi*) in the Hunter River region (Australia). Marine Biology 23, 221–228.
Saintilan, N., 2004. Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. Estuarine Coastal and Shelf Science 61, 591–601.
Shafroth, P.B., Stomberg, J.C., Patten, D.T., 2002. Riparian vegetation response to altered disturbance and stress regimes. Ecological Applications 12, 107–123.
Staples, D.J., Vance, D.J., 1986. Emigration of juvenile banana prawns, *Penaeus merguiensis*, from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. Marine Ecology Progress Series 27, 239–252.
Staples, D.J., Vance, D.J., Loneragan, N.R., 1995. Penaeid prawn recruitment variability: effect of the environment. In: Courtney, A.J., Cosgrove, M.G. (Eds.), Proceedings of the Workshop on Stock-Recruitment Relationships (SRR's). Australian Crustacean Fisheries. Queensland Department of Primary Industry, Southern Fisheries Centre, Deception Bay, Queensland, pp. 412–450.
Tyler, A.V., 1992. A context for recruitment correlation: why marine biologists should still look for them. Fisheries Oceanography 1, 97–107.
Vance, D.J., Staples, D.J., Kerr, D.J., 1985. Factors affecting year-to-year variation in the catch of banana prawns (*Penaeus merguiensis*) in the Gulf of Carpentaria, Australia. ECES Journal of Marine Science 42, 83–97.
Vance, D.J., Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R., 1998. Seasonal and annual variation in abundance of postlarval and juvenile banana prawns *Penaeus merguiensis* and environmental variation in two estuaries in tropical northeastern Australia: a six-year study. Marine Ecology Progress Series 163, 21–36.
Williams, J., Hindell, J.W., Swearer, S.E., Jenkins, G.P., 2012. Influence of freshwater flows on the distribution of eggs and larvae of black bream *Acanthopagrus butcheri* within a drought- affected estuary. Journal of Fish Biology 80, 2281–2301.
Williams, M.J., 1982. Natural food and feeding in the commercial sand crab *P. pelagicus* Linnaeus 1766 (Crustacea: Decapoda Portunidae) in Morton Bay, Queensland. Journal of Experimental Marine Biology and Ecology 59, 165–176.
Williams, M.J., Hill, B.J., 1982. Factors influencing pot catches and population estimates of the portunid crab *Scylla serrata*. Marine Biology 71, 187–192.

CSIRO PUBLISHING

www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2010, **61**, 615–620

Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh

Neil Saintilan[A,C] *and Debashish Mazumder*[B]

[A]Department of Environment Climate Change and Water, PO Box A290, Sydney South, NSW 1232, Australia.
[B]Australian Nuclear Science and Technology Organisation (ANSTO), PMB 1, Lucas Heights, Menai, NSW 2234, Australia.
[C]Corresponding author. Email: neil.saintilan@environment.nsw.gov.au

Abstract. Saltmarsh floristic diversity declines with increasing latitude on the Australian east coast, with the dominant tropical C_4 grass *Sporobolus virginicus* being replaced progressively by a suite of mostly succulent C_3 species. The temperate Towra Point saltmarsh consists of a mosaic of vegetation communities, including stands of the C_4 saltmarsh grass *Sporobolus virginicus*, and the C_3 succulents *Suaeda australis* and *Sarcocornia quinqueflora*. The contrasting stable isotope signatures of these plants provide an opportunity to determine the extent to which plant material is contributing to the diet of grazing invertebrates inhabiting these communities. The grazing crabs *Parasesarma erythrodactyla* and *Helograpsus haswellianus*, and the snail *Littoraria luteola*, were sampled for their carbon and nitrogen isotope signatures. In the *Sarcocornia* communities, crab and snail $\delta^{13}C$ signatures could not be matched to the signature of dominant plants, but were close to the fine benthic material on the marsh surface. In the *Sporobolus* community, the $\delta^{13}C$ signatures of the same species were enriched and closer to that of the dominant plant. Results suggest that grazing herbivores feed over very small spatial ranges within mosaics of vegetation on locally sourced benthic material, with *S. virginicus* plant material making a contribution to dietary carbon where present.

Additional keywords: estuary, photosynthetic pathway, stable isotope.

Introduction

Movement of energy (carbon) from autotrophic sources of production to higher-level consumers and predators is a fundamental organising principle of landscape ecology (Polis *et al.* 1997; Connolly *et al.* 2005). Early work within estuaries stressed the importance of hydrodynamic forces in moving carbon from productive inshore environments to offshore ecosystems of high secondary productivity, either through the direct outwelling of carbon (Odum *et al.* 1979; Nixon 1980; Dame and Allen 1996) or the transfer of carbon through successive trophic levels operating at successively wider geographic ranges (trophic relay: Kneib 1997, 2000).

The grazing invertebrate herbivores of the subtropical and temperate saltmarsh are now known to make a substantial contribution to the diet of small fish visiting the saltmarsh during the spring tide. In particular, larvae released by grapsid crabs during the monthly spring tide are a dominant component of the diet of many small fish visiting the saltmarsh (Mazumder *et al.* 2006; Hollingsworth and Connolly 2006). Mazumder *et al.* (2009) demonstrated that a temperate saltmarsh, when flooded, contained the highest concentration of larvae across a gradient of shallow nearshore habitats, and proposed the trophic relay hypothesis of Kneib (1997) to be a useful model for understanding the contribution of saltmarsh to the broader estuarine ecosystem.

The autotrophic component of the diet of grazing herbivores is likely therefore to be making a significant contribution to energy flows within the mangrove and saltmarsh ecosystems, and possibly the broader estuary. Several recent studies utilising stable isotopes have suggested that in many estuaries, the movement of carbon between autotrophs and primary consumers occurs at local scales (Loneragan *et al.* 1997; Chong *et al.* 2000; Dittel *et al.* 2000). A close trophic relationship between invertebrates and autotrophic sources of carbon has been demonstrated over scales of hundreds of metres (Hsieh *et al.* 2002) to less than 10 m (Guest *et al.* 2004). Guest and Connolly (2004) utilised the mangrove–saltmarsh boundary in a subtropical Australian estuary to study variability in invertebrate sources of carbon, taking advantage of the differing carbon isotope ($^{13}C:{}^{12}C$) ratios of the dominant mangrove (*Avicennia marina*, highly depleted in ^{13}C) and the dominant saltmarsh grass (*Sporobolus virginicus*, a C_4 plant and significantly less depleted). They showed a rapid transition in isotope ratios between these environments for the grazing crabs *Parasesarma erythrodactyla* and *Australoplax tridentata*, and the slug *Onchidina australis*. This result suggested that *S. virginicus* made a substantial contribution to the diet of grazing herbivores in the saltmarsh. However, their study and several others (France 1998; Bouillon *et al.* 2002; D. Mazumder, unpubl. data) have shown that the

© CSIRO 2010 10.1071/MF09187 1323-1650/10/050615

highly depleted signature of mangrove compared with mangrove herbivores indicates that microphytobenthos might have been a more important contributor to the diet in the mangrove habitat than mangrove leaf material in subtropical and temperate forests.

Saltmarsh floristic diversity increases with increasing latitude in Australia (Saintilan 2009), and between the subtropical Queensland saltmarshes studied by Guest and Connolly (2004) where *S. virginicus* is dominant, and the temperate saltmarshes of central and southern New South Wales, several saltmarsh species become increasingly important, notably *S. quinqueflora*, which forms a co-dominant saltmarsh plant in the Sydney region (Clarke and Hannon 1967). At Towra Point (34°01′S, 151°09′E), the largest saltmarsh in the region, *S. quinqueflora* and *S. virginicus* form a mosaic of small patches (tens to hundreds of square metres), possibly related to microtopographic variation through the marsh. The contrasting isotope signatures of these species (*S. quinqueflora* utilises the C_3 photosynthetic pathway and *S. virginicus* the C_4) makes possible the fine-scale assessment of sources of carbon contributing to the dominant grazing herbivores: the grapsid crabs *P. erythrodactyla* and *Helograpsus haswellianus*, and the snail *Littoraria luteola*, each of which are ubiquitously distributed through the saltmarsh.

We propose three possible sources of autotrophic production available to these herbivores in the saltmarsh: the cellulose of the two dominant plant species *S. virginicus* and *S. quinqueflora*; and the fine benthic organic material on the marsh surface dominated by microphytobenthos. By sampling within replicate patches of *Sarcocornia* community and *Sporobolus* community, we tested whether the carbon isotope signature of the invertebrates is consistently depleted within *Sporobolus* patches, implying a contribution from this source, and very small feeding ranges for these species. We also used dual stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to assess the most likely contributions to invertebrate diets across all patches.

Materials and methods

All specimens were sampled from the Towra Point saltmarsh in summer 2008–2009. Towra Point extends into Botany Bay, Sydney, separating Woolooware Bay from Weeney Bay (Fig. 1). The point is dissected along nearly half its length by an artificial levee (access road), which provides a degree of hydrological segregation between the Woolooware Bay saltmarsh and the Weeney Bay saltmarsh. Both saltmarsh plains are fringed by extensive mangrove (*Avicennia marina* dominant), and contain mosaics of four co-dominant saltmarsh plants; *Juncus kraussii*, *Suaeda australis*, *S. virginicus* and *S. quinqueflora*.

Two patches of *Sporobolus* community (patch sizes 170 m^2 and 280 m^2) and two patches of *Sarcocornia* community (200 m^2 and 340 m^2) were selected in each of the Weeney Bay and Woolooware Bay saltmarshes. Patches were selected on the basis of the floristic purity of the stand, and in both settings were in close proximity (within 100 m) and common geomorphic setting (all stands were situated in the lower saltmarsh zone on fluvial deltaic sand). Five adult individuals of each of the two dominant crab species, *Parasesarma erythrodactyla* (Grapsidae, size range: 17.4–18.8 mm) and *Helograpsus haswellianus* (Grapsidae, size range: 13.9–15.1 mm), and the snail *Littoraria luteola* (Littorinidae), were collected from each patch. Within each patch, five replicate samples were taken of the upper 1 cm of soil, for later division into fine and coarse benthic organic material. Five specimens of each of the dominant plant species within the saltmarsh (*S. virginicus*, *S. quinqueflora*, *J. kraussii* and *S. australis*) were also collected, but not at the patch scale, as previous studies have confirmed the low variability in $\delta^{13}C$ for these species over a range of spatial scales (Guest and Connolly 2004).

Sample preparation and analysis

Muscle tissues were collected from snails and the claws of crabs following removal of the hard shell. Lipid extractions were not undertaken as delipidation from muscle tissue causes only small (<1‰) isotope shifts in $\delta^{13}C$ and $\delta^{15}N$ (Sotiropoulos *et al.* 2004). Enough tissue was collected from each sample to make dry powder for isotope analysis. Samples were dried at 65°C for 72 h and then ground to a fine powder with mortar and pestle.

We divided the sediment samples in two groups. The whole-sediment samples are termed ‘coarse benthic organic matter’ (CBOM) and includes biological and geological materials including detritus, microphytobenthos bacteria and sediment. The second group, ‘fine benthic organic matter’ (FBOM), was separated from the whole sediment samples by sieving (mesh sizes of 0.25, 0.5, 1 and 4 mm) following the method of Loneragan *et al.* (1997). Benthic organic matter was then elutriated from the finest size-fractions (0.25–0.5 mm). A small quantity of 1 M hydrochloric acid was added to CBOM and FBOM sediment sub-samples and left for 3 h to remove the inorganic carbon present in the sediment (Polunin *et al.* 2001). The samples were then rinsed with distilled water, dried and ground to a fine powder. Because this acid-washing process results in enrichment of $\delta^{15}N$ (Pinnegar and Polunin 1999), untreated sediment sub-samples were analysed for $\delta^{15}N$.

All samples were analysed using a continuous-flow stable-isotope mass spectrometer (GV Instruments IsoPrime EA/IRMS). Stable isotope values were reported in delta (δ) units in parts per thousand (‰) relative to the international standard.

Two-factor Analysis of Variance (ANOVA) was conducted to compare $\delta^{13}C$ and $\delta^{15}N$ between samples collected from the treatments of setting (Woolooware Bay *v.* Weeney Bay) and habitat type (*Sporobolus* patches *v. Sarcocornia* patches). A three-source mixing model (Phillips 2001) was used with the assumption of 3.4‰ enrichment fractionation between trophic levels for $\delta^{15}N$ (Vander Zanden and Rasmussen 2001) and 1‰ for $\delta^{13}C$ (DeNiro and Epstein 1978) to explore the relative importance of potential food sources to the diet of crabs and the snail collected from the study sites.

Results

All plant species, except the C_4 plant *S. virginicus*, were highly depleted in the heavier isotope of carbon compared with the signatures of the grazing invertebrates (Fig. 2) and are unlikely to be a source of nutrition. Both species of crabs were significantly enriched in $\delta^{13}C$ over the *Sporobolus* communities compared with the *Sarcocornia* communities (*H. haswellianus*: $F_{1,9} = 36.3$, $P < 0.001$; *P. erythrodactyla*: $F_{1,9} = 46.1$, $P < 0.001$). There was no difference between sites in the extent of this enrichment, reflecting the relatively enriched signature of *S. virginicus*. The

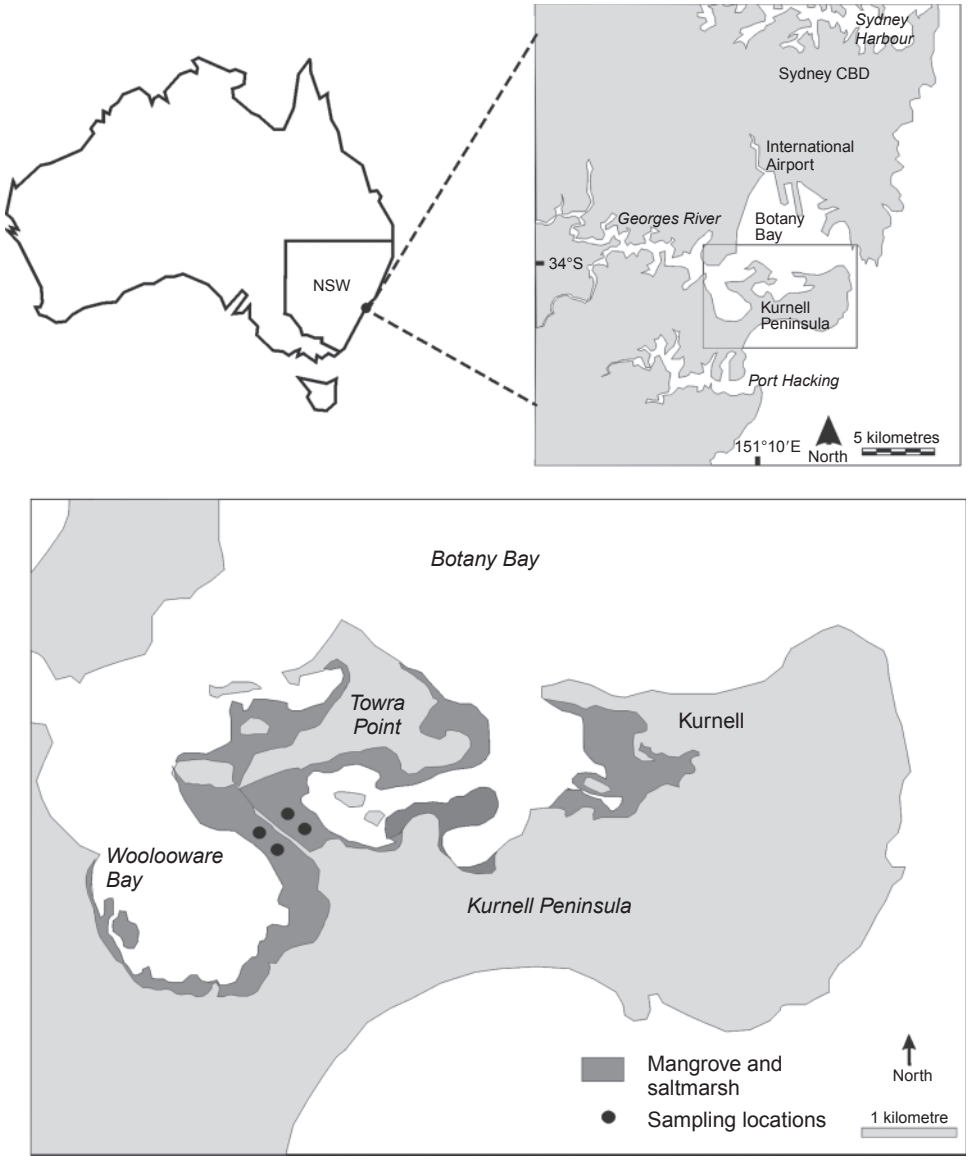


Fig. 1. Location of the Towra Point saltmarsh showing sampling locations.

snail *L. luteola* was also enriched in $\delta^{13}C$ over *Sporobolus* ($F_{1,9} = 5506$, $P < 0.001$), though more so in the Weeney Bay site (Site × Habitat interaction: $F_{1,9} = 46.8$, $P < 0.001$). FBOM and CBOM $\delta^{13}C$ signatures were also more enriched within *Sporobolus* patches than within *Sarcocornia* patches (FBOM: $F_{1,9} = 1174$, $P < 0.001$; CBOM: $F_{1,9} = 5856$, $P < 0.001$).

Nitrogen stable isotopes were consistently more enriched in the Woolooware Bay site than the Weeney Bay site (*H. haswellianus*: $F_{1,9} = 19.1$, $P < 0.001$; *P. erythrodactyla*: $F_{1,9} = 39.1$, $P < 0.001$; *L. luteola*: $F_{1,9} = 167.1$, $P < 0.001$; FBOM: $F_{1,9} = 19.8$, $P < 0.001$), and in the *Sporobolus* patches rather than the *Sarcocornia* patches (*P. erythrodactyla*: $F_{1,9} = 19.6$, $P < 0.001$; *L. luteola*: $F_{1,9} = 69.6$, $P < 0.001$; CBOM: $F_{1,9} = 21.3$, $P < 0.001$).

A three-source mixing model (Phillips 2001) was applied to three potential food sources in the *Sporobolus* patch (FBOM, CBOM and *S. virginicus*) and the *Sarcocornia* patch (FBOM, CBOM and *S. quinqueflora*). Results suggested that in the *Sarcocornia* patch, FBOM alone of the carbon sources sampled contributed to the diet of these species, explaining as much as 90% of carbon intake. In the *Sporobolus* patch, FBOM was again the dominant source of carbon, though *S. virginicus* plant material was making a contribution at ~20 percent of the diet of all three species.

Discussion

Primary sources of crustacean and gastropod dietary carbon

This study has demonstrated variability in the diet of grazing invertebrate herbivores in the saltmarsh at the patch scale (<500 m^2). A three-source mixing model indicated that FBOM was the dominant source of carbon for all grazing invertebrates

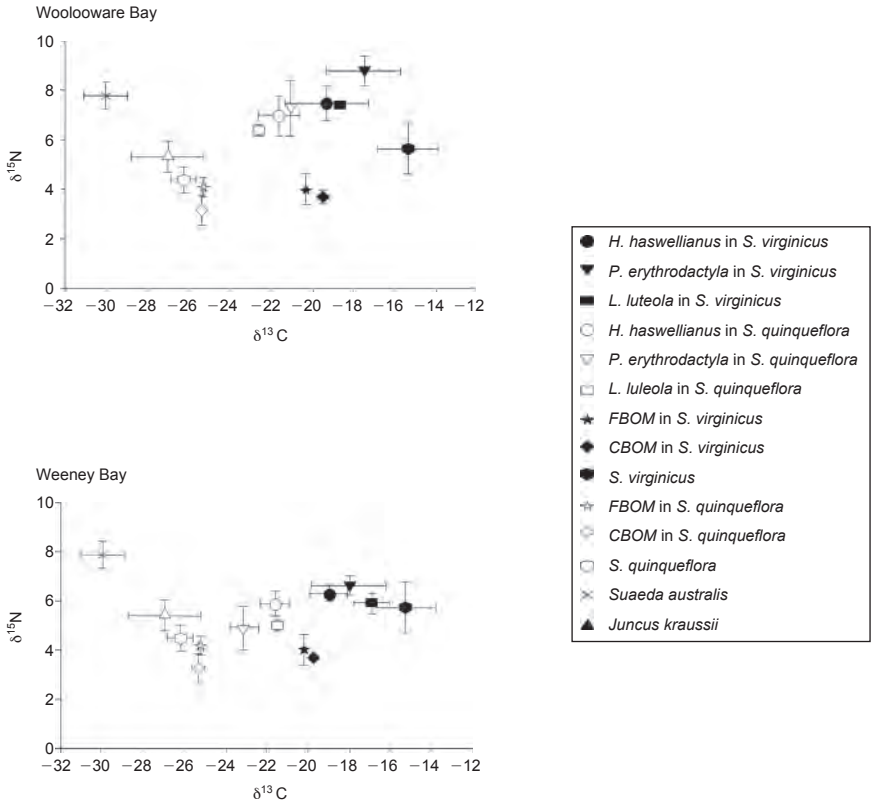


Fig. 2. Mean (±s.d.) $\delta^{13}C$ and $\delta^{15}N$ values of the macro-invertebrates, fine benthic organic matter (FBOM), coarse benthic organic matter (CBOM) and dominant plants at Woolooware Bay and Weeney Bay sites of the Towra Point saltmarsh.

in all patch types. For consumers in patches of *Sporobolus*, this saltmarsh grass was likely to be contributing ~20% of the dietary carbon of invertebrate consumers. This was reflected in the similarly enriched $\delta^{13}C$ values of crabs and molluscs sampled within these patches. The $\delta^{13}C$ values of *S. quinqueflora*, *S. australis* and *J. kraussii* were more depleted than that of *S. virginicus*. Resident invertebrates in the *Sarcocornia* patches were not as depleted as the adjacent autotrophs.

Within *Sarcocornia* habitats, FBOM was the only identified source of nutrition. The nitrogen isotope ratios of benthic organic material are consistently depleted 3–4‰ in relation to the grazing herbivores, typical of isotopic fractionation between single trophic levels (Minagawa and Wada 1984; Cabana and Rasmussen 1996; Post 2002). The low variability in FBOM isotope ratios between patches of *Sporobolus* and *Sarcocornia* would suggest that microphytobenthos might be an important contributor to this material, as opposed to detrital material derived from the standing vegetation. The alternative model of a mixed contribution of *S. virginicus* and *S. quinqueflora* to crabs within the *Sarcocornia* patches would seem unlikely given the highly localised movements of *P. erythrodactyla* (Guest *et al.* 2004) and most probably *H. haswellianus*.

Guest and Connolly (2004) similarly found crabs deriving carbon from local sources in subtropical estuarine wetlands in Queensland. The sampling gradient used in Guest and Connolly (2004) extended between homogenous *S. virginicus* and the mangrove forest, with the resulting crab carbon isotope ratios describing a sigmoidal curve centred near the interface of the two habitats. Their results were interpreted as a shift in dietary carbon between *S. virginicus* in the saltmarsh to microphytobenthos in the mangrove. In a subsequent study, Guest *et al.* (2006) used pitfall traps in a mark–recapture experiment to examine the range of movement of crabs along the mangrove–saltmarsh boundary, and found that over 90% of *P. erythrodactyla* and *Australoplax tridentata* (Ocypodidae) moved less than two metres from the point of original capture. Their conclusion was that the small home ranges of crabs explained the fine-scale relationships between isotope signatures and autotrophic sources.

Although *S. virginicus* alone among the macrophytes seems to be contributing to dietary carbon of grazing invertebrates in the saltmarsh at Towra Point, they show no preference for this habitat. Cochran (1982) suggested that food availability may be a factor contributing to the distribution of the snail species *Phallomedusa solida* in *S. quinqueflora* and *Ophicardelus* and *Pleuroloba* in *Juncus kraussii* and *S. virginicus*, although *L. luteola* was found commonly in both the *S. virginicus* and *S. quinqueflora* patches. Habitat type may, however, be influencing the distribution of *H. haswellianus*, which is absent from the mangrove and is found in higher abundance in *Sporobolus* patches than *Sarcocornia* patches at Towra Point (Mazumder and Saintilan 2003).

Gastropods are an important component of the saltmarsh ecosystem, making a numerically large contribution to

zooplankton exported from the saltmarsh (Mazumder *et al.* 2009), contributing to the diet of the toadfish *Tetractenos hamiltoni* (Hughes 1984; Kaly 1988) and yellow-finned bream *Acanthopagrus australis* (Kaly 1988; Mazumder *et al.* 2006). Roach (1998) has suggested that the contribution may be higher than indicated by gut content analysis, as fish spit out the indigestible shell, and the soft-bodied components are difficult to identify in the stomach.

Little is known of the diet of mollusc species found in Australian saltmarshes (Richardson *et al.* 1998; Ross *et al.* 2009). It is believed that most species feed on microscopic algae on the surface of the marsh (Hutchings and Recher 1974), including *L. luteola* (Reid 1986), although our study has suggested that plant detrital material might be contributing to the diet of this species, given the consistently depleted isotope signature within the *Sporobolus* patches. Indeed, there is little to distinguish the diet of gastropod and grapsid crabs in the saltmarsh on the basis of isotope signatures alone.

Latitudinal variation in carbon sources

The homogenous *S. virginicus* saltmarsh gives way in temperate climates to a more diverse saltmarsh community floristically, and at Towra Point *S. virginicus* forms small patches of no more than a few hundred square metres, interspersed with patches of *S. quinqueflora*, *J. kraussii* and *S. australis*. It is clear from the results of our study that not all of these species contribute equally to invertebrate diets. Our evidence supports the earlier work of Guest and Connolly (2004), which suggested *S. virginicus* as a source of nutrition for crabs. However, in the temperate saltmarsh, this is restricted to patches where the species is dominant, and even there, fine benthic organic material is the primary source of dietary carbon. All other saltmarsh species were too depleted in ^{13}C (*S. quinqueflora*: $\delta^{13}C$ 26.25‰; *J. kraussii*: 27.03‰; and *S. australis*: 30.02‰) to be making a contribution to the diet of crabs and the grazing snail *L. luteola*, including *S. quinqueflora* in patches dominated by this species.

The floristic dominance of *S. virginicus* in tropical climates therefore represents an important difference between tropical and temperate saltmarshes in autotrophic production. The C_4 photosynthetic pathway is more common in tropical monocots (Teeri and Stowe 1976), providing a higher light-use efficiency (Ehleringer *et al.* 1997). In temperate climates, the deleterious effect of low temperature negates the advantages of the C_4 pathway. We propose that on the east Australian coast the source of autotrophic carbon contributing to saltmarsh foodwebs shifts from plant to algal sources as C_3 plants become more common.

Acknowledgements

Rachel Melrose assisted with the collection of field samples. The Department of Environment Climate Change and Water (NSW) provided access to the Towra Point sites. Crab samples were collected under NSW Scientific Collection Permit P06/0005. Two anonymous referees are thanked for their constructive contributions.

References

Bouillon, S., Koedam, N., Raman, A., and Dehairs, F. (2002). Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. *Oecologia* **130**, 441–448. doi:10.1007/S004420100814

Cabana, G., and Rasmussen, J. B. (1996). Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences of the United States of America* **93**, 10 844–10 847. doi:10.1073/PNAS.93.20.10844

Chong, V. C., Low, C. B., and Ichikawa, T. (2000). Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. *Marine Biology* **138**, 72–86.

Clarke, L. D., and Hannon, N. J. (1967). The mangrove swamp and saltmarsh communities of the Sydney district. I. Vegetation, soil and climate. *Journal of Ecology* **55**, 753–771. doi:10.2307/2258423

Cochran, T. (1982). Factors affecting the distribution and abundance of the two pulmonate gastropods *Ophicardelus ornatus* and *Salinator solida* within a salt marsh at Warneet, Westernport Bay, Victoria. Honours thesis, The University of Melbourne.

Connolly, R. M., Gorman, D., and Guest, M. A. (2005). Movement of carbon among estuarine habitats and its assimilation by invertebrates. *Oecologia* **144**, 684–691. doi:10.1007/S00442-005-0167-4

Dame, R. F., and Allen, D. M. (1996). Between estuaries and the sea. *Journal of Experimental Marine Biology and Ecology* **200**, 169–185. doi:10.1016/S0022-0981(96)02642-1

DeNiro, M. J., and Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**, 495–506. doi:10.1016/0016-7037(78)90199-0

Dittel, A. I., Epifanio, C. E., Schwalm, S. M., Fantle, M. S., and Fogel, M. L. (2000). Carbon and nitrogen sources for juvenile blue crabs *Callinectes sapidus* in coastal wetlands. *Marine Ecology Progress Series* **147**, 31–47.

Ehleringer, J. R., Cerling, T. E., and Hellinker, B. R. (1997). C_4 photosynthesis, atmospheric CO_2 and climate. *Oecologia* **112**, 285–299. doi:10.1007/S004420050311

France, R. (1998). Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes. *Journal of Tropical Ecology* **14**, 413–425. doi:10.1017/S0266467498000315

Guest, M. A., and Connolly, R. M. (2004). Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. *Aquatic Ecology* **38**, 599–609. doi:10.1007/S10452-004-0442-1

Guest, M. A., Connolly, R. M., and Loneragan, N. R. (2004). Carbon movement and assimilation by invertebrates in estuarine habitats occurring at a scale of metres. *Marine Ecology Progress Series* **278**, 27–34. doi:10.3354/MEPS278027

Guest, M. A., Connolly, R. M., Lee, S. Y., Loneragan, N. R., and Breitfuss, M. J. (2006). Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement. *Oecologia* **148**, 88–96. doi:10.1007/S00442-005-0352-5

Hollingsworth, A., and Connolly, R. M. (2006). Feeding by fish visiting inundated subtropical saltmarsh. *Journal of Experimental Marine Biology and Ecology* **336**, 88–98. doi:10.1016/J.JEMBE.2006.04.008

Hsieh, H., Chen, C., Chen, Y., and Yang, H. (2002). Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary $\delta^{13}C$ and $\delta^{15}S$ signals. *Marine Ecology Progress Series* **227**, 145–155. doi:10.3354/MEPS227145

Hughes, J. M. (1984). A note on predation by toadfish *Spheroides* spp. on the mangrove snail *Littorina scabra*. In 'Focus on Stradbroke: New Information on North Stradbroke Island and Surrounding Areas 1974–1984'. (Eds R. J. Coleman, J. Covacevich and P. Davie.) pp. 312–314. (Boolarong Publications: Brisbane.)

Hutchings, P. A., and Recher, H. F. (1974). The fauna of Careel Bay with comments on the ecology of mangroves and seagrass communities. *Australian Zoologist* **18**, 99–127.

Kaly, U. L. (1988). Distribution, abundance and size in mangrove and saltmarsh gastropods. PhD thesis, University of Sydney.

Kneib, R. (1997). The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology Annual Review* **35**, 163–220.

Kneib, R. (2000). Saltmarsh ecoscapes and production transfer by estuarine nekton in the southeastern United States. In 'Concepts and Controversies

in Tidal Marsh Ecology'. (Eds M. P. Weinstein and D. A. Kreeger.) pp. 267–291. (Kluwer: Dordrecht.)

Loneragan, N. R., Bunn, S. E., and Kellaway, D. M. (1997). Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable isotope study. *Marine Biology* **130**, 289–300. doi:10.1007/S002270050248

Mazumder, D., and Saintilan, N. (2003). A comparison of sampling techniques in the assessment of burrowing crab abundance in saltmarsh and mangrove environments. *Wetlands (Australia)* **21**, 1–15.

Mazumder, D., Saintilan, N., and Williams, R. J. (2006). Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. *Marine and Freshwater Research* **57**, 193–199. doi:10.1071/MF05040

Mazumder, D., Saintilan, N., and Williams, R. J. (2009). Zooplankton inputs and outputs in the saltmarsh at Towra Point, Australia. *Wetlands Ecology and Management* **17**, 225–230. doi:10.1007/S11273-008-9102-X

Minagawa, M., and Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between δ^{15}N and animal age. *Geochimica et Cosmochimica Acta* **48**, 1135–1140. doi:10.1016/0016-7037(84)90204-7

Nixon, S. W. (1980). Between coastal marshes and coastal waters: a review of 20 years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In 'Estuarine and Wetland Processes'. (Eds P. Hamilton and K. B. MacDonald.) pp. 437–525. (Plenum: New York.)

Odum, W. E., Fisher, J. S., and Pickral, J. C. (1979). Factors controlling the flux of particulate organic carbon from estuarine wetlands. In 'Ecological Processes in Coastal and Marine Systems'. (Ed. R. J. Livingston.) pp. 69–80. (Plenum Press: New York.)

Phillips, D. L. (2001). Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* **127**, 166–170. doi:10.1007/S004420000571

Pinnegar, J. K., and Polunin, N. V. C. (1999). Differential fractionation of d13C and d15N among fish tissues: implications for the study of trophic interactions. *Functional Ecology* **13**, 225–231. doi:10.1046/J.1365-2435.1999.00301.X

Polis, G. A., Anderson, W. B., and Holt, R. D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**, 289–316. doi:10.1146/ANNUREV.ECOLSYS.28.1.289

Polunin, N. V. C., Morales-Nin, B., Pawsey, W. E., Carles, J. E., Pinnegar, J. K., and Moranta, J. (2001). Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. *Marine Ecology Progress Series* **220**, 13–23. doi:10.3354/MEPS220013

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**, 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Reid, D. G. (1986). 'The Littorinid Molluscs of Mangrove Forests in the Indo–Pacific Region.' (British Museum Natural History: London.)

Richardson, A. M. M., Swain, R., and Wong, V. (1998). Relationship between the crustacean and molluscan assemblages of Tasmanian saltmarshes and the vegetation and soil conditions. *Marine and Freshwater Research* **49**, 785–799. doi:10.1071/MF97097

Roach, A. C. (1998). Effects of predation on the size structure of the gastropod *Salinator solida* (Martens) populations at Towra Point, NSW, Australia. *Marine and Freshwater Research* **49**, 779–784. doi:10.1071/MF97098

Ross, P. M., Minchington, T. E., and Ponder, W. F. (2009). The ecology of molluscs in Australian saltmarshes. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp. 75–114. (CSIRO Publishing: Melbourne.)

Saintilan, N. (2009). Distribution of saltmarsh plants. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp. 23–44. (CSIRO Publishing: Melbourne.)

Sotiropoulos, M. A., Tonny, W. M., and Wassenaar, L. I. (2004). Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecology of Freshwater Fish* **13**, 155–160. doi:10.1111/J.1600-0633.2004.00056.X

Teeri, J. A., and Stowe, C. G. (1976). Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia* **23**, 1–12.

Vander Zanden, M. J., and Rasmussen, J. B. (2001). Variation in d15N and d13C trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography* **46**, 2061–2066.

Manuscript received 21 July 2009, accepted 23 November 2009

Vol. 487: 113–122, 2013
doi: 10.3354/meps10335

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 30

Application of isotope mixing models to discriminate dietary sources over small-scale patches in saltmarsh

Brendan Alderson[1,*], Debashish Mazumder[2], Neil Saintilan[3], Ken Zimmerman[1], Phil Mulry[1]

[1]University of Newcastle, Ourimbah Campus, Ourimbah, New South Wales 2258, Australia
[2]Australian Nuclear Science and Technology Organisation, Kirrawee DC, New South Wales 2232, Australia
[3]Office of Environment and Heritage, Sydney South, New South Wales 1232, Australia

ABSTRACT: Intertidal grazing crabs play an important role in estuarine ecosystems, transforming carbon fixed by autotrophs into forms available to a wide range of consumers. Whether the autotrophic carbon is derived primarily from intertidal vegetation or microalgae is an important question to be resolved, as the modification of estuaries alters the balance between these potential food sources, and restoration efforts are best guided by an understanding of the primary drivers of ecosystem energy flow. We utilised the mosaic of C_3 and C_4 vegetated patches in a temperate saltmarsh to clarify the relative contributions of potential sources of carbon and nitrogen to the diet of 2 species of grapsid crabs: *Paragrapsus laevis* and *Helograpsis haswellianus*. The 2 vegetation communities occupied the same position in relation to tidal elevation. We analysed stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to discriminate 3 potential sources of dietary carbon using an IsoSource mixing model: microphytobenthos (MPB); fine benthic organic matter (FBOM); and fresh plant material. We found enrichment of $\delta^{13}C$ and depletion of $\delta^{15}N$ in crabs sampled from patches of the C_4 grass *Sporobolus virginicus*, consistent with the use of C_4 derived carbon compared to those sampled in the C_3 chenopod *Sarcocornia quinqueflora*. However, microphytobenthos was similarly depleted within large patches of *S. virginicus*, implying uptake of dissolved inorganic carbon originating from plant respiration. Multiple-source mixing (IsoSource) models indicated a primary role for MPB and FBOM in crab diets, with locally derived plant material making little contribution to crab diet. The result contrasts with those of studies from subtropical and tropical systems.

KEY WORDS: Microphytobenthos · Grapsid crab · Saltmarsh · Intertidal · Stable isotopes · Carbon · Nitrogen

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Autotrophs occupying estuarine intertidal environments play an important role in fixing atmospheric and dissolved inorganic carbon, subsequently utilised in estuarine ecosystems (Kneib 1997, 2002) or sequestered and stored in estuarine soils (Chmura et al. 2003). A range of autotrophs contribute to the productivity of intertidal flats, including macrophytes (mangrove, saltmarsh and seagrass), phytoplankton, and microphytobenthos adhering to the surface sediment. Marine macroalgae may also be locally important (Karsten & West 1993).

Early studies emphasised the importance of plant detritus to estuarine and nearshore ecosystems, derived from both mangrove (Giddens et al. 1986,

*Email: brendan.alderson@cardno.com.au

© Inter-Research 2013 · www.int-res.com

Robertson 1986) and saltmarsh (Odum 1968). Observations of feeding behaviour of organisms (Robertson & Daniel 1989, Micheli 1993), and estimates of carbon mass balance led to conceptual models positioning macrophytic plant production as foundational to productive estuarine and nearshore ecosystems (Teal 1962, Lee 1999). However, 2 lines of evidence prompted a revision of sources of heterotrophic carbon. First, the high C:N ratio of mangrove plant detritus suggested that sole dependence on mangrove leaf material for nutrition was unlikely, even amongst leaf-shredding grapsid crabs (Skov & Hartnoll 2002). Secondly, the application of stable isotope ecology in intertidal environments demonstrated a disparity between grazing herbivore isotope signatures and macrophytes highly depleted in $\delta^{13}C$ (France 1998, Bouillon et al. 2002, Mazumder & Saintilan 2010). Attention has therefore turned to microphytobenthos (MPB) as an important contributing source of dietary carbon for intertidal heterotrophs (Bouillon et al. 2008).

The importance of MPB to the diet of intertidal crabs has been demonstrated by exclusion experiments (Reinsel 2004) and observation of naturally occurring and labelled isotopes. Oakes et al. (2010) used labelled isotopes to clarify the contribution of MPB and mangrove leaf material to the diet of grazing crabs and foraminifera. They found strong differences between species, with the grapsid crab *Parasesarma erythrodactyla* consuming predominantly leaf material and up to 33% MPB, while the ocypodid crab *Australoplax tridentata* consumed mostly MPB and minimal leaf material. These observations concurred with other studies indicating grapsids in mangrove relying more heavily on leaf litter (Lee 1998), while ocypodids in the same settings characteristically consume bacteria and MPB (Rodelli et al. 1984, Dye & Lasiak 1986).

The presence of the C_4 grass *Sporobolus virginicus* (salt couch) as an important component of the saltmarshes of eastern Australia provides an opportunity to test hypotheses concerning the relative contribution of saltmarsh plant material and MPB to the diet of saltmarsh heterotrophs. This is made possible by the narrow range of movement of crabs feeding in the saltmarsh — less than 10 m in studies in Australia and the USA (Guest et al. 2004, Morgan et al. 2006). Saintilan & Mazumder (2010) utilised the mosaic pattern of saltmarsh plants to compare the diet of crabs in the relatively $\delta^{13}C$-enriched *S. virginicus* patches with those in the $\delta^{13}C$-depleted *Sacrocornia quinqueflora* (samphire) patches. They found a consistent enrichment in crab $\delta^{13}C$ signatures within *S. virginicus* patches, suggesting a contribution of saltmarsh plant detritus to crab diet. In the present study, we sampled the obvious available carbon sources in replicate *S. virginicus* and *S. quinqueflora* patches to determine, through analysis of stable isotopes of carbon and nitrogen, the relative contribution of autotrophic sources to the diet of the 2 dominant species of saltmarsh crab; *Paragrapsus laevis* and *Helograpsus haswellianus*. We utilised a dual isotope mixing model (Phillips & Gregg 2003) to test probable sources of dietary carbon: the cellulose of plant material (the C_4 saltmarsh grass *S. virginicus* and the C_3 chenopod herb *S. quinqueflora*); MPB; and fine benthic organic material (FBOM) incorporating mostly decomposed detritus. Both species of crab were sampled in both habitats. Therefore, the sampling of crabs and probable food sources across habitats and sites allowed the testing of the following hypotheses:

(1) that crabs derive their dietary requirements from food sources available within small habitat patches,

(2) that the 2 common saltmarsh crab species are selective in their utilisation of plant material as a food source, and

(3) that MPB contributes significantly to crab diet in all patches.

MATERIALS AND METHODS

Study locations

The study was conducted at 2 separate locations containing saltmarsh habitat within Brisbane Water (Fig. 1), the marine entrance of the Hawkesbury-Nepean estuary to the north of Sydney, Australia. The locations included the saltmarsh areas of Empire Bay and Davistown.

Each of these locations were chosen for the study based on their vegetation coverage, types of saltmarsh vegetation present, their inundation characteristics and ease of access to each site. Generally, each location was dominated by the saltmarsh vegetation *Sarcocornia quinqueflora* and *Sporobolus virginicus*, with each generally present as homogenous patches separate from one another. The patches of saltmarsh at Empire Bay were larger (ca. 0.3–1 ha) than those at Davistown (ca. 0.1 ha). Adjacent fringing mangrove stands, which consisted primarily of *Avicennia marina*, were also present within both areas. Each location was generally inundated once a month for 9 mo of the year during spring tide events.

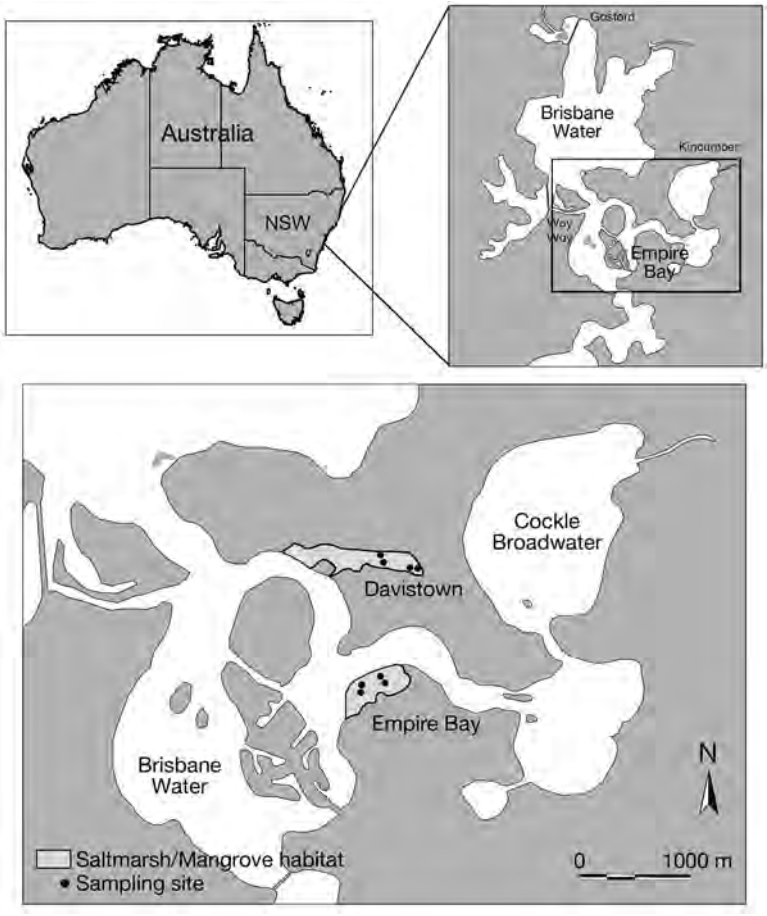


Fig. 1. Saltmarsh areas within Brisbane Water sampled during the study

Sampling methods

Pit traps (Salmon & Hyatt 1983) were used to sample shore crabs residing in saltmarsh habitat during the spring high tide in August 2009. Four traps were placed within each of 4 sites at each location (i.e. Empire Bay and Davistown), giving a total of 8 sites with 32 traps. To gain an understanding of the differences in isotopic signatures of shore crabs residing within different vegetation types, 2 of the 4 sites at each location were positioned within *Sporobolus virginicus*, whilst the other 2 sites were situated within *Sarcocornia quinqueflora*. On collection, crabs from the 4 pit traps at each site were combined and approximately 5 individuals of each of the 2 common species (*Paragrapsus laevis* and *Helograpsus haswellianus*) were collected where possible, placed into labelled jars and put into an ice slurry for further processing.

In addition to the collection of shore crab samples, potential food sources that consisted of various autotrophs present within saltmarsh habitat were collected for isotopic analyses. As it has been shown that plant species from saltmarsh habitat (i.e. *Sacrocornia quinqueflora*, *Sporobolus virginicus* etc.) have relatively low variability in $\delta^{13}C$ values over a range of spatial scales (Guest & Connolly 2005, Guest et al. 2006), only 3 replicate plant samples were taken of both *S. quinqueflora* and *S. virginicus* at each of the 2 locations (Empire Bay and Davistown). Three replicate sediment samples (which were later partitioned into FBOM and MPB) were collected from each of the 8 sites that were sampled for shore crabs. The plant samples were collected by cutting the vegetation at the base of the plant, whilst the sediment was collected by scraping off the top 1 cm layer of sediment (Melville & Connolly 2003) in an area approximately 20 × 20 cm from the saltmarsh surface.

Laboratory processing

Each shore crab was thoroughly rinsed with de-ionised water prior to processing. Muscle tissue was collected from the claws of the shore crabs, with care being taken not to include any hard shell fragments. Where possible, each replicate sample was taken from a single crab, although on some occasions where individual crabs were small, 2 crabs were used to make a single replicate. In general, 3 replicate crab samples of each species (i.e. *Paragrapsus laevis* and *Helograpsus haswellianus*) were obtained for each of the 8 sites, although at some sites a full complement of crab samples was unable to be achieved due to the low numbers of crabs collected.

Plant samples were thoroughly rinsed with de-ionised water prior to processing. Leaves were cut from the plant and placed into labelled Petri dishes ready for drying. Only leaf matter from each plant was used in each replicate.

Sediment samples were processed by separating out the FBOM and MPB from the entire sediment. Each sediment sample was firstly halved, with one half being used for FBOM samples and the other half used for MPB samples.

FBOM was separated from the entire sample by firstly rinsing the sediment through a series of sieves (0.25, 0.5, 1 and 4 mm) and then elutriating only the

0.25 mm sieve fraction to obtain the FBOM samples similar to the method of Saintilan & Mazumder (2010). A small quantity of 1 M hydrochloric acid was added to each FBOM sample and left for 3 h to remove any inorganic carbon present in the sediment (Polunin et al. 2001). The samples were then rinsed with de-ionised water and placed into labelled jars ready for drying. Because this acid-washing process results in enrichment of $\delta^{15}N$ (Pinnegar & Polunin 1999), untreated FBOM samples were analysed for $\delta^{15}N$. The treated acid-washed samples of FBOM were analysed for $\delta^{13}C$.

MPB was separated by first rinsing the sediment through 63 µm mesh to remove any infauna present within the sediment. Material passing through this mesh was then placed into jars and left to settle out. Once this had occurred, the top layer of water in each jar was decanted and 15 ml of the remaining sediment slurry was transferred to a centrifuge tube with 15 ml of colloidal silica (LUDOX™ AM30, density = 1.21) and centrifuged at 10 000 rpm (11 963 × *g*) for 10 min similar to the method of Guest et al. (2004). The band of materials (MPB) that formed at the top of the tube was then rinsed onto a glass fibre filter with de-ionised water. Any MPB material retained on the filter was carefully scraped into a labelled Petri dish ready for drying. It should be noted that not all MPB samples were able to be obtained as some samples, especially those from Davistown, generally had very little MPB present within the sediment.

All samples obtained (crab, plant, FBOM and MPB) were dried for 48 h at 50°C and ground to a fine powder before being weighed and placed into tin capsules ready for isotopic analyses. Samples were analysed using a continuous-flow stable isotope mass spectrometer (CF-IRMS, IsoPrime GV Instruments). The standard for carbon was BDH AnalaR Sucrose from cane sugar calibrated against Australian National University Sucrose (IAEA-C6). The standard for nitrogen was BDH AnalaR Ammonium Sulphate calibrated Ambient air and IAEA-Stable isotope values were reported in delta (δ) units in parts per thousand (‰) relative to the international standard and determined as follows:

$$X(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000 \quad (1)$$

where $X = \delta^{13}C$ or $\delta^{15}N$, and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$, respectively.

The full experimental design of the study, including the number of replicates that were collected/processed, is shown in Fig. 2.

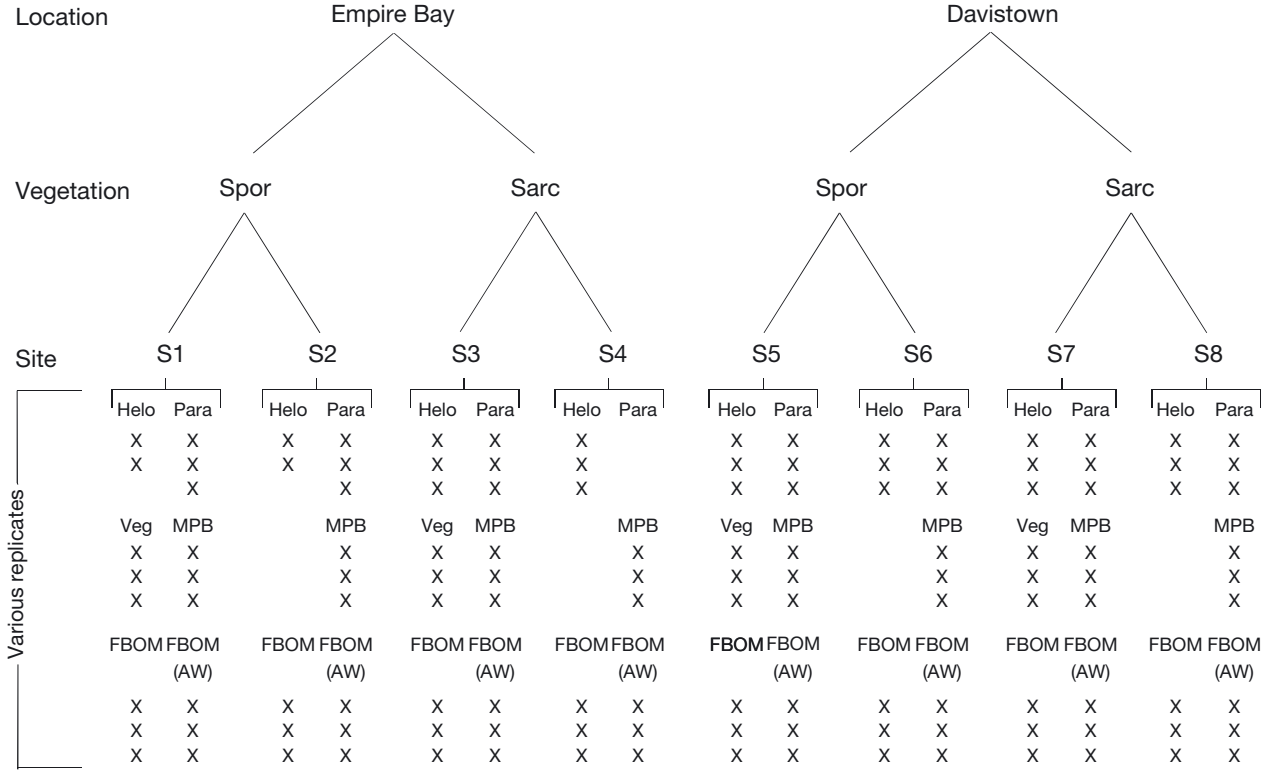


Fig. 2. Sampling design used throughout the study. Spor: *Sporobolus virginicus*; Sarc: *Sarcocornia quinqueflora*; Helo: *Helograpsus haswellianus*; Para: *Paragrapsus laevis*; Veg: vegetation; MPB: microphytobenthos; FBOM: fine benthic organic matter; AW: acid-washed

Statistical methods

Multifactorial permutational analysis of variance (PERMANOVA) was used to investigate the spatial variability of the various isotopic signatures obtained during the study. The advantages of this approach over traditional ANOVA are that there is no assumption that the data are normally distributed, and the test is not affected by unbalanced designs (i.e. different numbers of sites/replicates in different factors of the design). Furthermore, these analyses provide exact tests (i.e. the probability of rejecting the null hypothesis is the same as the value for alpha, which is conventionally 0.05) for each level in an experimental design and do not rely on interpolations from tabled values of *F* (Anderson et al. 2008).

Preliminary analyses of the data suggested that the factor of Site showed little variability in many of the variables analysed, often showing $p > 0.25$. In addition, not all compliments of samples could be obtained at each site for crabs and MPB. Therefore, to allow for a simpler interpretation of the analyses, it was decided that replicates from each site be effectively 'pooled' together and the factor of Site excluded from the analyses for all variables (i.e. crabs, MPB and FBOM). As vegetation samples were only collected from 1 site per vegetation type within each location, the factor of Site was already redundant in the analyses involving vegetation.

For crab isotope signatures, a 3-factor PERMANOVA was used to examine differences in crab isotopic signatures between locations, vegetation types and different crab species. For all autotrophs collected during the study (i.e. vegetation, FBOM and MPB), a 2-factor PERMANOVA was used to statistically compare their isotopic signatures between locations and vegetation types. Each factor used in the experimental design and their various attributes for the analyses were:

- Location (fixed, orthogonal factor consisting of 2 levels: Empire Bay and Davistown)
- Vegetation (fixed, orthogonal factor consisting of 2 levels: *Sacrocornia quinqueflora* and *Sporobolus virginicus*)
- Crab (fixed, orthogonal factor consisting of 2 levels: *Paragrapsus laevis* and *Helograpsus haswellianus*)

All analyses were univariate and were based on Euclidean distance matrices calculated by PRIMER v6 for Windows (PRIMER-E) using untransformed data. The variables analysed included $\delta^{13}C$ and $\delta^{15}N$ for crabs, vegetation, FBOM and MPB.

Where the p-value for a particular factor or interaction term was non-significant at a level greater than 0.25 (i.e. $p > 0.25$), the test was made more powerful by post-hoc pooling procedures (Winer et al. 1971, Anderson et al. 2008). When a significant result was achieved for an interaction term, post-hoc permutational *t*-tests were used (via PERMANOVA) to determine at which levels within the term these differences occurred at. Note that no pairwise tests were performed when Location, Vegetation or Crab were significant, as these factors only contained 2 levels, and thus no pairwise tests were required.

IsoSource mixing model

In addition to the above statistical analyses, a multiple-source mixing model (IsoSource; Phillips & Gregg 2003) was used to examine the relative contributions of potential food sources (autotrophs) to the diet of shore crabs (consumers) taken from Empire Bay and Davistown. This model attempts to calculate all possible combinations of the various potential food source contributions (as a percentage) in 1% increments, with combinations adding to within a pre-defined tolerance level of the consumer signature considered as feasible solutions.

Prior to any analyses, isotope signatures for autotrophs were corrected to allow for enrichment fractionation effects between trophic levels. $\delta^{13}C$ values were corrected for an enrichment of 0.4‰ and $\delta^{15}N$ values were corrected with a 2.3‰ enrichment value (McCutchan et al. 2003). All models were initially run with a tolerance level of 0.1‰, although when a solution was not obtained for a particular model, the tolerance level was increased incrementally by 0.05‰ until a solution was attained. This increase in the tolerance level was to help account for any uncertainty in the fractionation values used during each model run and the variability within consumer and producer isotope values (Currin et al. 2011).

Models were run for both crab species (*Paragrapsus laevis* and *Helograpsus haswellianus*) within each vegetation type (*Sacrocornia quinqueflora* and *Sporobolus virginicus*) at the 2 locations (Empire Bay and Davistown). For each of the 8 models, 3 potential food sources were included: the major vegetation from a particular patch (either *S. quinqueflora* or *S. virginicus* plant material depending on the type of habitat sampled), FBOM and MPB.

RESULTS

As expected, mean $\delta^{13}C$ values for *Sporobolus virginicus* plant material were significantly more enriched compared to those of *Sacrocornia quinqueflora* for both locations (Fig. 3); however, post-hoc pairwise tests detected significant differences in $\delta^{13}C$ for *S. quinqueflora* between Empire Bay and Davistown ($p = 0.0128$), which indicated isotope signatures for various vegetation types can vary within an estuary. *S. virginicus* was found to be significantly depleted in $\delta^{15}N$ compared to *S. quinqueflora* for both locations sampled (Table 1, Fig. 3).

A significant Location × Vegetation interaction was detected for FBOM $\delta^{13}C$ values (Table 1). FBOM and MPB collected from *Sporobolus* patches at Empire Bay were always more enriched in $\delta^{13}C$ than those collected from *Sarcocornia* patches at the same location (post-hoc pairwise $p = 0.0021$ for FBOM). This was in contrast to FBOM and MPB sampled from Davistown, with no distinct separation in $\delta^{13}C$ signatures between either patch types (Fig. 3).

Patterns for $\delta^{15}N$ values of FBOM and MPB were more consistent, with Location and Vegetation factors both showing a significant effects (Table 1). FBOM and MPB collected within *Sarcocornia* patches was always significantly enriched in $\delta^{15}N$ compared to FBOM and MPB in *Sporobolus* patches regardless of location (Fig. 3). In addition, mean $\delta^{15}N$ values for FBOM and MPB were always significantly enriched at Davistown compared to that at Empire Bay, irrespective of vegetation type (Fig. 3).

Helograpsus haswellianus was always significantly more enriched in $\delta^{13}C$ and $\delta^{15}N$ compared with *Paragrapsus laevis* sampled at the same location (Table 1, Fig. 2). Crabs of both species collected from Davistown were also always more enriched with $\delta^{15}N$ compared to Empire Bay (Table 1, Fig. 3). In addition, crabs sampled from *Sporobolus* patches were always more enriched in $\delta^{15}N$ compared to those collected from *Sarcocornia* patches regardless of location (Table 1, Fig. 3).

IsoSource mixing model results are presented in Table 2 for both locations. Both crab species collected from Empire Bay appeared to have similar diets, although the dominant source of food depended on the habitat type they were sampled from. MPB was clearly the dominant food source for both crab species residing within the *Sporobolus virginicus* habitat at Empire Bay, whereas FBOM contributed majorly to the diets of both crab species collected from *Sacrocornia quinqueflora* from the same location (Table 2).

In contrast, contributions from the various sources taken from Davistown were not as definitive as those from Empire Bay, with FBOM and MPB both contributing simultaneously to the diets of both crab species (Table 2). In addition, no clear patterns could be ascertained from the IsoSource results for either crab spe-

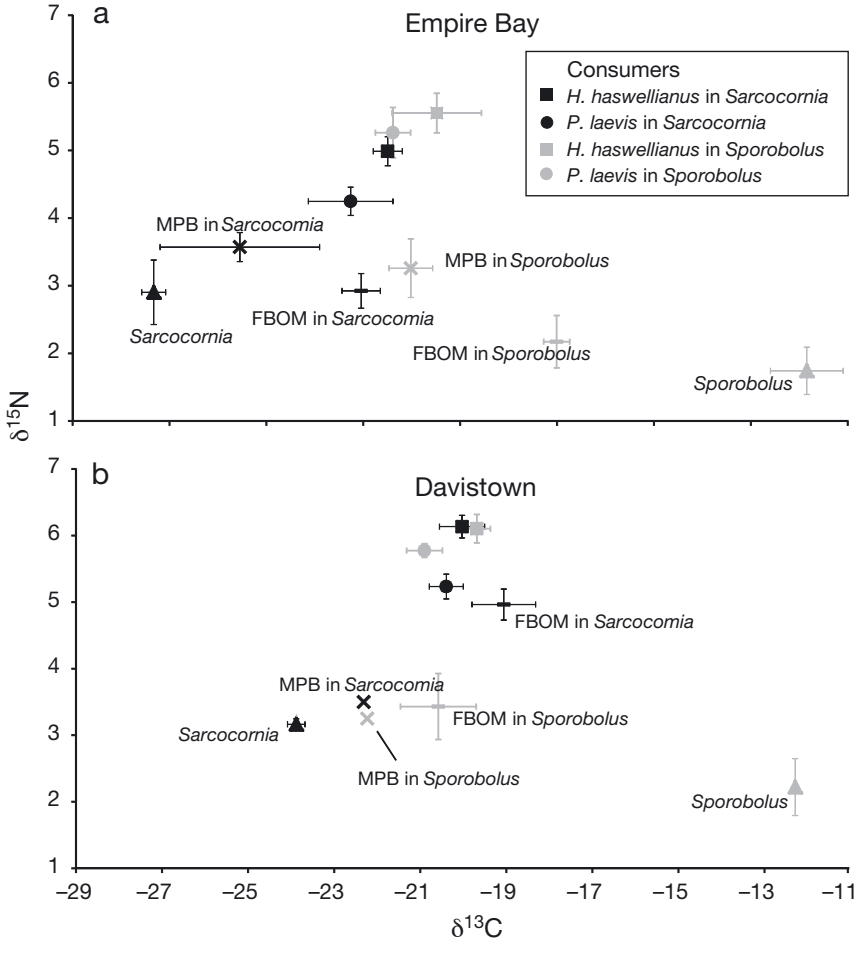


Fig. 3. Mean (±SE) $\delta^{13}C$ and $\delta^{15}N$ values for 2 species of shore crab (*Helograpsus haswellianus and Paragrapsus laevis*), 2 dominant vegetation types (*Sporobolus virginicus and Sarcocornia quinqueflora*), fine benthic organic matter (FBOM) and microphytobenthos (MPB) sampled from the (a) Empire Bay and (b) Davistown, Australia, saltmarshes

Table 1. Univariate PERMANOVA results for various isotope signatures sampled during the study. Significant factors ($p < 0.05$) are in **bold**. FBOM: fine benthic organic matter; MPB: microphytobenthos; LoxVe: Location/Vegetation interaction; VexCr: Vegetation/Crab interaction

(a) $\delta^{13}C$ Source of variation	df	MS	Pseudo-*F*	P(perm)
Crab				
Location	1	0.277	0.241	0.628
Vegetation	1	1.925	1.679	0.204
Crab	**1**	**6.857**	**5.980**	**0.020**
LoxVe	1	2.714	2.367	0.135
Pooled	38	1.147		
Vegetation				
Location	1	0.750	1.503	–
Vegetation	1	471.540	945.690	–
LoxVe	**1**	**2.667**	**5.348**	**0.046**
Residual	8	0.499		
FBOM				
Location	1	0.025	0.006	–
Vegetation	1	13.544	3.480	–
LoxVe	**1**	**59.023**	**15.166**	**0.001**
Residual	20	3.892		
MPB				
Location	1	7.444	2.699	0.132
Vegetation	**1**	**17.819**	**6.461**	**0.020**
Pooled	12	2.758		

(b) $\delta^{15}N$ Source of variation	df	MS	Pseudo-*F*	P(perm)
Crab				
Location	**1**	**6.721**	**23.782**	**0.000**
Vegetation	**1**	**2.935**	**10.386**	**0.002**
Crab	**1**	**3.419**	**12.099**	**0.001**
LoxVe	1	0.799	2.826	0.106
VexCr	1	0.715	2.529	0.123
Pooled	37	0.283		
Vegetation				
Location	1	0.410	1.130	0.309
Vegetation	**1**	**3.320**	**9.149**	**0.023**
Pooled	9	0.363		
FBOM				
Location	**1**	**16.319**	**20.903**	**0.000**
Vegetation	**1**	**7.825**	**10.024**	**0.005**
Pooled	21	0.781		
MPB				
Location	**1**	**43.402**	**9.015**	**0.011**
Vegetation	**1**	**40.840**	**8.483**	**0.016**
LoxVe	1	7.282	1.513	0.234
Residual	11	4.815		

Table 2. Range of feasible contributions (%) of various potential food sources to *Helograpsus haswellianus* and *Paragrapsus laevis* sampled from different vegetation types at Empire Bay and Davistown, Australia, based on $\delta^{13}C$ and $\delta^{15}N$ isotope values as determined by IsoSource (Phillips & Gregg 2003). Minimum tolerance values that provided a solution for each model run are also indicated. FBOM: fine benthic organic matter; MPB: microphytobenthos

Habitat	Producer	Empire Bay				Davistown			
		H. haswellianus		*P. laevis*		*H. haswellianus*		*P. laevis*	
		Median	1^{st}–99^{th} percentile	Median	1^{st}–99^{th} percentile	Median	1^{st}–99^{th} percentile	Median	1^{st}–99^{th} percentile
Sarcocornia	*S. quinqueflora*	0	0–2	19	0–36	5	0–15	4	0–12
	FBOM	98	97–100	79	61–99	50	46–53	23	20–25
	MPB	1	0–3	2	0–5	45	32–54	73	63–80
	Tolerance (‰)	0.25		1		0.4		0.9	
Sporobolus	*S. virginicus*	1	0–2	0	0–0	2	2–2	2	0–4
	FBOM	3	0–7	0	0–1	96	95–99	46	29–67
	MPB	96	93–99	99	99–100	1	0–3	52	32–67
	Tolerance (‰)	0.10		0.80		0.40		0.20	

cies taken from the 2 types of saltmarsh vegetation from this location.

Modelling results suggested that fresh plant material contributed very little to the diets of crabs sampled from both locations, although results suggest that *Sacrocornia quinqueflora* did contribute nearly 20% to the diet of *Paragrapsus laevis* collected from this vegetation type at Empire Bay (Table 2).

DISCUSSION

Previous studies have demonstrated the limited foraging range of crabs in intertidal environments (Guest et al. 2006). A capture-recapture experiment demonstrated that grapsid crabs rarely moved more than 2 m from their burrow, a behaviour possibly associated with burrow defence, and common

amongst grapsids (Fratini et al. 2000, Skov & Hartnoll 2002). Given this behaviour, it is possible to utilise the fine-scale mosaic of C_3 and C_4-dominated vegetated habitats in the intertidal saltmarsh to test hypotheses concerning the relative importance of plant and algal sources to crab diets. The study tests both the proportional contribution of macrophytic and microphytic nutritional sources, and the spatial scale over which these sources are likely to be accessed for 2 species of intertidal burrowing crab.

The consistent enrichment of crab signatures where collected from patches of the C_4 grass *Sporobolus virginicus* suggests the contribution of carbon fixed by this species. The importance of *S. virginicus* to saltmarsh crab diet has been previously argued by Guest et al. (2006), and Saintilan & Mazumder (2010). However, the presence of *S. virginicus* as a dominant vegetation type could be influencing the isotope signature of the microphytobenthos, by contributing to the local pool of dissolved inorganic carbon (DIC). This hypothesis has been suggested by Guest et al. (2006) in explaining the slight depletion of MPB signatures in mangrove forests in Queensland. Given that both *S. virginicus* and FBOM were too highly enriched in $\delta^{13}C$ to be contributing directly to crab diet at Empire Bay, the enrichment observed in crab $\delta^{13}C$ might have been due to the enrichment of MPB with carbon originally fixed by *S. virginicus*. This was not the case in the smaller *Sporobolus* patches at Davistown, suggesting that a patch size threshold exists before the enriched DIC can be distinguished in MPB from the background DIC originating from the relatively depleted *Sarcocornia* and the mangrove *Avicennia marina*, which fringes the estuary.

The possibility of a secondary influence of macrophyte isotopic signatures mediated through aquatic microphytes incorporating DIC should present a note of caution in the interpretation of aquatic foodwebs, and in this case, depletion of crab signatures across *Sporobolus viriginicus* saltmarsh is primarily due to MPB according to our IsoSource modelling.

In general, crabs were selecting the food source of greatest nutritional value, as indicated by C:N ratios. The contribution of living plant material was minimal at all sites reflecting the high C:N ratio of *Sacrocornia quinqueflora* and *Sporobolus virginicus* (average 22.9 and 25.1, respectively). In the *S. virginicus* habitat at Empire Bay, crabs fed on MPB (mean C:N 7.6, compared with mean FBOM C:N 12.5). In the *S. quinqueflora* zone, preference switched to FBOM, which had the lower C:N ratio on average. In all other situations, MPB and FBOM C:N ratios were equivalent, and crabs utilised both sources.

However, we cannot exclude differences in the availability of MPB as a potential explanation in the utilisation of this source. Several of our sites had little measurable MPB, and while crabs do not by their grazing exhaust availability of MPB (Ribeiro & Iribarne 2011), they may encounter fluctuating density of MPB in the upper intertidal zone with seasonal, tidal and diurnal phases (Reinsel 2004, Ribeiro & Iribarne 2011) that may differ between habitats and sites. Regional differences in the relative contribution of algal and detrital sources to crab diet have been recorded elsewhere, and are a notable distinction between east and west coast US coastal ecosystems (Kwak & Zedler 1997). The result suggests that in temperate Australian locations crabs feed primarily on FBOM and MPB rather than fresh plant material in saltmarsh, in common with mangrove (Mazumder & Saintilan 2010), and in contrast to crabs in mangrove and saltmarsh in subtropical and tropical estuaries (Lee 1998, Guest et al. 2004, Nordhaus et al. 2011). For example, Oakes et al. (2010) used isotope enrichment to demonstrate that MPB contributed one-third of the nutrition requirements of *Parasesarma erythrodactyla* and mangrove leaf detritus up to 80% in a subtropical Australian mangrove forest.

The 2 crab species sampled play an important role in the saltmarsh and associated estuarine ecosystem, transforming autotrophic carbon into forms available to a range of consumers (Mazumder et al. 2009). Larval outwelling from the saltmarsh during spring tidal phases contributes substantially to the diet of several species of estuarine fish (Hollingsworth & Connolly 2006, Mazumder et al. 2006) including several of commercial importance. The relative importance of macrophytic and microphytic carbon to these ecosystem processes is an important consideration in ecosystem management and the setting of restoration targets, and is likely to vary between geographic settings (Tue et al. 2012). We propose that assessment and modelling of these contributions will depend on an improved understanding of transfers of dissolved inorganic carbon between autotrophs, aided by the application of additional tracers (Melville & Connolly 2003, Fry 2013).

Acknowledgements. D. Tome, R. Slingsby, D. Baird-Bower and F. Erskine assisted with the collection of field samples. J. Iles and R. Diocares provided advice on the preparation of samples for stable isotope analyses. Dr. S. Hollins supported the isotopic analyses of samples. Crab samples were collected under NSW Scientific Collection Permit P07/0122-2.0. The research was supported by an Australian Postgraduate Award (Industry) to B.A.

LITERATURE CITED

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Bouillon S, Koedam N, Raman A, Dehairs F (2002) Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130:441–448

Bouillon S, Connolly RM, Lee SY (2008) Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J Sea Res 59:44–58

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. Global Biogeochem Cycles 17:1111, doi:10.1029/2002GB001917

Currin CA, Levin LA, Talley TS, Michener R, Talley D (2011) The role of cyanobacteria in Southern California salt marsh food webs. Mar Ecol 32:346–363

Dye AH, Lasiak TA (1986) Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical mangrove sediment. Mar Ecol Prog Ser 32:259–267

France R (1998) Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes. J Trop Ecol 14:413–425

Fratini S, Cannicci S, Vannini M (2000) Competition and interaction between *Neosarmatium smithi* (crustacea: Grapsidae) and *Terebralia palustris* (mollusca: Gastropoda) in a Kenyan mangrove. Mar Biol 137:309–316

Fry B (2013) Alternative approaches for solving underdetermined isotope mixing problems. Mar Ecol Prog Ser 472: 1–13

Giddins RL, Lucas JS, Neilson MJ, Richards GN (1986) Feeding ecology of the mangrove crab *Neosarmatium smithi* (crustacea: Decapode: Sesarmidae). Mar Ecol Prog Ser 33:147–155

Guest MA, Connolly RM (2005) Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. Aquat Ecol 38:599–609

Guest MA, Connolly RM, Loneragan NR (2004) Carbon movement and assimilation by invertebrates in estuarine habitats at a scale of metres. Mar Ecol Prog Ser 278: 27–34

Guest MA, Connolly RM, Lee SY, Loneragan NR, Breitfuss MJ (2006) Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement. Oecologia 148:88–96

Hollingsworth A, Connolly RM (2006) Feeding by fish visiting inundated subtropical saltmarsh. J Exp Mar Biol Ecol 336:88–98

Karsten U, West J (1993) Ecophysiological studies on six species of the mangrove red algal genus *Caloglossa.* Funct Plant Biol 20:729–739

Kneib RT (1997) The role of tidal marshes in the ecology of estuarine nekton. Oceanogr Mar Biol Annu Rev 35: 163–220

Kneib RT (2002) Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Springer, Dordrecht, p 267–291

Kwak TJ, Zedler JB (1997) Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia 110:262–277

Lee SY (1998) Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar Freshw Res 49:335–343

Lee SY (1999) Tropical mangrove ecology: physical and biotic factors influencing ecosystem structure and function. Aust J Ecol 24:355–366

Mazumder D, Saintilan N (2010) Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. Wetlands 30: 375–380

Mazumder D, Saintilan N, Williams RJ (2006) Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. Mar Freshw Res 57:193–199

Mazumder D, Saintilan N, Williams R (2009) Zooplankton inputs and outputs in the saltmarsh at Towra Point, Australia. Wetlands Ecol Manag 17:225–230

McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390

Melville AJ, Connolly RM (2003) Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136:499–507

Micheli F (1993) Feeding ecology of mangrove crabs in north eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii.* J Exp Mar Biol Ecol 171:165–186

Morgan S, Spilseth S, Page H, Brooks A, Grosholz E (2006) Spatial and temporal movement of the lined shore crab *Pachygrapsus crassipes* in salt marshes and its utility as an indicator of habitat condition. Mar Ecol Prog Ser 314: 271–281

Nordhaus I, Salewski T, Jennerjahn TC (2011) Food preferences of mangrove crabs related to leaf nitrogen compounds in the Segara Anakan lagoon, Java, Indonesia. J Sea Res 65:414–426

Oakes JM, Connolly RM, Revill AT (2010) Isotope enrichment in mangrove forests separates microphytobenthos and detritus as carbon sources for animals. Limnol Oceanogr 55:393–402

Odum EP (1968) Evaluating the productivity of coastal and estuarine water. Proceedings of the Second Sea Grant Conference, University of Rhode Island, Newport, RI, p 63–64

Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261–269

Pinnegar JK, Polunin NVC (1999) Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implications for the study of trophic interactions. Funct Ecol 13:225–231

Polunin NVC, Morales-Nin B, Pawsey WE, Cartes JE, Pinnegar JK, Moranta J (2001) Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. Mar Ecol Prog Ser 220:13–23

Reinsel KA (2004) Impact of fiddler crab foraging and tidal inundation on an intertidal sandflat: season-dependent effects in one tidal cycle. J Exp Mar Biol Ecol 313:1–17

Ribeiro PD, Iribarne OO (2011) Coupling between microphytobenthic biomass and fiddler crab feeding. J Exp Mar Biol Ecol 407:147–154

Robertson AI (1986) Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. J Exp Mar Biol Ecol 102:237–248

Robertson AI, Daniel PA (1989) The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. Oecologia 78:191–198

Rodelli MR, Gearing JN, Gearing PJ, Marshall N, Sasekumar A (1984) Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. Oecologia 61:326–333

Saintilan N, Mazumder D (2010) Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. Mar Freshw Res 61:615–620

Salmon M, Hyatt GW (1983) Spatial and temporal aspects of reproduction in North Carolina fiddler crabs (*Uca pugilator bosc*). J Exp Mar Biol Ecol 70:21–43

Skov M, Hartnoll R (2002) Paradoxical selective feeding on a low-nutrient diet: Why do mangrove crabs eat leaves? Oecologia 131:1–7

Teal JM (1962) Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614–624

Tue NT, Hamaoka H, Sogabe A, Quy TD, Nhuan MT, Omori K (2012) Food sources of macro-invertebrates in an important mangrove ecosystem of Vietnam determined by dual stable isotope signatures. J Sea Res 72:14–21

Winer B, Brown D, Michels K (1971) Statistical principles in experimental design. McGraw-Hill, New York, NY

Editorial responsibility: Steven Morgan, Bodega Bay, California, USA

Submitted: August 7, 2012; Accepted: March 12, 2013
Proofs received from author(s): July 10, 2013

Wetlands Ecology and Management (2005) 13: 457–467
DOI 10.1007/s11273-004-0814-2
© Springer 2005

Temporal variations in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia

Debashish Mazumder[1,*], Neil Saintilan[2] and Robert J. Williams[3]
*[1]Institute for Nuclear Geophysiology, Australian Nuclear Science and Technology Organisation (ANSTO), PMB 1, Lucas Heights, Menai 2234, New South Wales, Australia; [2]Centre for Environmental Restoration and Stewardship, Australian Catholic University, Mackillop Campus, North Sydney, P.O. Box 968, NSW 2059, Australia; [3]New South Wales Fisheries, 202 Nicholson Pde, Cronulla, NSW 2230, Australia; *Author for correspondence (e-mail: debashish.mazumder@ansto.gov.au)*

Received 11 November 2003; accepted in revised form 21 June 2004

Abstract

Fish assemblages utilising saltmarsh and mangrove during spring tides were surveyed over a 12-month period using buoyant pop nets. A total of 48 net releases in the saltmarsh identified 16 species, at a density of 0.56 fish m^{-2}, with six species being of commercial importance. The same number of releases within the mangrove collected a total of 23 species at a density of 0.76 fish m^{-2}. However, fish density was higher within the saltmarsh than the adjacent mangrove when corrected for water volume. Multidimensional scaling revealed different assemblages of fish in the two habitats, with higher numbers of *Ambassis jacksoniensis* and *Pseudomugil* sp. in the saltmarsh and higher numbers of *Mugilogobius* sp. and *Acanthopagrus australis* in the mangrove. The result suggests a potentially significant role for saltmarsh as a fish habitat in the estuaries of southeast Australia.

Introduction

Considerable evidence has demonstrated the association of mangrove and tidal creeks with juvenile fish and an inferred role of the former as nursery habitats in Australia (Gibbs 1985; Morton et al. 1988; Morton 1990; Saenger 1994; Blaber et al. 1995; Laegdsgaard and Johnson 1995; Halliday and Young 1996; Williams et al. 1996). These habitats provide a source of food for fish, prawns and crabs (Bell et al. 1984; Robertson and Duke 1987, 1990; Vance et al. 1990). In contrast, very little is known about the fish associated with Australian saltmarsh, which typically occurs landward of mangrove forests and higher in the inter-tidal zone, and consequently have shorter and less frequent periods of inundation (Thomas and Connolly 2001). To date most of our knowledge of fish communities in saltmarsh is gained from investigations in the USA (Talbot and Able 1984; Kneib and Wagner 1997) and Europe.

The few saltmarsh investigations conducted in Australia have considered the presence of fish in creeks rather than on the flats. Studies have been done on the abundance of juveniles of economically important species in tropical Australia (Davis 1988), in a tidal inlet adjacent to a saltmarsh in the subtropical region of southeast Queensland (Morton et al. 1987) and in a saltmarsh creek in Wallis Lake in temperate Australia (Gibbs 1986). When the flats *per se* were sampled, Connolly et al. (1997) recorded only 19 individuals from two species sampled from temperate saltmarsh in the Barker Inlet – Port River estuary, South Australia. Surveys from flats in subtropical Queensland provide a contrast, with 23 species taken during spring tides, with economically important species contributing substantially to the catch (Thomas

and Connolly 2001). No studies have been reported between these latitudinal extremes for southeastern Australia.

In the present study we compared fish catch on saltmarsh flat and adjacent mangrove at Towra Point, Botany Bay. The study area is mid-way between the surveys of Connolly et al. (1997) and Thomas and Connolly (2001). The primary aim of the research was to test the popular assumption that mangroves support a higher richness and abundance of nekton than saltmarsh when both are flooded. The study is of additional significance in that the area of saltmarsh in New South Wales is in decline due to encroachment by mangrove (Saintilan and Williams 1999, 2000). Saltmarsh is not protected under the Fisheries Management Act (1994), which protects mangrove to the mean high water mark.

Methods

Study site

The study compared temporal variation of nekton catch in mangrove and saltmarsh flats at Towra Point Nature Reserve, in Botany Bay (Figure 1). The reserve is a relatively undisturbed sandy marine delta with mangrove forest dominated by *Avicennia marina* (McGuinness 1990). The lower saltmarsh was dominated by a *Sarcocornia quinqueflora*/*Sporobolus virginicus* association, with *Triglochin striata* growing in less well-drained positions. *Juncus krausii* and *Suaeda australis* were also present in higher elevation environments (Clarke and Hannon 1967; Adam et al. 1988). Inundation of the saltmarsh occurs normally during Spring tides and sometimes when there are extended wet weather conditions. The marsh is inundated through breaks in a natural levee bank that creates a sharp boundary between the mangrove and saltmarsh along most of the Woolooware Bay side of the wetland.

Fish collection

Buoyant pop nets (Michael et al. 1989; Connolly 1994) were employed in the saltmarsh and adjacent mangrove flats to sample fish during the spring tide. The pop nets are 5.5 m square, elevating to a maximum height of 1.5 m, with nylon mesh of 0.6 mm. The top of the mesh was attached to 20 mm diameter PVC pipe, sealed for floatation. The base of the net was secured tightly to the marsh surface using tent pegs, with the nets hidden prior to release inside shallow trenches. Nets were weighed down with four concrete blocks attached with nylon rope to a remote point approximately 30 m from the nets. The net was released from this remote point at the peak of the tide. Four replicate pop nets were set in saltmarsh and four replicate pop nets in the mangrove forest. Nets were placed randomly in the lower saltmarsh (*Sarcocornia*/*Sporobolus* zone), and randomly in the mangrove zone. Fish samples were collected monthly during spring high tides (>1.8 m) from March 2001 to February 2002 when saltmarsh flats as well as mangrove were inundated by tidal water. Water temperature, tide height and time of sampling were recorded.

Statistical methods

Univariate analysis (ANOVA) and *post hoc* Student–Newman–Kuels (SNK) tests were performed using GMAV5 (Underwood and Chapman 1989) to determine the significance of differences of fish abundance between saltmarsh and mangrove in different seasons. Two-way analyses of variance were used (Underwood 1997) with season as the first factor with four levels (1 = autumn; 2 = winter; 3 = spring and 4 = summer) which were orthogonal and fixed. Habitat was considered as second factor with two levels (1 = saltmarsh and 2 = mangrove) which were orthogonal and fixed. Margalef's index (d) $d=(S-1)/\log(N)$ (Margalef 1969) was used to determine species richness between and within habitats in different seasons.

Differences in assemblages of fish between saltmarsh and mangrove were examined using Bray–Curtis measures of dissimilarity (Bray and Curtis 1957) with square root transformed data. Non-metric multidimensional scaling (nMDS) plots were also used to demonstrate the patterns of fish assemblages in different seasons between habitats (Clarke and Warwick 2001). Multivariate techniques such as ANOSIM (Clarke and Warwick 2001) were used to test the statistical significance

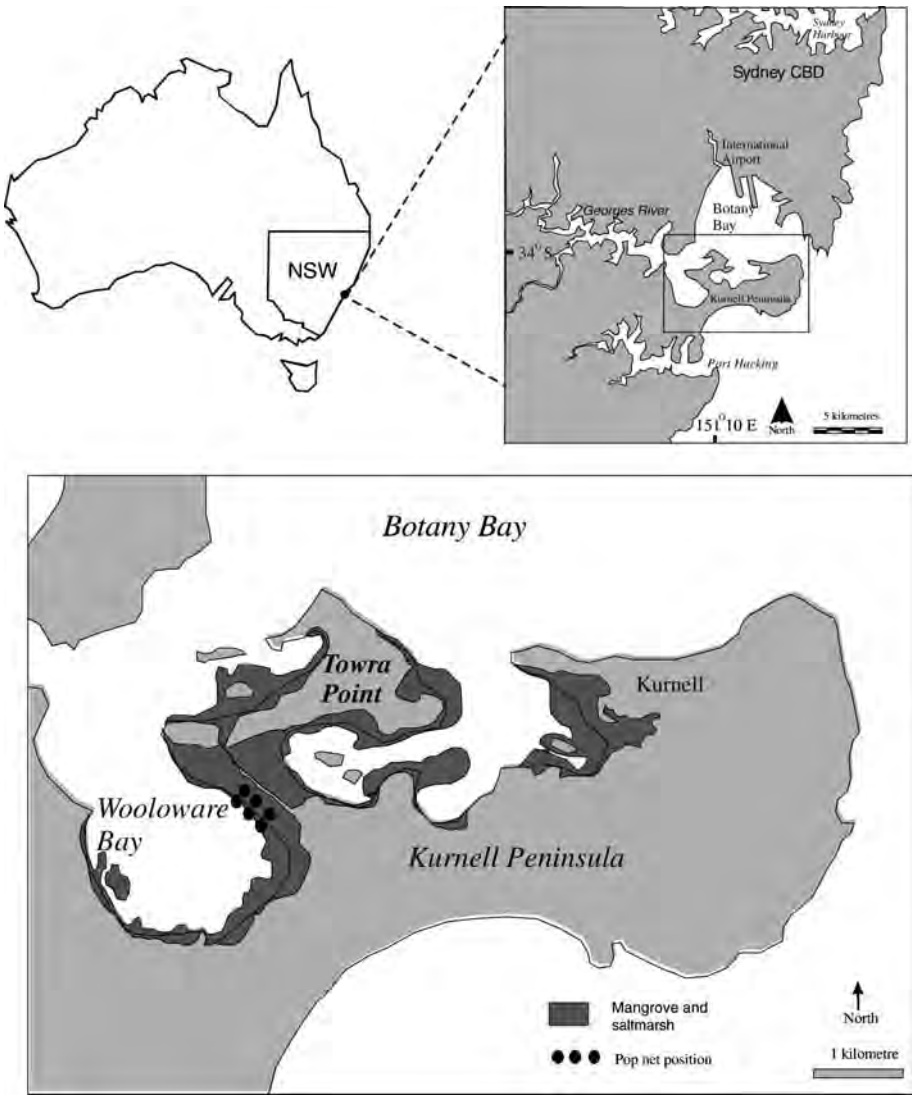


Figure 1. Map of Australia showing the location of study site, Towra Point, Botany Bay, Sydney, NSW.

of differences between the fish assemblages of habitats. The contribution made by particular species to differences in species assemblages was determined using SIMPER (similarity percentages-species contribution, Clarke and Warwick 2001) for habitats.

Links between environmental variables and fish assemblages were explored using BIOENV (Clarke and Warwick 2001) in saltmarsh. Cyclicity in the distribution of monthly samples in mangrove and saltmarsh was tested using the RELATE procedure in Primer Version 5 (Clarke and Warwick 2001).

Results

Twenty-six species of fish were caught at the study site, 16 species from the saltmarsh and 25 species from the mangrove (Table 1). *Ambassis jacksoniensis* was most abundant species in the saltmarsh contributing 43.0% of the total catch by number, followed by *Gobiopterus semivestitus* (18.7%), *Pseudomugil signifer* (9.3%) and *Gerres subfasciatus* (6.6%). Six of the 16 species found in the saltmarsh were of commercial significance, whereas within the mangrove, 12 of 25 species were of commercial significance. *A. jacksoniensis*

Table 1. Species caught from saltmarsh and mangrove with pop nets at Towra Point 2001–2002.

Family	Genus/species	Common name	% Contribution to catch									
			Autumn (March–May)		Winter (June–August)		Spring (Sept.–Nov.)		Summer (Dec.–Feb.)		All season	
			Salt.	Mang.	Salt.	Mang.	Salt.	Mang.	Salt.	Mang.	Salt.	Mang.
Finfish												
Atherinidae	*Pseudomugil signafer*	Blue eye	8.40	0.00	25.45	4.35	4.41	3.55	1.60	1.90	9.29	2.33
Gobiidae	*Pseudogobius olorum*	Blue spot goby	0.00	0.00	0.00	10.14	0.98	4.86	25.13	7.58	5.99	4.38
Gobiidae	*Arenigobius bifrenatus*	Bridled goby	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.90	0.00	0.63
Gobiidae	*Mugilogobius stigmaticus*	Checkered mangrove goby	0.38	8.91	1.82	10.14	0.98	0.00	2.14	12.80	1.22	5.46
Tetraodontidae	*Tetractenos hamiltoni*	Common toad	0.00	0.00	0.00	1.45	2.54	0.00	0.53	2.37	0.73	0.54
Platycephalidae	*Platycephalus fuscus*	Dusky flathead*	0.00	0.00	0.61	4.35	0.49	0.00	3.74	2.84	1.10	0.81
Mugilidae	*Liza argenta*	Flat tail mullet*	0.00	1.32	0.00	1.45	1.47	3.36	1.07	1.90	0.61	2.42
Gobiidae	*Gobiopterus semivestitus*	Glass goby	4.20	6.27	15.76	11.59	46.56	5.61	11.23	0.00	18.70	5.10
Chandidae	*Ambassis jacksoniensis*	Glassfish	70.99	0.00	29.70	5.80	25.98	54.58	34.22	4.27	43.03	27.28
Bothidae	*Ammotretis rostratus*	Large toothed flounder*	0.00	0.00	0.00	0.00	0.00	1.50	0.00	0.00	0.00	0.72
Gobiidae	*Redigobius macrostoma*	Largemouth goby	0.00	0.00	0.00	2.90	0.00	0.93	0.00	0.00	0.00	0.63
Girellidae	*Girella tricuspidata*	Luderick*	0.00	0.00	0.00	4.35	0.00	1.87	0.00	0.00	0.00	1.16
Gobiidae	*Mugilogobius paludis*	Mangrove goby	0.00	38.28	3.03	24.64	2.54	12.52	2.14	8.53	1.71	19.50
Poeciliidae	*Gambusia holbrooki*	Mosquito fish	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.12	0.00
Mugilidae	*Myxus elongatus*	Sand mullet*	0.00	0.00	1.21	0.00	0.00	0.00	1.60	0.47	0.61	0.09
Sillaginidae	*Sillago clliata*	Sand whiting*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.74	0.00	0.89
Mugilidae	*Mugil cephalus*	Sea mullet*	0.00	0.00	0.00	0.00	1.47	0.00	0.00	0.95	0.37	0.18
Gerreidae	*Gerres subfasciatus*	Silver biddy*	11.38	23.76	3.64	0.00	0.98	0.19	8.02	18.96	6.60	10.11
Gobiidae	*Taenioides mordax*	Snake head goby	0.00	15.51	0.00	5.80	0.00	4.11	0.00	0.00	0.00	6.53
Sparidae	*Rhabdosargus sarba*	Tarwhine*	0.00	0.00	0.00	2.90	0.00	0.00	0.00	2.37	0.00	0.63
Teraponidae	*Pelates quadrilineatus*	Trumpeter*	0.00	2.64	0.00	0.00	0.00	0.00	0.00	2.84	0.00	1.25
Sparidae	*Acanthopagrus australis*	Yellow fin bream*	3.44	0.99	0.00	8.70	1.96	4.86	4.28	12.80	2.57	5.55
Crustaceans												
Alpheidae	*Alpheus edwardsi*	Common pistol shrimp	0.00	0.66	0.00	1.45	0.00	0.19	0.00	0.00	0.00	0.36
Atyidae	*Macrobrachium intermedium*	Grass shrimp	0.76	0.66	18.75	0.00	5.88	0.56	3.74	9.95	6.36	2.33
Penaeidae	*Metapenaeus macleayi*	School prawn*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.84	0.00	0.54
Total no. of species			7	11	9	15	14	15	14	18	16	25
Total no. of fish			262	303	165	69	204	535	187	211	818	1118
No. of fish m^{-2}			0.72	0.83	0.45	0.19	0.56	1.47	0.51	0.58	0.56	0.76

The asterisk (*) designates species of commercial and or recreational significance.

was also the most abundant species in mangrove and contributed 27.3% of the catch, followed by *Mugilogobius paludis* (19.5%), *G. subfasciatus* (10.1%) and *Taenioides mordax* (6.5%).

Seven species of fish (*A. jacksoniensis*, *P. signifer*, *G. semivestitus*, *Mugilogobius stigmaticus*, *M. paludis*, *G. subfasciatus*, and *Acanthopagrus australis)* and one crustacean species, *Macrobrachium intermedium*, were found in saltmarsh as well as mangrove through the year with varying abundance between seasons (Table 1). Abundances of these species were similar between environments.

Analysis of similarities (ANOSIM) for commercial species showed a significant difference (ANOSIM: $p < 0.01$) between saltmarsh and mangrove. Eight species of fish (*Pelates quadrilineatus*, *Sillago cilliata*, *Rhabdosargus sarba*, *Ammotretis rostratus*, *Girella tricuspidata*, *Redigobius macrostoma*, *Arenigobius bifrenatus* and *T. mordax)*, and two crustacean species (*Metapenaeus macleayi* and *Alpheus edwardsi)* were found only in mangrove over the 12-month sampling period (Table 1).

Some species exhibited seasonal variability in abundance, and overall a bimodal pattern of spring and autumn abundance was evident for many of the most common species (Figure 2). Abundances of *A. jacksoniensis* and *M. paludis* were high in autumn and spring while *G. subfasciatus* was abundant in autumn. A distinct peak abundance in the Spring was observed for *G. semivestitus* (Figure 2).

Fish abundance and species richness

ANOVA results showed that fish abundance within saltmarsh did not vary among seasons ($p = 0.81$, Table 2). Analysis of variance using Margalef's measure of species richness between seasons in saltmarsh showed no significance difference between seasons for species richness.

ANOVA results for fish abundance within mangrove showed that fish abundance differed significantly between seasons ($p < 0.01$, Table 3). The *post hoc* SNK test showed fish abundance in

Table 2. ANOVA results for fish abundance between seasons in saltmarsh using pop nets at Towra Point, Botany Bay, NSW: Cochran's test $C = 0.8285$.

Source of variation	DF	MS	*F*	*p*
Season	3	143.69	0.31	0.81
Residual	44	465.74		
Total	47			

Table 3. ANOVA results for fish abundance between seasons in mangrove using pop nets at Towra Point, Botany Bay, NSW: Cochran's test $C = 0.6004$.

Source of variation	DF	MS	*F*	*p*
Season	3	21.60	3.69	0.0188
Residual	44	5.86		
Total	47			

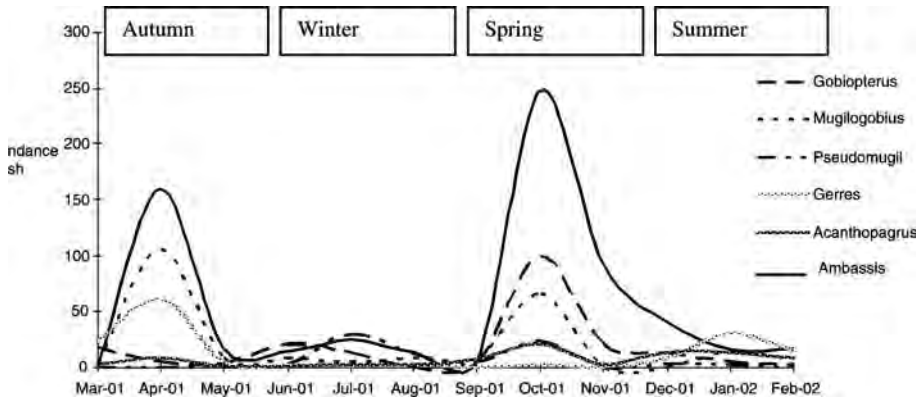


Figure 2. Abundance of most common fish on saltmarsh and on mangrove during Spring high tide at Towra Point using pop nets, March 2001–February 2002.

Table 4. Two way analysis results for fish abundance between seasons and habitats at Towra Point, Botany Bay, NSW: Cochran's test $C = 0.6373$.

Source of variation	DF	MS	F	p
Season	3	1965.02	2.08	0.109
Habitat	1	937.50	0.99	0.322
Season × habitat	3	1368.52	1.45	0.234
Residual	88	946.28		
Total	95			

winter significantly higher than spring. Fish abundance between autumn and winter, spring and summer, winter and summer, autumn and summer, autumn and spring were found not to vary significantly.

Analysis of variance using Margalef's measure of species richness between seasons in mangrove found no significant difference between seasons.

ANOVA results showed that fish abundance in saltmarsh and mangrove did not vary between seasons ($p = 0.10$) and no significant difference was found in fish abundance between habitats ($p = 0.32$, Table 4). The *post hoc* SNK test for fish abundance between saltmarsh and mangrove in different seasons showed fish abundance in spring in mangrove to be significantly higher than saltmarsh. Fish abundance between saltmarsh and mangrove in autumn, winter and summer were found not to vary significantly (Figure 3). The overall density of fish in saltmarsh and mangrove were 0.56 fish m^{-2} in saltmarsh and 0.76 fish m^{-2} for mangrove.

Fish assemblages in saltmarsh and mangrove

nMDS ordinations showed different assemblages of fish in saltmarsh and mangrove in all seasons (Figure 4).

Analysis of similarities (ANOSIM) shows that fish assemblages in saltmarsh and mangrove differed significantly in autumn (ANOSIM: $p < 0.001$), winter (ANOSIM: $p < 0.001$), spring (ANOSIM: $p < 0.004$) and summer (ANOSIM: $p < 0.001$). SIMPER analysis suggested the dissimilarity between the two habitats in autumn appears primarily due to the higher abundance of *A. jacksoniensis* in saltmarsh and its absence from the mangrove, and the presence of *M. paludis* and *T. mordax* in mangrove and their absence from the saltmarsh (Table 5). In winter the dissimilarity between the two habitats appears primarily due to the greater abundance of *A. jacksoniensis*, *P. signafer* and *M. intermedium* in saltmarsh than mangrove, and the presence *A. australis* in mangrove only. The dissimilarity between the two habitats in spring appears primarily due to the higher abundance of *G. semivestitus* in saltmarsh, and *A. jacksoniensis*, *M. paludis*, *T. mordax* and *G. tricuspidata* in the mangrove. In summer the dissimilarity appears primarily due to higher abundance of *A. jacksoniensis* and *Pseudogobius olorum* in saltmarsh, *G. subfasciatus*, *A. australis* and *M. stigmaticus* in mangrove and absence of *P. quadrilineatus* and *S. cilliata* in saltmarsh, respectively (Table 5).

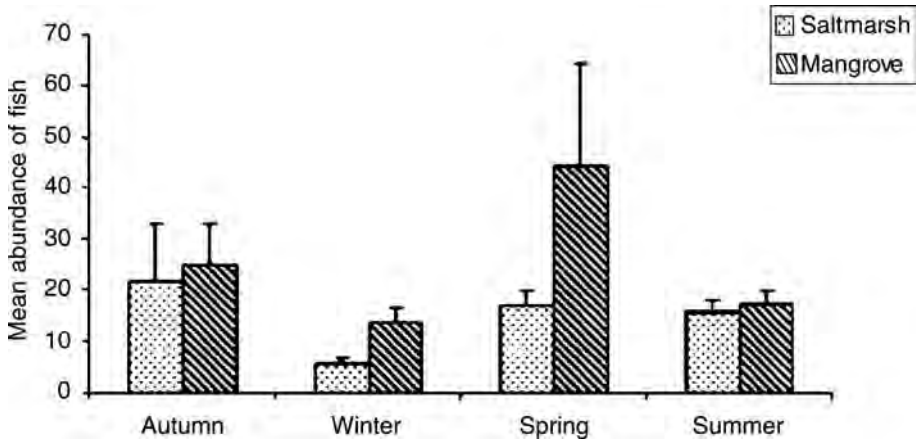


Figure 3. Mean abundance (+SE) of fish in Towra Point saltmarsh and mangrove in different seasons using pop nets, 2001–2002: $n = 96$.

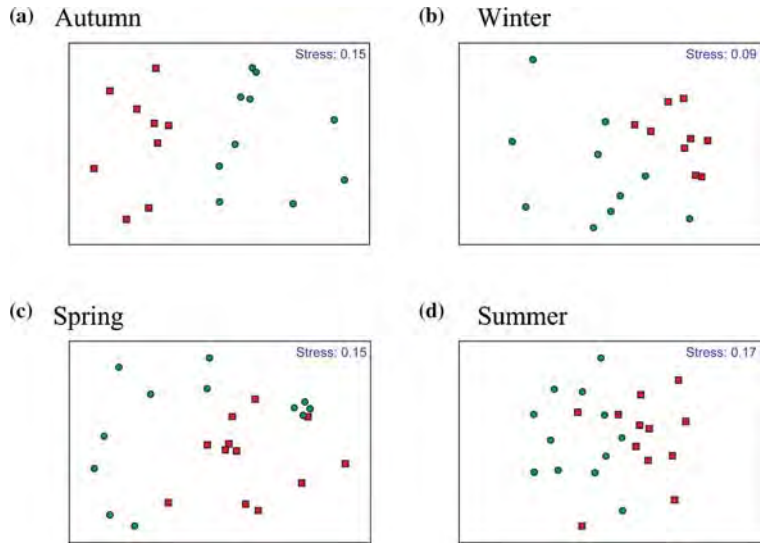


Figure 4. nMDS ordinations differentiating assemblages of fish in saltmarsh from those in mangrove in different seasons at Towra Point using pop nets.

Analysis of similarities (ANOSIM) for different seasons showed that the assemblages of fish in saltmarsh differed between autumn and winter (ANOSIM: $p < 0.049$), autumn and spring (ANOSIM: $p < 0.017$), winter and summer (ANOSIM: $p < 0.038$) and spring and summer (ANOSIM: $p < 0.029$). No significant difference was observed in fish assemblages within saltmarsh between autumn and summer (ANOSIM: $p > 0.256$) and winter and spring (ANOSIM: $p > 0.319$) (Table 6). Within the mangrove, differences in fish assemblages were found between all seasons, with the exception of autumn and summer ($p = 0.059$, Table 6).

The RELATE procedure in PRIMER tests for seriation in samples, determining whether consecutive samples are more similar than a random permutation of sample labels, and whether samples approach the original assemblage after (in this case) the annual cycle. The results of matched similarity matrices (RELATE) results for cyclicity in monthly catch through the year showed a significantly greater cyclicity than would be the case in a random distribution for saltmarsh ($p < 0.04$) as well as mangrove ($p < 0.003$) (Figure 5).

Biota and environmental matching (BIOENV) results for correlation between environmental variables and fish assemblages in saltmarsh showed no correlations between time of sampling and fish assemblages (weighted Spearman rank correlation $\rho = 0.100$), tide height and fish assemblages ($\rho = 0.096$) and temperature and fish assemblages ($\rho = 0.112$) or between any combination of these variables.

Discussion

The study has demonstrated that during spring tides the catch of fish in saltmarsh at Towra Point approaches that of adjacent mangrove. The mean density of the 16 species of fish caught in saltmarsh was 0.56 fish m^{-2} from 48 pop net releases. In a comparable study, Thomas and Connolly (2001) collected a total of 23 species from 134 pop net releases with density ranging up to 0.46 fish m^{-2} from the subtropical saltmarsh in Queensland. The nets used by Thomas and Connolly (2001) were smaller in size (25 m^2) than the nets used in the present study (30.25 m^2). The current study suggests a greater abundance but lower diversity of fish in the temperate saltmarsh of Towra Point compared with the subtropical saltmarsh in Queensland.

We found the density of fish to be slightly higher in mangrove (0.76 fish m^{-2}) than saltmarsh, The present study found 25 species of fish in mangrove among which 12 species were of the commercial importance. Several studies conducted in Austra-

Table 5. SIMPER analysis was used to derive the percent contribution of fish species to differentiation between saltmarsh and mangrove in different seasons using pop nets at Towra Point, Botany Bay, 2001–2002.

Species	Autumn, Saltmarsh *versus* Mangrove (ANOSIM: $p < 0.001$)			Species	Winter, Saltmarsh *versus* Mangrove (ANOSIM: $p < 0.001$)			Species	Spring, Saltmarsh *versus* Mangrove (ANOSIM: $p < 0.004$)			Species	Summer, Saltmarsh *versus* Mangrove (ANOSIM: $p < 0.001$)		
	Av. Abund salt.	Av. Abund mang.	% Contrib. to dissim.		Av. Abund salt.	Av. Abund mang.	% Contrib. to dissim.		Av. Abund salt.	Av. Abund mang.	% Contrib. to dissim.		Av. Abund salt.	Av. Abund mang.	% Contrib. to dissim.
Ambassis jacksoniensis	20.67	0.00	23.50	*A. jacksoniensis*	5.44	0.40	20.44	*A. jacksoniensis*	4.42	24.33	21.12	*A. jacksoniensis*	5.33	0.75	15.63
Mugilogobius paludis	0.00	11.60	20.32	*P. signafer*	4.67	0.30	13.80	*G. semivestitus*	7.92	2.50	16.87	*G. subfasciatus*	1.25	3.33	10.41
Pseudomugil signafer	2.44	0.00	4.87	*G. semivestitus*	2.89	0.80	12.28	*M. paludis*	0.42	5.58	8.05	*P. olorum*	3.92	1.33	9.29
Acanthopagrus australis	1.00	0.30	4.79	*M. intermedium*	3.44	0.00	10.70	*A. australis*	0.33	2.17	7.98	*A. australis*	0.67	2.25	8.63
Gobiopterus semivestitus	1.22	1.90	7.82	*M. paludis*	0.56	1.70	8.77	*T. mordax*	0.00	1.83	5.92	*G. semivestitus*	1.75	0.00	7.59
Gerres subfasciatus	3.44	7.20	14.26	*G. subfasciatus*	0.67	0.00	5.82	*L. argenta*	0.25	1.50	5.61	*P. quadrilineatus*	0.00	0.50	2.47
Taenioides mordax	0.00	4.70	4.89	*A. australis*	0.00	0.60	5.34	*G. tricuspidata*	0.00	0.83	3.78	*S. clliata*	0.00	0.83	2.97
Mugilogobius stigmaticus	0.11	2.70	8.27	*M. stigmaticus*	0.33	0.70	5.39	Unidentified sp.	0.67	0.58	5.43	*M. intermedium*	0.58	1.75	6.90
Macrobrachium intermedium	0.22	0.20	2.79	*P. olorum*	0.00	0.70	3.29	*P. signafer*	0.75	1.58	5.31	*M. paludis*	0.33	1.50	6.40
				P. fuscus	0.11	0.30	2.95	*P. olorum*	0.17	2.17	5.22	*P. fuscus*	0.58	0.50	4.74
				T. mordax	0.00	0.40	2.32	*M. intermedium*	1.00	0.25	3.21	*L. argenta*	0.17	0.33	3.11
								T. hamiltoni	0.42	0.00	2.60	*T. hamiltoni*	0.08	0.42	2.73
												R. sarba	0.00	0.42	2.55

Table 6. ANOSIM results for fish assemblages in different seasons within saltmarsh and mangrove at Towra Point, 2001–2002.

Season	Saltmarsh, significance level (%)	Mangrove, significance level (%)
Autumn *versus* Winter	4.9	2.5
Autumn *versus* Spring	1.7	0.1
Autumn *versus* Summer	25.6	5.9
Winter *versus* Spring	31.9	2.1
Winter *versus* Summer	3.8	2.7
Spring *versus* Summer	2.9	0.2

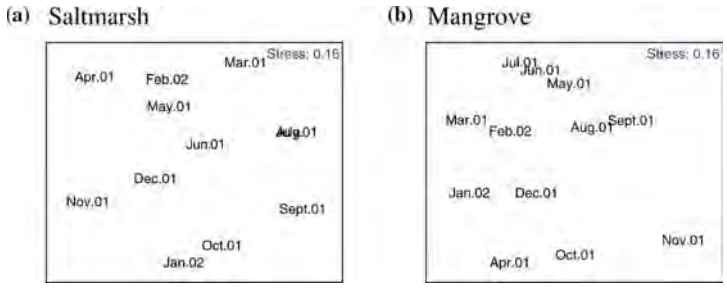


Figure 5. nMDS ordinations showing distribution of monthly fish assemblages in saltmarsh and mangrove at Towra Point using pop nets.

lian mangroves have suggested importance of this habitat (Blaber et al. 1985; Robertson and Duke 1987; Laegdsgaard and Johnson 1995) though these studies were concentrated in tropical and subtropical situations. Recently Clynick and Chapman (2002) surveyed fish in temperate mangroves and adjacent mudflats, revealing little difference in density.

The present study found seven species of fish in both saltmarsh and mangrove throughout the year, of which four families (Chandidae, Atherinidae, Gobiidae and Gerreidae) were dominant. This is similar to the findings of Bell (1984) who reported two of these families (Atherinidae, Gobiidae and Chandidae) as common in the fish community of temperate tidal mangrove creek in Botany Bay. Chandidae, Atherinidae, Gobiidae were common families among others in Alligator Creek, Lockhart River and Escape River in tropical Australia (Robertson and Duke 1987).

Thomas and Connolly (2001) found fish assemblages in subtropical saltmarshes in Queensland varied between winter and summer. A strong seasonal change in fish assemblages has also been reported by Morton et al. (1987) for subtidal creeks of saltmarshes, and by Rountree and Able (1993) for New Jersey polyhaline marsh creeks in the USA. The present study observed autumn and spring peaks in the abundance of many of the common species, including *A. jacksoniensis*, and *M. paludis*. Other common species showed peak abundance in either spring (*G. subfasciatus)* or autumn (*G. semivestitus*. Bell (1980) and Anon (1981) found recruitment of some juvenile species of fish to mangrove creek habitat when water temperatures are at maximum during summer. However, the present study found no correlation between fish assemblages and water temperature, or with sampling hour or tidal height. The cyclicity of fish assemblages in saltmarsh and mangrove suggests the assemblages approached their original composition after 12 months.

While a different assemblage of fish is found in saltmarsh compared to mangrove, there is little to distinguish the two habitats in terms of overall abundance and density of fish. Commercially important species were more likely to be found in the mangrove, though some were also found in the saltmarsh. The results strongly suggest that despite infrequent inundation by tides saltmarsh does play a role as a fish habitat and further protection is needed regarding the legislation and associated policies that protect this habitat.

Acknowledgements

The study was supported by the Australian Postgraduate Award (Industry), from the Australian Research Council (ARC), with support from New South Wales Fisheries (NSWF) and the New South Wales Department of Infrastructure Planning and Natural Resources (DIPNR). The National Parks and Wildlife Service provided access to the site. The authors also acknowledge the assistance of several field volunteers especially Kamal Hossain, Kerrylee Rogers, Swapan Paul, Abdul Halim Miah, and Rifat.

References

Adam P., Wilson N.C. and Huntley B. 1988. The phytosociology of coastal saltmarsh vegetation in New South Wales. Wetlands (Australia) 7: 35–84.

Anon. 1981. The ecology of fish in Botany Bay – biology of commercially and recreationally important species. State Pollution Control Commission of New South Wales. Report. No. BBS23B.

Bell J.D. 1980. Aspects of the ecology of fourteen economically important fish species in Botany Bay, New South Wales, with special emphasis on habitat utilisation and a decision of the effects of man-induced habitat changes. MSc thesis, Macquarie University.

Bell J.D., Pollard D.A., Burchmore J.J., Pease B.C. and Middleton M.J. 1984. Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. Aust. J. Marine Freshwater Res. 35: 33–46.

Blaber S.J.M., Young J.W. and Dunning M.C. 1985. Community structure and zoogeographic affinities of the coastal fishes of the Dampier Region of north-western Australia. Aust. J. Mar. Freshwater Res. 36: 247–266.

Blaber S.J.M., Brewer D.T. and Salini J.P. 1995. Fish communities and the nursery role of shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. Estuar. Coast. Shelf Sci. 40: 177–193.

Bray J.R. and Curtis J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325–349.

Clark L.D. and Hannon N.J. 1967. The mangrove swamp and saltmarsh communities of the Sydney district. I. Vegetation, soil and climate. J. Ecol. 55: 753–771.

Clarke K.R. and Warwick R.M. 2001. Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd ed. PRIMER-E, Plymouth, UK.

Clynick B. and Chapman M.G. 2002. Assemblages of small fish in patchy mangrove forest in Sydney Harbour. Mar. Freshwater Res. 53: 669–677.

Connolly M.R. 1994. Comparison of fish catches from a buoyant pop net and beach seine net in a shallow seagrass habitat. Mar. Ecol. Prog. Ser. 109: 305–309.

Connolly R.M., Dalton A. and Bass D.A. 1997. Fish use of an inundated saltmarsh flat in a temperate Australian estuary. Aust. J. Ecol. 22: 222–226.

Davis T.L.O. 1988. Temporal changes in the fish fauna entering a tidal swamp system in tropical Australia. Environ. Biol. Fish. 21: 185–194.

Gibbs P.J. 1985. The fauna and fisheries of Wallis Lake. Wallis Lake – present and future. Australian Marine Science Association (NSW Branch) and Coast and Wetland Society, Occasional paper series.

Gibbs P.J. 1986. The fauna and fishery of Wallis Lake. In: Wallis Lake: Present and Future. Occasional papers of the Australian Marine Science Association, Sydney, NSW, pp. 1–7.

Halliday I.A. and Young W.R. 1996. Density, biomass and species composition of fish in a subtropical *Rhizophora stylosa* mangrove forest. Mar. Freshwater Res. (Australia) 47(4): 609–615.

Kneib R.T. and Wagner S.L. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. Mar. Ecol. Prog. Ser. 106: 227–238.

Laegdsgaard P. and Johnson C.R. 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Mar. Ecol. Prog. Ser. 126: 67–81.

Margalef R. 1969. Perspectives in Ecological Theory. University of Chicago Press, Chicago.

McGuinness K.A. 1990. Effects of oil spills on macro-invertebrates and mangrove forests in Botany Bay, New South Wales, Australia. J. Exp. Mar. Biol. Ecol. 142: 121–135.

Michael R.D., Holland E.L. and Zigler J.S. 1989. Comparison of fish catches with buoyant pop nets and seines in vegetated and non-vegetated habitats. North Am. J. Fish. Manage. 9: 249–253.

Morton R.M. 1990. Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. Mar. Biol. 105: 385–394.

Morton R.M., Pollock B.R. and Beumer J.P. 1987. The occurrence and diet of fishes in a tidal inlet to a saltmarsh in southern Moreton Bay, Queensland. Aust. J. Ecol. 12: 217–237.

Morton R.M., Beumer J.P. and Pollock B.R. 1988. Fishes of a subtropical Australian saltmarsh and their predation upon mosquitoes. Environ. Biol. Fish. 21(3): 185–194.

Robertson A.I. and Duke N.C. 1987. Mangrove as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangrove and other near shore habitats in tropical Australia. Mar. Biol. 96: 193–205.

Robertson A.I. and Duke N.C. 1990. Mangrove fish communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. Mar. Biol. 104: 369–379.

Rountree R.A. and Able K.W. 1993. Diet variation in decapod crustacean and fish assemblages in New Jersey polyhaline marsh creeks. Estuar. Coast. Shelf Sci. 37: 181–201.

Saenger P.E. 1994. Mangrove and saltmarsh. In: Hammond L.S. and Synnot R.N. (eds), Marine Biology. Longman Cheshire Pty Ltd., Melbourne, Australia, pp. 238–256.

Saintilan N. and Williams R.J. 2000. The decline of saltmarsh in southeast Australia: result of recent surveys. Wetlands (Australia) 18: 49–54.

Saintilan N. and Williams R.J. 1999. Mangrove transgression into saltmarsh environments in New South Wales, Australia. Global Ecol. Biogeogr. 8: 117–124.

Talbot C.W. and Able K.W. 1984. Composition and distribution of larval fishes in New Jersey high marshes. Estuaries 7: 434–43.

Thomas E.B. and Connolly R.M. 2001. Fish use of subtropical saltmarshes in Queensland, Australia: relationships with vegetation, water depth and distance onto the marsh. Mar. Ecol. Prog. Ser. 209: 275–288.

Underwood A.J. 1997. Experiments in Ecology: Their Ecological Design and Interpretation Using Analysis of Variance. University Press, Cambridge, UK.

Underwood A.J. and Chapman M.G. 1989. GMAV5 for Windows. Institute of Marine Ecology, University of Sydney, Australia.

Vance D.J.M., Haywood D.E. and Staples J. 1990. Use of Mangrove Estuary as a Nursery Area by postlarval and juvenile banana prawns, *Penaeus merguiensis* de Man, in Northern Australia. Estuar. Coast. Shelf Sci. 31: 689–701.

Williams R.J., Hannan J., Balashov V. and Watford F.A. 1996. The changing estuarine fish and decapod crustacean community of western Kooragang Island, NSW, Australia. In: Wetlands for the Future, INTECOL'S V International Wetlands Conference. Conference Programme and Book of Abstracts. Encore Productions, WA, Australia, pp. 118–119.

CSIRO PUBLISHING

www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2011, **62**, 11–19

Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses

Debashish Mazumder[A,D], *Neil Saintilan*[B], *Robert J. Williams*[C] *and Ron Szymczak*[A]

[A]Australian Nuclear Science and Technology Organisation, Locked Bag 2001, Kirrawee DC, NSW 2232, Australia.
[B]New South Wales Department of Environment Climate Change and Water, Rivers and Wetlands Unit, PO Box A 290, Sydney, NSW 1232, Australia.
[C]New South Wales Department of Industry and Investment, Systems Research Branch, Aquatic Ecosystems Research Unit, PO Box 21, Cronulla, NSW 2230, Australia.
[D]Corresponding author. Email: debashish.mazumder@ansto.gov.au

Abstract. Juveniles of commercially important fish species congregate in shallow vegetated estuarine habitats during high tides. Considerable debate has centred on whether the significance of these habitats lies in their provision of greater feeding opportunities, or shelter from predation afforded by greater structural complexity. We tested the hypothesis that an inundated mangrove and saltmarsh wetland provided feeding opportunities for itinerant species, and that the contribution of wetland primary producers and grazing herbivores could be identified in their diet, using stable isotopes of carbon and nitrogen. Potential sources of dietary carbon included mangrove, saltmarsh, seagrass, seagrass epiphytic material and benthic organic material. Saltmarsh plants (mostly *Sporobolus virginicus* and *Juncus kraussii*) and fine benthic organic material appeared to be the primary sources of dietary carbon for the resident grazing herbivores in the wetlands, based on IsoSource mixing models. During high tide, species of itinerant fish enter the mangrove and, when inundated, the saltmarsh, and feed primarily on crab larvae and copepods. Fine benthic organic matter, seagrass epiphyte, and C_3 and C_4 plant materials also supplement the diet of some fish. The crab larvae therefore provide a significant source of nutrition and an important link between the intertidal wetlands and the adjacent estuarine ecosystem. The carnivorous fish *Acanthopagrus australis*, at the highest trophic level, hunted within or adjacent to the mangrove–saltmarsh wetland and fed on several lower-order consumers within the wetland. The present study highlights the significance of mangrove and saltmarsh wetlands as a feeding habitat for resident grazers and itinerant nekton.

Keywords: mangrove, nekton, saltmarsh, seagrass, stable isotopes, trophic connectivity.

Introduction

Estuaries are nursery habitats for many species of fish, prawns and crabs (e.g. Blaber 2000; Abrantes and Sheaves 2009). Some species spend the majority of their life in the estuary, whereas others are temporary visitors from the inshore marine water or coastal rivers. The abundance and diversity of nekton in an estuary are influenced by hydrological linkages with the open ocean (Saintilan 2004), and the variety and area of habitats (Jones *et al.* 1986; Nicolas *et al.* 2010). The shallow and vegetated habitats that fringe estuaries are of particular importance to juvenile fish (e.g. Loneragan *et al.* 1986; Hannan and Williams 1998; Martinho *et al.* 2007) that congregate in areas of high structural complexity (Nagelkerken *et al.* 2000; Beyst *et al.* 2002; Trebitz *et al.* 2009) or turbidity (Robertson and Blaber 1992). It has been suggested that this behaviour is a means of avoiding predators (Bell and Worthington 1992; Gray *et al.* 1996; Chiu and Abrahams 2010), but the shallow vegetated estuarine habitats also provide unique opportunities for feeding (Haynes and Quinn 1995; Grimaldo *et al.* 2009).

An understanding of nutrient and energy flow and trophic linkages in estuarine food webs is essential for developing ecological models for sustainable management of ecosystems. For example, models of the impacts of fishing pressure require reference points where trophic interactions between functional groups are identified (Gislason *et al.* 2000; Robinson and Frid 2003). Identification of linkages between high-trophic-order species (particularly those of commercial and recreational importance) and different habitat resources (e.g. saltmarsh, mangrove and seagrass) is fundamental to resource management, but may not be sufficient if predator–prey interactions are unclear. Christensen (1996) cites several case studies in which projections of fishing impacts were confounded by secondary

© CSIRO 2011 10.1071/MF10076 1323-1650/11/010011

impacts on prey species populations, and Saintilan *et al.* (2008) implicated predator-mediated changes in juvenile fish abundance at Towra Point, New South Wales, following the closure of the estuary to commercial fishing.

Stable isotopes can be applied to assist in the clarification of the relative importance of different primary carbon sources (terrestrial and aquatic macrophytes, benthic algae and phytoplankton), and the trophic position of a range of consumers in estuarine ecosystems (Loneragan *et al.* 1997; Bouillon *et al.* 2002; Abrantes and Sheaves 2009). In contrast to earlier studies in trophic systems (e.g. Robertson 1986; Robertson and Daniel 1989), several isotope studies over the past decade have questioned the contribution of mangrove and saltmarsh plants to energy flows within estuarine ecosystems. These studies have shown that carbon isotope signatures of grazing organisms that convert autotrophic production into protein seldom reflect the carbon isotope ratios of dominant macrophytes, and are often more closely associated with either benthic, epiphytic or phytoplanktonic algae (Lee 2000; Bouillon *et al.* 2002; Mazumder and Saintilan 2010). Further, in a study applying isotopes of carbon and nitrogen to a linked mangrove–saltmarsh ecosystem, Marguillier *et al.* (1997) demonstrated that even species visiting the mangrove ecosystem fed primarily in the nearby seagrass.

Resolving the energy flow in coastal ecosystems is important to our understanding of the conservation significance of fringing wetlands in south-east Australia, which are used by a range of fish species (Thomas and Connolly 2001; Crinall and Hindell 2004; Mazumder *et al.* 2005). The use of intertidal habitats may be influenced by the availability of nearby heterogeneous habitat types (Irlandi and Crawford 1997; Skilleter *et al.* 2005), most notably seagrass (Jelbart *et al.* 2007; Saintilan *et al.* 2007). To model trophic connectivity between habitats and species, and between predators and prey, carbon and nitrogen stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were measured in a variety of ecosystem components collected from the mangrove, saltmarsh and seagrass habitats of Towra Point, New South Wales, Australia.

The Towra Point wetlands are the most extensive intertidal wetlands in the Sydney region and provide habitat to a diverse assemblage of intertidal invertebrates and visiting nekton (Mazumder *et al.* 2005). Fish of several species move from the fringing seagrass into the mangrove and saltmarsh during high tides (Saintilan *et al.* 2007), including significant species in terms of biomass (*Ambassis jacksoniensis*) and commercial significance (*Liza argentea*, *Acanthopagrus australis*), where gut content analysis has suggested they feed on crab larvae and other products of the wetland (Mazumder *et al.* 2006).

The analysis of stable isotopes from a range of organisms using this wetland would reveal the primary sources of autotrophic production for these species, and the trophic linkages within the food web. Specifically, the aim of this study was to test three distinct hypotheses: (1) whether stable carbon and nitrogen isotope ratios could be used to cluster species into functional trophic groups, (2) whether stable isotope signatures of the saltmarsh grazers corresponded to the isotope signatures of the primary sources of carbon and nitrogen available in the saltmarsh and (3) whether the isotope signatures of itinerant (high-tide) visitors to the mangrove and saltmarsh wetland reflected locally available sources of carbon and nitrogen.

Materials and methods

Study area

The Towra Point Nature Reserve is in Botany Bay, New South Wales (Fig. 1) and is characterised by the presence of extensive saltmarsh dominated by a *Sarcocornia quinqueflora–Sporobolus virginicus* association, with *Triglochin striata* growing in less well-drained positions. *Juncus kraussii* and *Suaeda australis* are also present in higher-elevation environments (Clarke and Hannon 1967; Adam *et al.* 1988). The mangrove area is dominated by *Avicennia marina*, and the seagrass by *Zostera capricorni* (McGuinness 1990). A total of 23 species of nekton (Mazumder *et al.* 2005) and four species of crabs (Mazumder and Saintilan 2003) have been found in the saltmarsh and mangrove habitats at Towra Point.

Sample collection

Samples were collected in the saltmarsh, mangrove and seagrass habitats of Towra Point. Following a sensitivity analysis by Mazumder *et al.* (2008), five specimens of each species and five replicates of benthic material were sought. Six species of plant, epiphytic material from *Z. capricorni*, and sediment from each intertidal habitat, were collected on one field excursion (Table 1). Over December 2005 to July 2006, replicate samples of four species of invertebrates, two categories of zooplankton, and four species of fish were obtained. The collected taxa represented the dominant species by biomass.

Saltmarsh, mangrove, seagrass and seagrass epiphytes were chosen to represent the potential sources of carbon and nitrogen to be transferred to aquatic food webs. The common vascular saltmarsh species (*Sarcocornia quinqueflora* and *Juncus kraussii*), mangrove species (*Avicennia marina* and *Aegiceras corniculatum*) and seagrass (*Zostera capricorni*) are C_3 species, whereas the saltmarsh grass *Sporobolus virginicus* is a C_4 species. Five leaves of separate plants were hand-picked randomly from saltmarsh, mangrove and seagrass. Epiphytes were separated from the *Z. capricorni* leaves in the laboratory by scraping with a scalpel. No attempt was made to identify epiphyte taxa. Scraped material was subsequently washed with distilled water, dried and ground to fine powder for stable isotope analysis.

The dominant crab species *Helograpsus haswellianus* and *Parasesarma erythrodactyla* were collected from saltmarsh using pit-traps (see Salmon and Hyatt 1983). A common snail, *Salinator solida*, was collected from saltmarsh by hand. Crabs and snails were frozen for laboratory analysis.

Sediment scrapings were collected from the top 1 cm of surface sediment (Melville and Connolly 2003) from saltmarsh and mangrove habitats. The samples were washed through 4-mm, 1-mm, 0.5-mm and 0.25-mm sieves following the method of Loneragan *et al.* (1997). Material elutriated from the finest size-fractions (0.25–0.5 mm) was labelled 'fine benthic organic matter' (FBOM). As stable isotopes used in trophic ecology rely on C fixed in the organic form (Mateo *et al.* 2008), acid-washing of sediment samples was performed before analysis. To avoid bias introduced by inorganic C, a small quantity of 1 M hydrochloric acid was added to sediment subsamples and left for 3 h to remove the inorganic carbon present in the sediment (Polunin *et al.* 2001). The samples were then

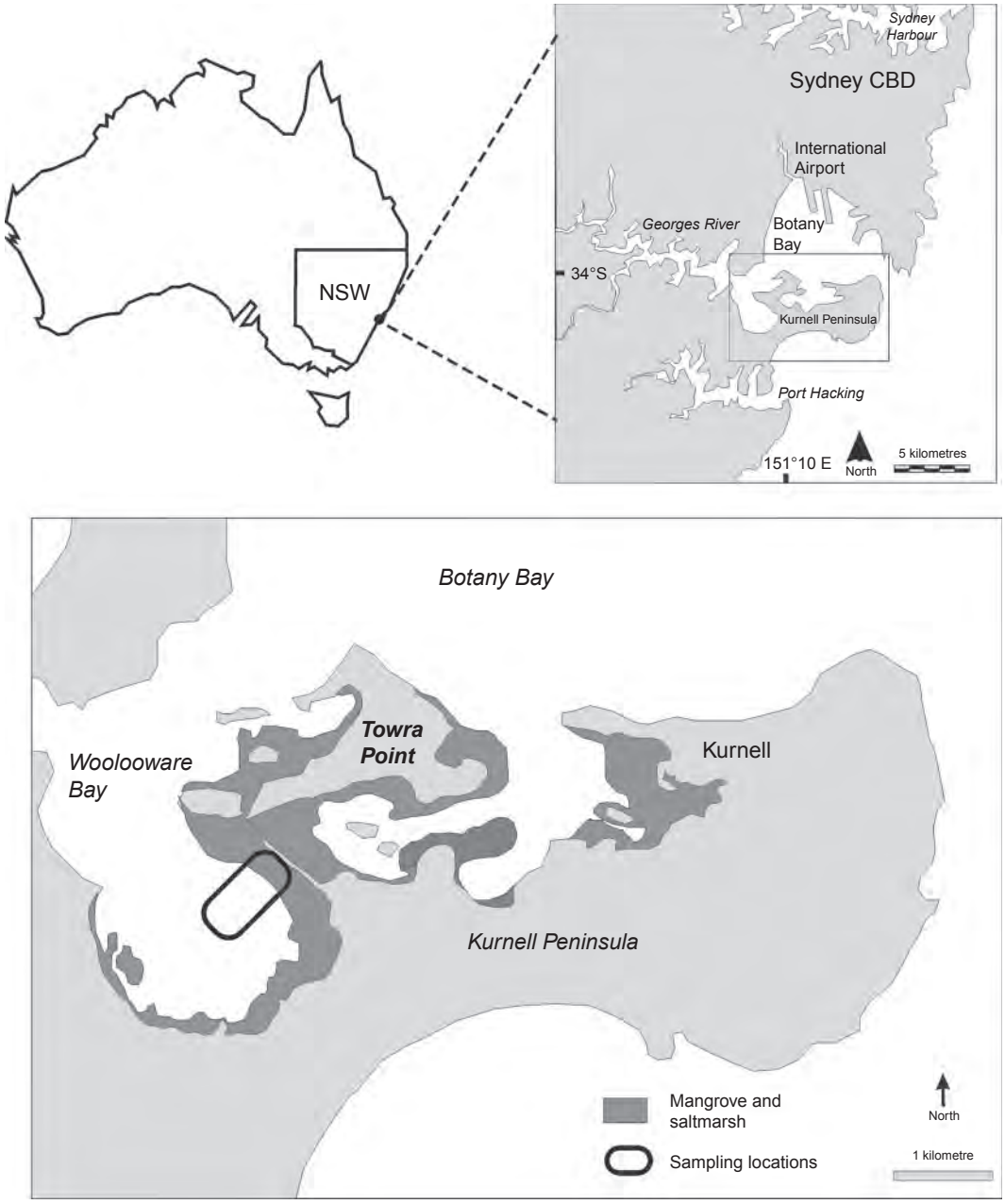


Fig. 1. Location of the Towra Point study sites, Sydney, New South Wales, Australia.

rinsed with distilled water, dried and ground to a fine powder. Because this acid-washing process results in enrichment of $\delta^{15}N$ (Pinnegar and Polunin 1999), untreated sediment sub-samples were analysed for $\delta^{15}N$.

Previous research at Towra Point indicated that the breeding period of *H. haswellianus* was from March to October, and that of *P. erythrodactyla* was from November to February (Mazumder 2004). Ovigerous females of these two crab species were collected from saltmarsh in December 2005 and June 2006 just before high spring tide using pit-traps and kept in an aquarium. Within a few days, crabs released their larvae. Newly hatched larvae were then collected and washed with distilled water, dried and ground to fine powder for stable isotope analysis. Isotope signatures of these two larval species were pooled in the analysis.

Copepods were collected using a 150-μm mesh plankton net. The plankton net was towed from a boat adjacent to the mangrove fringe. The catch was frozen immediately for laboratory processing. In the laboratory, samples were cleaned of detritus, and copepods were separated from other zooplankton under a dissecting microscope, washed with distilled water, dried and ground to fine powder for stable isotope analysis. No attempt was made to differentiate copepods to species level. Fish (*Pseudomugil signifer*, *Liza argentea*, *Ambassis jacksoniensis*,

Table 1. Specimens collected from Towra Point during 2005–06 for carbon and nitrogen stable isotope analysis

Family	Scientific name	*n*	Length range (mm)	Comments
Benthos				
Chenopodiaceae	*Sarcornia quinqueflora*	5	–	C3 plant, leaf material
Juncaeae	*Juncus kraussii*	5	–	C3 plant, leaf material
Avicenniaceae	*Avicennia marina*	5	–	C3 plant, leaf material
Myrsinaceae	*Aegiceras corniculatum*	5	–	C3 plant, leaf material
Gramineae	*Sporobolus virginicus*	5	–	C4 plant, leaf material
Zosteraceae	*Zostera capricorni*	5	–	C3 plant, leaf material
Seagrass epiphyte		5*		Epiphytic materials from the *Zostera* leaves
Benthic sediment		5*		Benthic sediment from saltmarsh and mangrove
Grapsidae	*Helograpsus haswellianus*	5	19–21	Adults
Grapsidae	*Parasesarma erythrodactyla*	5	20–22	Adults
Chalcidoidea	*Salinator solida*	5	4–5	Adults
Nekton				
	Copepod	5*	Not measured	Adults
Grapsidae	*Helograpsus haswellianus*	5*	Not measured	Newly hatched larvae
	Parasesarma erythrodactyla		Not measured	Newly hatched larvae
Palaemonidae	*Macrobrachium intermedium*	5	35–42	Adults
Pseudomugilidae	*Pseudomugil signifer*	5	30–35	Adults
Chandidae	*Ambassis jacksoniensis*	5	44–43	Adults
Sparidae	*Acanthopagrus australis*	5	193–410	Adults

*Five replicates from pooled samples.

Acanthopagrus australis) and invertebrates (*Macrobrachium intermedium*) were collected from the saltmarsh and mangrove habitats using fyke and seine nets (mesh size 2 mm) and frozen instantly for laboratory processing.

Sample processing

Sample processing was undertaken in a filtered-air Room Laboratory (Class 3500) and powder-less laboratory gloves were worn at all times to minimise C and N contamination. Plants, invertebrates and fish brought in from the field were washed with distilled water and kept frozen until processed. Plant materials were dried at 65°C for 72 h and then ground to a fine powder with a Retsch three-dimensional Vibrator Mill (Type-MM-2: Haan, Germany).

White muscle tissue from the dorsal region of fish was collected, as this tissue has been shown to be representative of overall stable isotope signatures in fish and to be less variable than other tissues (Hesslein *et al.* 1993; Pinnegar and Polunin 1999). Lipid extractions were not undertaken, as delipidation from muscle tissue appears to lead to only small (<1‰) isotope shifts in $\delta^{13}C$ and $\delta^{15}N$ values (Sotiropoulos *et al.* 2004). For macro-invertebrates, only muscle tissues were collected, following the removal of the exoskeleton. Muscle tissue samples were dried at 65°C for 72 h and then ground to a fine powder with a mortar and pestle. After processing, samples were loaded in tin capsules and analysed on a continuous-flow stable isotope ratio mass spectrometer (GV Instruments IsoPrime EA/IRMS, Manchester, UK).

Functional categories were defined on the basis of cluster analysis. Cluster analysis (PRIMER v6 statistical software: Clarke and Warwick 2001) was performed using Bray–Curtis measures of similarities with square-root-transformed data from the isotope ratios of carbon and nitrogen of the specimens. Trophic position (TPO) of species was calculated using the formula reported by Post (2002):

$$\mathrm{TPO} = \lambda + (\delta^{15}N_{\mathrm{organism}} - \delta^{15}N_{\mathrm{base\ of\ food\ web}})/3.4, \qquad (1)$$

where λ is the trophic level used to estimate $\delta^{15}N_{\mathrm{base\ of\ food\ web}}$. In this study, fine benthic organic matter (FBOM) was identified as the likely base trophic resource (i.e. trophic level = 1).

Modelling contribution of food sources to the diet of consumers

Mean isotopic ($\delta^{13}C$ and $\delta^{15}N$) values were used as inputs to an IsoSource mixing model (Phillips and Gregg 2003) to estimate the possible contributions of the different diet sources to the isotopic makeup of the consumers. Prior to modelling, the mean isotopic values were adjusted by 1‰ enrichment fractionation of $\delta^{13}C$ (DeNiro and Epstein 1978) and 3.4‰ fractionation of $\delta^{15}N$ (Vander Zanden and Rasmussen 2001). However, for grazers (crabs and the snail), a fractionation for $\delta^{15}N$ of 2.2‰ was used (McCutchan *et al.* 2003). A tolerance of 0.01% was used in the IsoSource model. Model results were reported as means and lower and upper ranges (1st and 99th percentiles), representing estimates of percentages of food items in the diet of consumer species.

Results

Trophic grouping based on isotopic values

Six trophic categories were identified in the cluster analysis (Fig. 2). Mean values for $\delta^{13}C$ and $\delta^{15}N$ were separated into two distinct plant groups. The C_4 plant (*S. virginicus*) and C_3 seagrass (*Z. capricorni*) were enriched compared with the intertidal

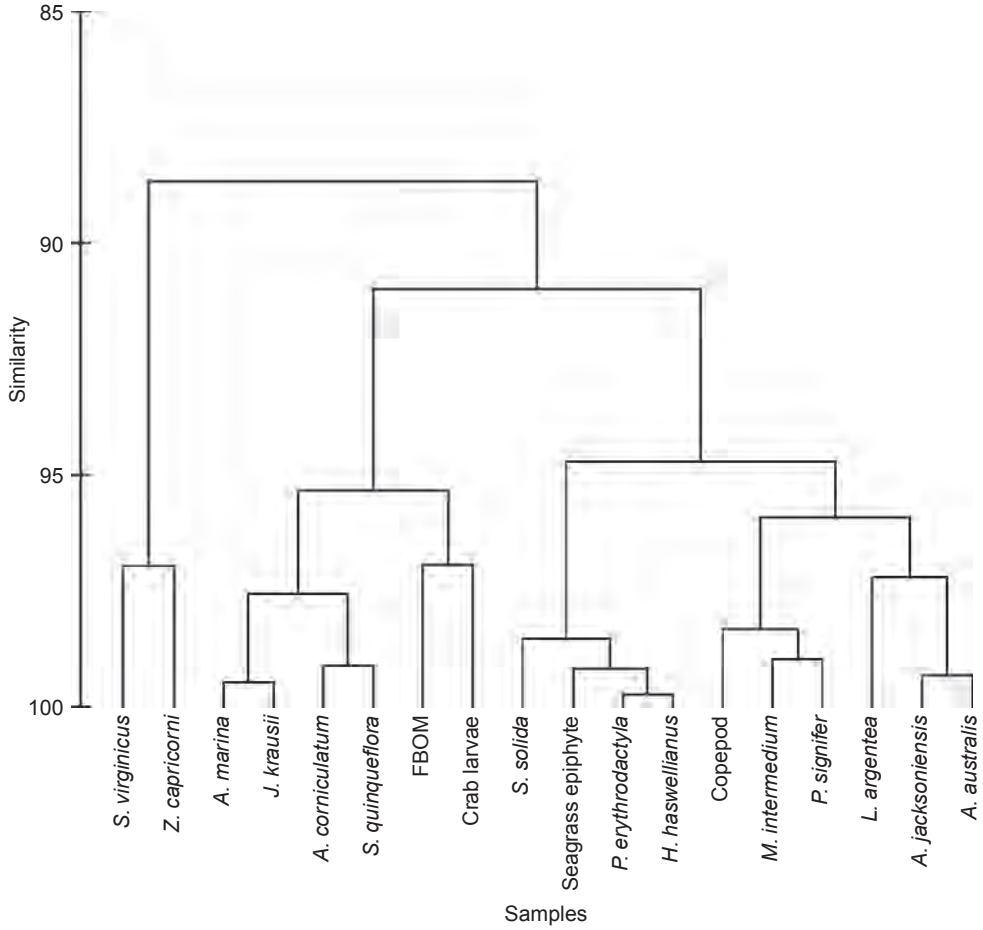


Fig. 2. Cluster analysis showing assemblages of species based on their trophic functionality. Stable C and N isotope values of species were used to draw trophic hierarchical grouping.

C_3 plants and clustered together in the ordination. FBOM and crab larvae were positioned together between the two plant groups (Fig. 3). Isotopic signatures of grazers (snail and crabs) ranged from −18.50‰ to −19.90‰ for carbon and 7.70‰ to 8.00‰ for nitrogen. Carbon isotope values of grazers were enriched compared with the C_3 plant group, and depleted compared with the C_4 (*S. virginicus*) and submerged (*Z. capricorni*) plant groups.

Adult crabs and snails grouped into a grazer category, although seagrass epiphytes also fell in this group. The copepod sample grouped with *M. intermedium* and *P. signifer* into an omnivore category. The carnivore category consisted of the species *L. argentea*, *A. jacksoniensis* and *A. australis*. *L. argentea* separated from the other two species in the carnivore category, but was positioned closely with the omnivore group (Fig. 3). Mean $\delta^{15}N$ values of the carnivore group were the most enriched compared with species in the other trophic categories.

Trophic linkages between mangrove–saltmarsh resources, grazers and itinerant nekton

Nitrogen isotope values of grazers were enriched compared with both plant groups, and the trophic position of these primary consumers ranged from 1.5 to 1.9. IsoSource mixing models showed the diets of *H. haswellianus*, *P. erythrodactyla* and the snail *S. solida* to be similar. The C_4 plant *S. virginicus* and FBOM were important contributors to the diets of these species (Table 2).

Mean $\delta^{13}C$ values in the omnivore group ranged from −23.62‰ to −21.56‰, and mean $\delta^{15}N$ values ranged from 9.42‰ to 10.22‰. The trophic position of this group ranged from 2.3 to 2.5 (Fig. 3). Copepods, crab larvae and seagrass epiphytic materials were the leading sources of nutrition in this category, although C_3 and C_4 plants, and FBOM, were also important contributors (Table 2). Juvenile *L. argentea*, which clustered in the carnivore category, fed on the same food items as the omnivore group, but was distinguished by a dominant contribution of copepods to their diet, according to the IsoSource model.

Mean $\delta^{13}C$ values in the carnivore group ranged from −21.38‰ to −20.30‰, and mean $\delta^{15}N$ values of species in the carnivore group were enriched compared with other trophic categories. Trophic positions of species included in the carnivore group ranged from 2.8 to 3.7 (Fig. 3). IsoSource analyses on the diets of carnivores showed that crab larvae and copepods were the major contributors to the diet of *A. jacksonien*sis.

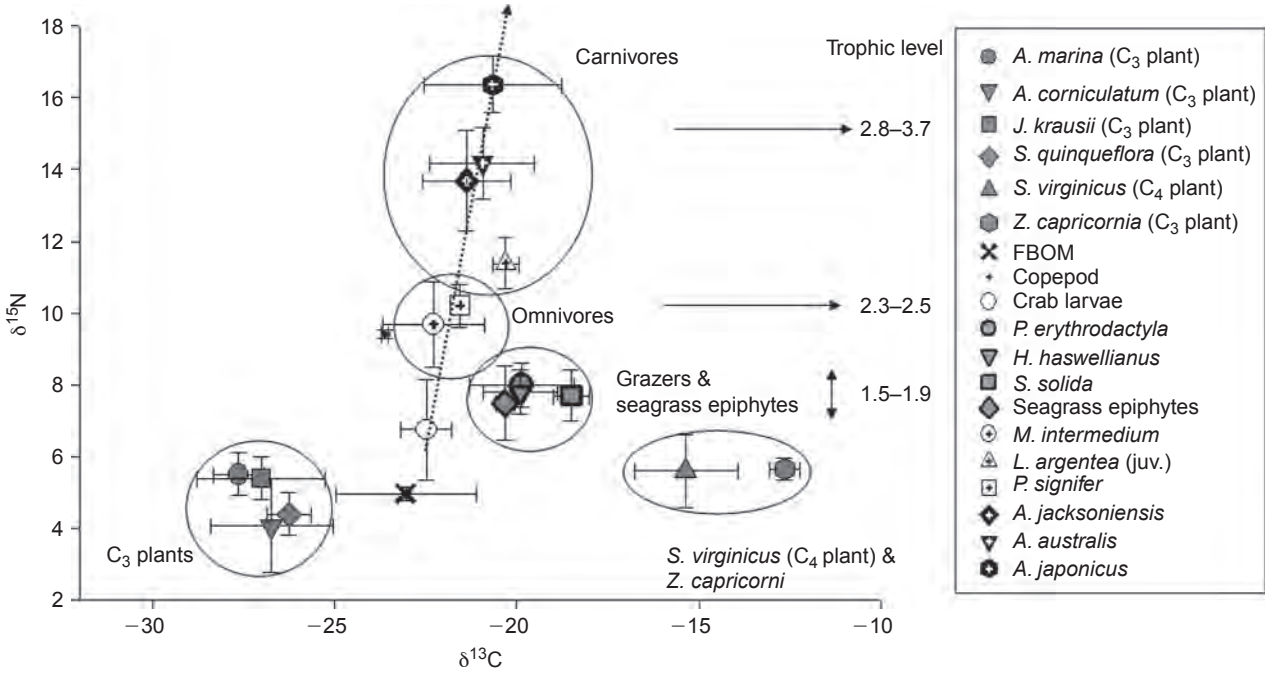


Fig. 3. Dual isotope plot of $\delta^{13}C$ and $\delta^{15}N$ showing trophic interactions between different ecosystem components and trophic level of consumers in different functional categories of the Towra Point, NSW, 2005–06.

Table 2. Probable dietary sources of consumers in the Towra Point wetland based on IsoSource modelling calculations
Mean percent contribution, and 1st and 99th percentiles of the distribution of feasible solutions of each source to consumer diet. FBOM, fine benthic organic matter

Dietary source	Mean percent contribution to consumer diet (1st–99th percentiles)							
	A. australis	*A. jacksoniensis*	*L. argentea*	*P. signifier*	*M. intermedium*	*H. haswellianus*	*P. erythrodactyla*	*S. solida*
M. intermedium	63 (57–68)	–	–	–	–	–	–	–
P. erythrodactyla	0.9 (0–3)	–	–	–	–	–	–	–
H. haswellianus	0.9 (0–4)	–	–	–	–	–	–	–
S. solida	0.1 (0–2)	–	–	–	–	–	–	–
A. jacksoniensis	27 (25–29)	–	–	–	–	–	–	–
P. signifer	8 (0–18)	–	–	–	–	–	–	–
Crab larvae	–	48 (0–94)	5 (0–7)	25 (0–77)	21 (0–65)	–	–	–
Copepods	–	31 (0–62)	49 (28–63)	21 (6–37)	13 (0–27)	–	–	–
Seagrass epiphytes	–	21 (5–37)	25 (0–69)	17 (0–51)	14 (0–44)	–	–	–
C_3 plants	–	–	1 (0–5)	14 (0–31)	28 (7–46)	–	–	–
C_4 plants	–	–	18 (0–29)	7 (0–22)	6 (0–19)	–	–	–
S. quinqueflora	–	–	–	–	–	10 (1–19)	6 (1–10)	11 (3–20)
J. kraussii	–	–	–	–	–	20 (2–36)	9 (1–18)	17 (1–32)
S. virginicus	–	–	–	–	–	42 (37–47)	35 (33–38)	60 (55–64)
FBOM	–	–	2 (0–7)	16 (0–45)	18 (0–56)	28 (16–42)	50 (43–56)	12 (1–24)

A. australis, *M. intermedium*, *A. jacksoniensis* and *P. signifier*, as well as other lower-order consumers (Table 2).

Discussion

The segregation of trophic components is a helpful tool in the development of conceptual models of ecosystem function (Robinson and Frid 2003). Our hypothesis that cluster analysis of stable isotope data could be used to group species into meaningful trophic guilds corresponding to published accounts of dietary preference was supported. The three consumer groups identified in this study correspond to the herbivore, zoobenthi-planktivore and piscivore–benthivore groups identified by Marguillier *et al.* (1997) in a linked mangrove–seagrass ecosystem in Kenya, though in our study there is less evidence of omnivory at the highest trophic level. At the lowest trophic level are FBOM and the autotrophs, the latter being distinguished on the basis of carbon isotope ratios between the emergent C_3 plants

(*A. marina*, *A. corniculatum*, *S. quinqueflora* and *J. kraussii*) and the seagrass *Z. capricorni*, along with the C_4 marsh grass *S. virginicus*.

The grazers form a cluster at the next trophic level, consisting of two sampled species of grapsid crab (*H. haswellianus*, *P. erythrodactyla*) and the snail *S. solida.* These herbivores are permanent residents of the mangrove and saltmarsh following a brief planktonic stage. Our hypothesis, that local sources of autotrophic production would dominate the diet of grazing herbivores, is supported, although saltmarsh species predominated, and mangrove leaf material was not an important source of nutrition. The minor importance of mangroves as a source of nutrition, as opposed to benthic and phytoplanktonic algae and saltmarsh in estuarine ecosystems, has been noted in several other studies (Riera *et al.* 1999; Lee 2000; Bouillon *et al.* 2002).

The third trophic level at the site is taxonomically diverse, including the Copepoda, the shrimp *M. intermedium*, a small fish *P. signifier*, and juveniles of the fish species *L. argentea*. The grazing herbivores appear too depleted in $\delta^{15}N$, and too enriched in $\delta^{13}C$, to be making a direct contribution to the omnivores, other than through the provision of larvae. The newly-hatched larvae of the crabs are sufficiently enriched in $\delta^{15}N$ to be positioned as an important link between the autotrophic production and the higher-level consumers, and this is supported by gut-content studies at Towra Point (Mazumder *et al.* 2006). Other food items sourced by the omnivore group include copepods, seagrass epiphytic materials, fine benthic organic matter and C_3 and C_4 plant materials.

Omnivorous nekton species are itinerant visitors to the Towra Point marsh, occupying the seagrass habitat at low tide and moving into the mangrove and saltmarsh during high tide (Saintilan *et al.* 2007). *Z. capricorni*, a C_3 plant and the only seagrass species at the site, is isotopically distinct from the emergent intertidal C_3 macrophytes, principally because the dissolved $\delta^{13}C$ within seawater is similar to that of C_4 plants, though anatomical evidence suggests that seagrasses do not use the C_4 photosynthetic pathway (Benedict *et al.* 1980). The $\delta^{13}C$ value of seagrass (−12.65‰) is far more enriched than the taxa present in the omnivore group, suggesting a negligible contribution to the latter. The low contribution of seagrass carbon to food webs was also reported by Moncreiff and Sullivan (2001), Kieckbusch *et al.* (2004) and Lugendo *et al.* (2006). The mixing model indicates that the $\delta^{13}C$ of seagrass epiphyte material (−20.31‰) contributes considerably to the diet of the omnivore species.

The fourth trophic level, on the basis of nitrogen isotope fractionation, is the carnivores. This group includes juvenile *L. argentea* and adults of *A. jacksoniensis* and *A. australis*, all species commonly encountered in the mangrove and saltmarsh of south-eastern Australia at high tide (Mazumder *et al.* 2005; Platell and Freewater 2009). Mixing model results suggest that *L. argentea* feeds on the same range of prey items as the omnivores, but that it is grouped in the carnivore cluster because of the higher proportional contribution of copepods to their diet. Our results suggest that crab larvae and copepods are the most important components of the diet of *A. jacksoniensis*. Stomach content analysis of *A. jacksoniensis* at Towra Point (Mazumder *et al.* 2006) the NSW central coast (Platell and Freewater 2009) and south-east Queensland (Hollingsworth and Connolly 2006) found high proportions of crab larvae in the stomachs of individuals of this fish species. *A. australis* is the largest of the sampled predators in the wetland and alone of the carnivores is able to feed on *M. intermedium*, *A. jacksoniensis* and *P. signifier*, as well as on other lower-order nekton species. The finding supports the suggestion by Saintilan *et al.* (2008) that the closure of a fishery targeting this species may have contributed to surveyed declines in *M. intermedium* and *P. signifer* in the wetlands.

One of the top predators in south-east Australian estuaries is the mulloway *A. japonicus*. This species has never been observed hunting in the intertidal wetlands, but for comparative purposes, isotope data for *A. japonicus* sampled near Towra Point (Taylor and Mazumder 2010) have been included in Fig. 3. Over a range of estuaries, stomach-content analysis revealed forage fish were the most important components of the diet of adult *A. japonicus* (Taylor *et al.* 2006). The wide range of carbon isotope values for *A. japonicus* shown in Fig. 3 may reflect its mobility and range of diet, but it appears that itinerant nekton feeding in the mangrove and saltmarsh wetlands form a staple component.

The study illustrates the potential significance of trophic relay between the intertidal environment and the broader estuarine environment (Kneib 1997). Although grazers feed on locally available autotrophic material (Saintilan and Mazumder 2010), their larvae, being released to the water column and re-distributed by the tide, provide a link between the wetland and itinerant fish that occupy a wider range of environments beyond the wetland. Although the mangrove and saltmarsh are inundated for a fraction of the time of the adjacent estuarine environments, several species of nekton appear to visit the mangrove and saltmarsh wetland to feed on materials that are only available, or available in higher concentrations, within these habitats. These species in turn become significant components of the diet of several commercially important species.

Acknowledgements

We acknowledge Ms. Val Sadler and Mr. Alan Williams (ANSTO) for assisting the stable isotope sample preparation and analysis, support and encouragement by Dr Suzanne Hollins and John Twining (ANSTO) and Dr Mathew Johansen (ANSTO) for assisting mixing model calculation. The NSW Department of Environment Climate Change and Water provided access to the Towra Point Nature Reserve. Daniel Large (DECCW) is thanked for assistance with copepod sampling. Also, we thank two anonymous referees and Professor Andrew Boulton for providing helpful comments. This research was conducted under NSW Fisheries Scientific Research Permit F89/1598–3.0 and NSW Department of Environment, Climate Change and Water Scientific Licence S12527. Animal ethics approval was granted by the Director General's Animal Ethics Committee of the Department of Primary Industries, project number 02/3477.

References

Abrantes, K., and Sheaves, M. (2009). Food-web structure in a near-pristine mangrove area of the Australian wet tropics. *Estuarine, Coastal and Shelf Science* **82**, 597–607. doi:10.1016/J.ECSS.2009.02.021

Adam, P., Wilson, N. C., and Huntley, B. (1988). The phytosociology of coastal saltmarsh vegetation in New South Wales. *Wetlands (Australia)* **7**, 35–84.

Bell, J. D., and Worthington, D. C. (1992). Links between estuaries and coastal rocky reefs in the lives of fishes from south-eastern Australia. In 'Proceedings of the Second International Temperate Reef Symposium,

Auckland, New Zealand'. (Ed. C. N. Battershill.) pp. 85–91. (NIWA Marine: Wellington.)

Benedict, C. R., Wong, W. W. L., and Wong, J. H. H. (1980). Fractionation of the stable isotopes of inorganic carbon by seagrasses. *Plant Physiology* **65**, 512–517.

Beyst, B., Hostens, K., and Mees, J. (2002). Factors influencing the spatial variation in fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium. *Journal of the Marine Biological Association of the United Kingdom* **82**, 181–187. doi:10.1017/S0025315402005337

Blaber, S. J. M. (2000). 'Tropical Estuarine Fishes: Ecology, Exploitation and Conservation.' (Blackwell Scientific: Oxford.)

Bouillon, S., Raman, A. V., Dauby, P., and Dehairs, F. (2002). Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Predesh, India). *Estuarine, Coastal and Shelf Science* **54**, 901–913. doi:10.1006/ECSS.2001.0864

Chiu, S., and Abrahams, M. V. (2010). Effects of turbidity and risk of predation on habitat selection decisions by fathead minnow (*Pimephales promelas*). *Environmental Biology of Fishes* **87**, 309–316. doi:10.1007/S10641-010-9599-8

Christensen, V. (1996). Managing fisheries involving predator and prey species. *Reviews in Fish Biology and Fisheries* **6**, 417–442. doi:10.1007/BF00164324

Clarke, L. D., and Hannon, N. J. (1967). The mangrove swamp and saltmarsh communities of the Sydney district. I. Vegetation, soil and climate. *Journal of Ecology* **55**, 753–771. doi:10.2307/2258423

Clarke, K. R., and Warwick, R. M. (2001). 'Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation.' 2nd edn. (PRIMER-E: Plymouth.)

Crinall, S. M., and Hindell, J. S. (2004). Assessing the use of saltmarsh flats by fish in a temperate Australian embayment. *Estuaries* **27**, 728–739. doi:10.1007/BF02907656

DeNiro, M. J., and Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**, 495–506. doi:10.1016/0016-7037(78)90199-0

Gislason, H., Sinclair, M., Sainsbury, K., and O'Boyle, R. (2000). Symposium overview: incorporating ecosystem objectives within fisheries management. *ICES Journal of Marine Science* **57**, 468–475. doi:10.1006/JMSC.2000.0741

Gray, C. A., McElligot, D. J., and Chick, R. C. (1996). Intra- and inter-estuary difference in assemblages of fishes associated with shallow seagrass and bare sand. *Marine and Freshwater Research* **47**, 723–735. doi:10.1071/MF9960723

Grimaldo, L. F., Stewart, A. R., and Kimmerer, W. (2009). Dietary segregation of pelagic and littoral fish assemblages in a highly modified tidal freshwater estuary. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* **1**, 200–217. doi:10.1577/C08-013.1

Hannan, J. C., and Williams, R. J. (1998). Recruitment of juvenile marine fishes to seagrass habitat in a temperate Australian estuary. *Estuaries* **21**, 29–51. doi:10.2307/1352545

Haynes, D., and Quinn, G. P. (1995). Temporal and spatial variability in community structure of a sandy intertidal beach, Cape Paterson, Victoria, Australia. *Marine and Freshwater Research* **46**, 931–942. doi:10.1071/MF9950931

Hesslein, R. H., Hallard, K. A., and Ramlal, P. (1993). Replacement of sulfur, carbon, and nitrogen in tissue of growing broad white fish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2071–2076. doi:10.1139/F93-230

Hollingsworth, A., and Connolly, R. M. (2006). Feeding by fish visiting inundated subtropical saltmarsh. *Journal of Experimental Marine Biology and Ecology* **336**, 88–98. doi:10.1016/J.JEMBE.2006.04.008

Irlandi, E. A., and Crawford, M. K. (1997). Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of estuarine fish. *Oecologia* **110**, 222–230. doi:10.1007/S004420050154

Jelbart, J. E., Ross, P. M., and Connolly, R. M. (2007). Fish assemblages in seagrass beds are influenced by the proximity of mangrove forests. *Marine Biology* **150**, 993–1002. doi:10.1007/S00227-006-0419-9

Jones, A. R., Watson-Russell, C. J., and Murry, A. (1986). Spatial patterns in the macrobenthic communities of the Hawkesbury Estuary, New South Wales. *Marine and Freshwater Research* **37**, 521–543. doi:10.1071/MF9860521

Kieckbusch, D. K., Koch, M. S., Serafy, J. E., and Anderson, W. T. (2004). Trophic linkages among primary producers and consumers in fringing mangroves of subtropical lagoons. *Bulletin of Marine Science* **74**, 271–285.

Kneib, R. T. (1997). The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology Annual Review* **35**, 163–220.

Lee, S. Y. (2000). Carbon dynamics of Deep Bay, eastern Pearl River estuary, China. II: Trophic relationship based on carbon- and nitrogen-stable isotopes. *Marine Ecology Progress Series* **205**, 1–10. doi:10.3354/MEPS205001

Loneragan, N. R., Potter, I. C., Lenanton, R. C. J., and Caputi, N. (1986). Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. *Marine Biology* **92**, 575–586. doi:10.1007/BF00392517

Loneragan, N. R., Bunn, S. E., and Kellaway, D. M. (1997). Are mangroves and seagrass sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. *Marine Biology* **130**, 289–300. doi:10.1007/S002270050248

Lugendo, B. R., Nagelkerken, I., van der Velde, G., and Mgaya, Y. D. (2006). The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas for juvenile fishes in Chwaka Bay, Zanzibar: gut content and stable isotope analyses. *Journal of Fish Biology* **69**, 1639–1661. doi:10.1111/J.1095-8649.2006.01231.X

Marguillier, S., van der Velde, G., Dehairs, F., Hemminga, M. A., and Rajagopal, S. (1997). Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}C$ and $\delta^{15}N$. *Marine Ecology Progress Series* **151**, 115–121. doi:10.3354/MEPS151115

Martinho, F., Leitão, R., Neto, J. M., Cabral, H. N., Marques, J. C., and Pardal, M. A. (2007). The use of nursery areas by juvenile fish in a temperate estuary, Portugal. *Hydrobiologia* **587**, 281–290. doi:10.1007/S10750-007-0689-3

Mateo, M. A., Serrano, O., Serrano, L., and Michener, R. H. (2008). Effects of sample preparation on stable isotope ratios of carbon and nitrogen in marine invertebrates: implications for food web studies using stable isotopes. *Oecologia* **157**, 105–115. doi:10.1007/S00442-008-1052-8

Mazumder, D. (2004). Contribution of saltmarsh to temperate estuarine fish in southeast Australia. Ph.D. Thesis, Australian Catholic University, Sydney.

Mazumder, D., and Saintilan, N. (2003). A comparison of sampling techniques in the assessment of burrowing crab abundance in saltmarsh and mangrove environments. *Wetlands (Australia)* **21**, 1–15.

Mazumder, D., and Saintilan, N. (2010). Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. *Wetlands* **30**, 375–380. doi:10.1007/S13157-010-0021-2

Mazumder, D., Saintilan, N., and Williams, R. (2005). Temporal variations in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. *Wetlands Ecology and Management* **13**, 457–467. doi:10.1007/S11273-004-0814-2

Mazumder, D., Saintilan, N., and Williams, R. (2006). Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. *Marine and Freshwater Research* **57**, 193–199. doi:10.1071/MF05040

Mazumder, D., Williams, R. J., Reid, D., Saintilan, N., and Szymczak, R. (2008). Variability of stable isotope ratios of glassfish (*Ambassis jacksoniensis*) from mangrove/saltmarsh environments in southeast Australia and implications for choosing sample size. *Environmental Bioindicators* **3**, 114–123. doi:10.1080/15555270802266003

McCutchan, J. H., Lewis, W. M., Kendall, C., and McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen and sulfur. *Oikos* **102**, 378–390. doi:10.1034/J.1600-0706.2003.12098.X

McGuinness, K. A. (1990). Effects of oil spills on macro-invertebrates of saltmarshes and mangrove forests in Botany Bay, New South Wales, Australia. *Journal of Experimental Marine Biology and Ecology* **142**, 121–135. doi:10.1016/0022-0981(90)90141-X

Melville, A. J., and Connolly, R. M. (2003). Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. *Oecologia* **136**, 499–507. doi:10.1007/S00442-003-1302-8

Moncreiff, C. A., and Sullivan, M. J. (2001). Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. *Marine Ecology Progress Series* **215**, 93–106. doi:10.3354/MEPS215093

Nagelkerken, I., van der Velde, G., Gorissen, M. W., Meijer, G. J., van't Hof, T., *et al.* (2000). Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for importance coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science* **51**, 31–44. doi:10.1006/ECSS.2000.0617

Nicolas, D., Lobry, J., Le Pape, O., and Boët, P. (2010). Functional diversity in European estuaries: relating the composition of fish assemblages to the abiotic environment. *Estuarine, Coastal and Shelf Science* **88**, 329–338. doi:10.1016/J.ECSS.2010.04.010

Phillips, D. L., and Gregg, J. W. (2003). Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136**, 261–269. doi:10.1007/S00442-003-1218-3

Pinnegar, J. K., and Polunin, N. V. C. (1999). Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implications for the study of trophic interactions. *Functional Ecology* **13**, 225–231. doi:10.1046/J.1365-2435.1999.00301.X

Platell, M. E., and Freewater, P. (2009). Importance of saltmarsh to fish species of a large south-eastern Australian estuary during a spring tide cycle. *Marine and Freshwater Research* **60**, 936–941. doi:10.1071/MF08164

Polunin, N. V. C., Morales-Nin, B., Pawsey, W. E., Cartes, J. E., Pinnegar, J. K., *et al.* (2001). Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. *Marine Ecology Progress Series* **220**, 13–23. doi:10.3354/MEPS220013

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**, 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Riera, P., Stal, L. J., Nieuwenhuize, J., Richard, P., Blanchard, G., *et al.* (1999). Determination of food sources for benthic invertebrates in a salt marsh (Aiguillon Bay, France) by carbon and nitrogen stable isotopes: importance of locally produced sources. *Marine Ecology Progress Series* **187**, 301–307. doi:10.3354/MEPS187301

Robertson, A. I. (1986). Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in north-eastern Australia. *Journal of Experimental Marine Biology and Ecology* **102**, 237–248. doi:10.1016/0022-0981(86)90179-6

Robertson, A. I., and Blaber, S. J. M. (1992). Plankton, epibenthos and fish communities. *Coastal and Estuarine Studies* **41**, 173–224.

Robertson, A. I., and Daniel, P. A. (1989). The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia* **78**, 191–198. doi:10.1007/BF00377155

Robinson, L. A., and Frid, C. L. J. (2003). Dynamic ecosystem models and the evaluation of ecosystem effects of fishing: can we make meaningful predictions? *Aquatic Conservation: Marine and Freshwater Ecosystems* **13**, 5–20. doi:10.1002/AQC.506

Saintilan, N. (2004). Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine, Coastal and Shelf Science* **61**, 591–601. doi:10.1016/J.ECSS.2004.07.002

Saintilan, N., and Mazumder, D. (2010). Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. *Marine and Freshwater Research* **61**, 615–620. doi:10.1071/MF09187

Saintilan, N., Hossain, K., and Mazumder, D. (2007). Linkages between seagrass, mangrove and saltmarsh fish habitat in the Botany Bay estuary, New South Wales. *Wetlands Ecology and Management* **15**, 277–286. doi:10.1007/S11273-006-9028-0

Saintilan, N., Mazumder, D., and Cranney, K. (2008). Changes to fish assemblages visiting estuarine wetlands following the closure of commercial fishing in Botany Bay, Australia. *Aquatic Ecosystem Health & Management* **11**, 441–449. doi:10.1080/14634980802515823

Salmon, M., and Hyatt, G. W. (1983). Spatial and temporal aspects of reduction in North Carolina fiddler crabs (*Uca pugilator* Bosc.). *Journal of Experimental Marine Biology and Ecology* **70**, 21–43. doi:10.1016/0022-0981(83)90146-6

Skilleter, G. A., Olds, A., Loneragan, N. R., and Zharikov, Y. (2005). The value of patches of intertidal seagrass to prawns depends on their proximity to mangroves. *Marine Biology* **147**, 353–365. doi:10.1007/S00227-005-1580-2

Sotiropoulos, M. A., Tonny, W. M., and Wassenaar, L. I. (2004). Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecology Freshwater Fish* **13**, 155–160. doi:10.1111/J.1600-0633.2004.00056.X

Taylor, M. D., Fielder, D. S., and Suthers, I. M. (2006). Spatial and ontogenetic variation in the diet of wild and stocked mulloway (*Argyrosomus japonicus*, Sciaenidae) in Australian estuaries. *Estuaries and Coasts* **29**, 785–793.

Taylor, D. M., and Mazumder, D. (2010). Stable isotopes reveal post-release trophodynamic and ontogenetic changes in a released finfish, mulloway (*Argyrosomus japonicus*). *Marine and Freshwater Research* **61**, 302–308.

Thomas, E. B., and Connolly, R. M. (2001). Fish use of subtropical saltmarshes in Queensland, Australia: relationships with vegetation, water depth and distance onto the marsh. *Marine Ecology Progress Series* **209**, 275–288. doi:10.3354/MEPS209275

Trebitz, A. S., Brazner, J. C., Danz, N. P., Pearson, M. S., Peterson, G. S., *et al.* (2009). Geographic, anthropogenic, and habitat influences on Great Lakes coastal wetland fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 1328–1342. doi:10.1139/F09-089

Vander Zanden, M. J., and Rasmussen, J. B. (2001). Variation in $\delta^{13}C$ and $\delta^{15}N$ trophic fractionation: implications for aquatic food web studies. *Limnology and Oceanography* **46**, 2061–2066. doi:10.4319/LO.2001.46.8.2061

Manuscript received 19 March 2010, accepted 2 October 2010

Wetlands (2010) 30:375–380
DOI 10.1007/s13157-010-0021-2

NOTE

Mangrove Leaves are Not an Important Source of Dietary Carbon and Nitrogen for Crabs in Temperate Australian Mangroves

Debashish Mazumder · Neil Saintilan

Received: 12 August 2009 / Accepted: 29 November 2009 / Published online: 3 March 2010
© Society of Wetland Scientists 2010

Abstract The carbon and nitrogen stable isotope ratios of the mangrove sesarmid crabs *Parasesarma erythrodactyla, Paragrapsus laevis,* and *Helograpsus haswellianus* were measured from sites in arid and humid temperate Australia, and compared with potential food sources. Crab stable isotope ratios were uniform and consistent with published values from subtropical Queensland. Fresh and decomposed leaves of the dominant mangrove *Avicennia marina* were discounted as a potential food source, being too depleted in their $\delta^{13}C$ and $\delta^{15}N$ signatures compared to crabs to have made a substantial contribution to the diet. A three-source mixing model indicated that fine benthic organic material was the primary food source. Mangrove epiphyte and highly decomposed mangrove leaf material were too depleted in $\delta^{15}N$ to be contributing to crab diet.

Keywords Estuarine · Food habits · Isotope · Sesamaridae · Trophic

Introduction

The suggestion that mangrove crabs are responsible for processing large proportions of mangrove leaf litter was first advocated by Robertson (1986) and Giddens et al. (1986). Subsequent field and laboratory work has confirmed the leaf processing role of crabs in settings ranging from Hong Kong (Lee 1989; Kwok and Lee 1995; Lee 1997), tropical northern Australia (Robertson and Daniel 1989; Micheli 1993), subtropical Australia (Camilleri 1992), Thailand (Poovachiranon and Tantichodok 1991), Malaysia (Ashton 2002), South Africa (Emmerson and McGwynne 1993; Steinke et al. 1993), east Africa (Dahdouh-Geubas et al. 1997, 1999; Olafsson et al. 2002), Florida (Erickson et al. 2003), and Brazil (Nordhaus et al. 2006).

The proportion of mangrove forest leaf production consumed by crabs has often been found to be high (Lee 1998). Nordhaus et al. (2006) found *Ucides cordatus* consumed 81.3% of *Rhizophora mangle* leaf production in a Brazilian mangrove forest. In northern Australia, sesarmid herbivory accounted for 71% of *Ceriops* leaf production, 79% of *Bruguiera* leaf production, and 33% of *Avicennia marina* leaf production (Robertson and Daniel 1989).

Studies over a wide geographic range have shown that mangrove litter can constitute a large proportion of sesarmid crab diet. *Sesarma meinerti* was found to consume both *Bruguiera gymnorrhiza* and *Avicennia marina* leaves in a South African mangrove forest (temperate), with mangrove leaf litter forming 74.6% of the diet (Steinke et al. 1993). In east Africa *Neosarmatium meinerti* consumed the leaves of *Avicennia marina* as a primary diet source, supplemented by animal material (Dahdouh-Geubas et al. 1997). Malley (1978) found the gut content of *Chiromanthes onychophorum* to consist of 95% by volume mangrove leaf fragments in peninsular Malaysia.

The widely reported consumption of mangrove leaves by crabs presents a paradox. Mangrove leaves have high tannin contents and C/N ratios that exceed 17, ratios that are too high to be considered suitable to sustain nutrition

D. Mazumder (✉)
Australian Nuclear Science and Technology Organisation,
PMB 1, Menai, NSW 2234, Australia
e-mail: debashish.mazumder@ansto.gov.au

N. Saintilan
New South Wales Department of Environment Climate Change and Water, Rivers and Wetlands Unit,
P.O. Box A 290, Sydney, NSW 1232, Australia

(Skov and Hartnoll 2002). The hypothesis that decomposition within burrows decreases the C/N ratio, making the leaf more palatable, was rejected by Skov and Hartnoll (2002) who found no difference in N concentration or C/N ratios between senescent leaves and fragments of leaves collected from burrows. They concluded that mangrove leaves in any state of decomposition are unlikely to fulfil the nutritional requirements of crabs.

The recent application of stable isotopes to the study of crab diets has cast further question on the dietary importance of mangrove leaves to crabs. France (1998) used carbon and nitrogen isotope ratios of fiddler crabs in Puerto Rico to demonstrate a dietary preference for microalgae (cyanobacteria) over vascular plant detritus. Bouillon et al. (2002) found most C signatures of mangrove intertidal invertebrates in southeast India to be too enriched relative to the mangrove leaf signal to support the hypothesis that mangrove-derived carbon is assimilated in any significant way. In sub-tropical Australia the $\delta^{13}C$ signatures of two species of shorecrabs (*Australoplax tridentate* and *Parasesarma erythrodactyla*) were enriched compared to the dominant mangrove *Avicennia marina* but corresponded to microphytobenthos (Guest et al. 2004, 2006). Although *Parasesarma erythrodactyla* has been observed feeding on mangrove leaves in the region (Camilleri 1992) this is not reflected in the stable isotope signatures (Guest and Connolly 2004).

This study is the first to apply stable isotopes of carbon and nitrogen to determine the importance of mangrove leaves to the diet of crabs in a temperate mangrove setting. Throughout southern Australia, the dominant mangrove is *Avicennia marina*, a species known to be predated by crabs in tropical and subtropical mangrove ecosystems elsewhere (Robertson and Daniel 1989; Camilleri 1989; Dahdouh-Guebas et al. 1999; Olafsson et al. 2002). The range of *Avicennia marina* in temperate southern Australia extends from the humid east, where *Parasesarma erythrodactyla* and *Paragrapsis laevis* are the dominant grapsids (Mazumder and Saintilan 2003), to the arid south, where *Helograpsus haswellianus* is the dominant crab in mangrove forests (Imgraben and Dittmann 2009). Our hypothesis is that the stable isotope signatures of the grazing crabs will correspond to the isotope signatures of the dominant mangrove, *Avicennia marina*, if this species was the primary source of dietary carbon and nitrogen.

Materials and Methods

Site Description

Samples were collected from the mangrove forests of Towra Point, Botany Bay (24° 01′24″ S; 151° 09′15″ E), and Middle Beach mangrove forest at South Australia (34° 36′29″ S; 138° 24′38″ E). Towra Point was selected within the humid temperate region because of its large extent and relatively undisturbed condition. The Towra Point saltmarsh is dominated by a *Sarcocornia quinqueflora/Sporobolus virginicus* association (Clarke and Hannon 1967; Adam et al. 1988) and extends for 250 m shoreward of the mangrove. *Avicennia marina* dominates the mangrove forest, which fringes Woolooware Bay to a width of approximately 100 m. The small burrowing shore crabs *Heloecius cordiformis*, *Parasesarma erythrodactyla*, and *Paragrapsus laevis* are abundant in the mangrove (Mazumder and Saintilan 2003). Towra Point is the largest intertidal wetland in the Sydney region and one of the most pristine, occurring within an Aquatic Reserve. The vegetation and inundation characteristics of the study area are similar to other mangrove habitats in the region (Rogers and Saintilan 2002).

Middle Beach is situated on the shores of the Gulf St. Vincent, about 40–50 km north of the city of Adelaide, South Australia. The mangrove area is inundated daily and consists solely of *Avicennia marina*.

Sample Collection

We collected the samples from all species of macrophyte in the mangroves (*Avicennia marina* at Middle Beach; *Avicennia marina*, *Aegiceras corniculatum* at Towra Point) including fresh samples and decomposing leaves sources from the forest floor. All other known autotrophs at Towra Point were sampled, including mangrove algal epiphytes (by hand picking from the pneumatophores of five randomly located trees of each species), and fine and coarse benthic organic material, five replicates of which were collected from the top 1 cm of surface sediment (after Melville and Connolly 2003) in the vicinity of the crab pit-fall traps. Five adult individuals of each burrowing crab species *H. haswellianus* (from Middle Beach mangrove), *P. laevis* and *P. erythrodactyla* (from Towra Point mangrove) were collected using pit-traps (Salmon and Hyatt 1983; Mazumder and Saintilan 2003). All plant and animal material was kept on ice in transit, washed in deionized water, and then frozen until ready for processing.

Sample Preparation and Analysis

Muscle tissues were collected from claws following removal of the exoskeleton. Muscle, leaf, and epiphytic algal samples were dried at 65°C for 72 h and then ground to a fine powder first with mortar and pestle and subsequently with a Retsch three dimensional Vibrator Mill (Type-MM-2).

We divided the sediment samples into two size fractions. The whole sediment samples were called "coarse benthic organic matter" (CBOM) as they included both biological and clastic materials (i.e., detritus, microphytobenthos, etc.). Second group was termed "fine benthic organic matter" (FBOM) which was separated from whole sediment samples through a series of sieves. Sediment samples were washed through 4 mm, 1 mm, 0.5 mm, and 0.25 mm sieves following the method of Loneragan et al. (1997). Benthic organic matter was then elutriated from the finest size-fractions (0.25 to 0.5 mm). A small quantity of 1 M hydrochloric acid was added to FBOM sediment sub-samples and left for 3 h to remove the inorganic carbon present in the sediment (Polunin et al. 2001). The samples were then rinsed with distilled water, dried, and ground to a fine powder. Since acid washing can result in enrichment of $\delta^{15}N$ (Pinnegar and Polunin 1999), untreated sediment sub-samples were analyzed for $\delta^{15}N$.

All samples were analyzed using a continuous flow stable isotope mass spectrometer (GV Instruments IsoPrime EA/IRMS). Stable isotope values were reported in delta (δ) units in parts per thousand (‰) relative to the international standard and determined as follows:

$$\delta x\ (^{0}/_{00}) = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000$$

where x = $\delta^{13}C$ or $\delta^{15}N$, and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively.

A three source mixing model (Phillips 2001) was used with the assumption of 2.5‰ enrichment fractionation between trophic levels for $\delta^{15}N$ (Vanderklift and Ponsard 2003) and 1‰ for $\delta^{13}C$ (DeNiro and Epstein 1978) to explore the relative importance of potential food sources to the diet of crabs collected from the Towra Point study site.

Results

Parasesarma erythrodactyla (n=5) had an average carapace width of 20.6 mm (s.d.±0.1), while *Paragrapsus laevis* (n=5) had an average carapace width of 25.6 mm (s.d.±2.6). *Helograpsus haswellianus* (n=5) from Middle Beach Mangrove forest, South Australia had an average carapace width 12.3 mm (s.d.±1.5).

The carbon isotope ratio of the mangrove crabs sampled were remarkably uniform, ranging from *Paragrapsus laevis* in New South Wales ($\delta^{13}C$ −21.0±2.2‰) and *Helograpsus haswellianus* in South Australia ($\delta^{13}C$ −21.4±1.3‰), to *Parasesarma erythrodactyla* in New South Wales ($\delta^{13}C$ −22.0±0.4‰), which corresponds precisely to the carbon isotope ratio for the same species in subtropical Queensland, reported by Guest and Connolly (2004) as −22.0±0.2‰.

Carbon and nitrogen isotope signatures of *P. laevis* and *P. erythrodactyla* at Towra Point were enriched compared to mangrove leaves and mangrove epiphytes (Fig. 1). Similarly, both $\delta^{13}C$ and $\delta^{15}N$ signatures for *H. haswellianus* at the Middle Beach site were enriched compared to *A. marina* sampled at that location (Fig. 1).

Mangrove epiphytes had the most depleted carbon and nitrogen isotope ratios and were eliminated as a potential source of crab diet in our three-source mixing models. Fine and coarse benthic organic matter were enriched in $\delta^{13}C$ compared to autotrophs. Our mixing model suggested that FBOM contributed most of all sampled carbon sources to the diet of the two crab species. Highly decomposed mangrove leaf material, although slightly enriched in $\delta^{13}C$ compared to fresh leaf material, was heavily depleted in $\delta^{15}N$, and was excluded as a potential source of dietary carbon in the mixing models.

Discussion

Two previous studies on mangrove crab diets in temperate Australia have cast doubt on the importance of mangrove leaf litter as a source of nutrition. Saintilan et al. (2000) found no evidence of leaf litter consumption by *Parasesarma erythrodactyla* or *Heloecius cordiformis* through direct observation. Imgraben and Dittmann (2009) found little evidence to support the hypothesis that mangrove crabs consume litter of *Avicennia marina* in South Australia. Laboratory studies using the dominant South Australian mangrove crab, *Helograpsus haswellianus*, showed no predation on fresh leaves or propagules of *Avicennia marina*, and low rates of predation on slightly decomposed leaves by females only (Imgraben and Dittmann 2009).

The evidence from stable isotopes presented here supports these observations. In concord with several published accounts of mangrove crab isotope signatures from tropical and subtropical regions (Rodelli et al. 1984 in Malaysia; France 1998 in Puerto Rico; Bouillon et al. 2002 in India) we found a 3–11‰ enrichment of carbon isotope ratios of crabs compared to mangrove leaves, well beyond the range attributable to trophic fractionation. Our mixing models indicated that it is unlikely that any of the grapsid crab species were utilizing mangrove leaf litter as an important source of nutrition. This may be because of the high C/N values of mangrove leaves (Skov and Hartnoll 2002) being beyond a range suitable for sustainable nutrition (Russell-Hunter 1970).

To resolve this paradox several authors have suggested a "leaf aging hypothesis" whereby crabs plaster leaves to

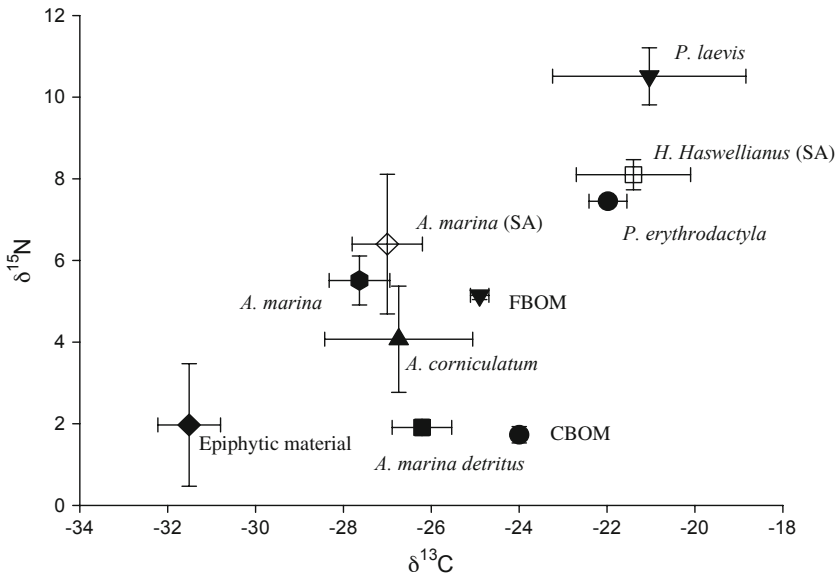


Fig. 1 Stable isotope ratios (‰) of mangrove shore crabs, mangrove leaves, epiphytes and benthic organic matter collected from mangrove habitat at Towra Point and Middle beach mangrove forest. (*FBOM* fine benthic organic matter; *CBOM* coarse benthic organic matter)

their burrow walls (Giddens et al. 1986) allowing leaching of tannins (Neilson et al. 1986) and an increase in N content during breakdown by microbial activity (Wafar et al. 1997). However, in a study of C/N ratios of leaves excavated from burrows Skov and Hartnoll (2002) could find no significant difference between the C/N ratios of excavated leaf fragments and fresh leaves. While our decomposing leaf samples were slightly enriched in ^{13}C compared to fresh leaves (~1‰), the ^{15}N ratios were substantially depleted compared with fresh leaves (~4‰) and could not be contributing to the comparatively enriched ^{15}N ratios of the crabs.

Other obvious potential sources of carbon sampled included epiphytic algae found on mangrove pneumatophores, and benthic organic material. Mangrove epiphytic algae was highly depleted in both carbon and nitrogen and did not contribute to our mixing models. Fine benthic organic matter was closest to the signature of crabs, and our mixing models indicated this to be the primary food sources for all species sampled. Observations of the feeding behaviour of crabs in these environments provide additional support for this model, with crabs of all species appearing to feed off the surface layer of sediment (McGuinness 1997; Mazumder and Saintilan 2003). Fine benthic organic material consists of a range of carbon sources that were not separately sampled, although which could be selectively consumed by crabs. Of these, microphytobenthos (including nitrogen-fixing cyanobacteria) has been postulated as an important contributor to crab diets in several studies (Robertson 1986; Alongi 1988; Bouillon et al. 2002; Guest et al. 2004). France (1998) found a wide discrepancy between sediment organic matter and crab stable isotope signatures in Puerto Rico, which was reconciled when benthic cyanobacteria was isolated. Published values for benthic microalgae (~$\delta^{13}C$−20: France 1998; Connolly 2003) indicate this to be a relatively enriched component of the fine benthic organic material, and would explain the enrichment of our crab signatures relative to our measures of our $\delta^{13}C$ for this material.

Mangrove leaves have been cited as the primary source of grapsid crab diet across latitudes ranging from temperate (Steinke et al. 1993), subtropical (Camilleri 1992), or tropical (Robertson and Daniel 1989), with evidence including leaf tethering (Smith and Daniel 1989), laboratory studies (Micheli 1993; Kwok and Lee 1995), and gut content analysis (Malley 1978; Leh and Sasekumar 1985; Dahdouh-Guebas et al. 1999). The distinction between conclusions drawn from stable isotope studies and those from leaf tethering and gut content analysis are therefore puzzling. It is also possible that in some situations rates of leaf predation, when measured using leaf tethering, have been over-estimated, as suggested by Saintilan et al. (2000). Where it occurs, rates of assimilation may also be low for mangrove leaves compared with other food sources, as suggested by Lee (1998). Skov and Hartnoll (2002) propose that crabs shred leaves to improve the nutritional value of their immediate environment, including the substrate, a strategy observed in other highly territorial grazers.

Acknowledgments The authors acknowledge Mrs. Gitanjali Katrak, School of Biological Science, Flinders University, SA for collecting crab and mangrove leaves from Middle Beach mangrove forest, SA. Dr. Suzanne Hollins (ANSTO) for advice and logistic support. The Department of Environment Climate Change and Water (NSW) provided access to the Towra Point sites. Crab samples were collected under NSW Scientific Collection Permit P06/0005. The helpful comments of two anonymous referees are gratefully acknowledged.

References

Adam P, Wilson NC, Huntley B (1988) The phytosociology of coastal saltmarsh vegetation in New South Wales. Wetlands (Australia) 7:35–57

Alongi DM (1988) Bacterial productivity and microbial biomass in tropical mangrove sediments. Microbial Ecology 15:59–79

Ashton EC (2002) Mangrove sesarmid crab feeding experiments in Peninsular Malaysia. Journal of Experimental Marine Biology and Ecology 273:97–119

Bouillon S, Koedam N, Raman A, Dehairs F (2002) Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130:441–448

Camilleri JC (1989) Leaf choice by crustaceans in a mangrove forest in Queensland. Marine Biology 102:453–459

Camilleri JC (1992) Leaf-litter processing by invertebrates in a mangrove forest in Queensland. Marine Biology 114:139–145

Clarke LD, Hannon NJ (1967) The mangrove swamp and saltmarsh communities of the Sydney district. I. Vegetation, soil and climate. Journal of Ecology 55:753–771

Connolly RM (2003) Differences in trophodynamics of commercially important fish between artificial waterways and natural coastal wetlands. Estuarine Coastal and Shelf Science 58:929–936

Dahdouh-Geubas F, Verneirt M, Tack JF, Koedam N (1997) Food preferences of Neosarmatium meinerti de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 137:83–87

Dahdouh-Guebas F, Giuggioli MA, Oluoch A, Vannini M, Cannicci S (1999) Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. Bulletin of Marine Science 64:291–297

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506

Emmerson WD, McGwynne LE (1993) Feeding and assimilation of mangrove leaves by the crab *Sesarma meinerti* De Man in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. Journal of Experimental Marine Biology and Ecology 157:41–53

Erickson AA, Saltis M, Bell SS, Dawes CJ (2003) Herbivore feeding preferences as measured by leaf damage and stomatal ingestion: a mangrove crab example. Journal of Experimental Marine Biology and Ecology 289:123–138

France R (1998) Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes. Journal of Tropical Ecology 14:413–425

Giddens RL, Lucas JS, Neilson MJ, Richards GN (1986) Feeding ecology of the mangrove crab *Neosarmatium smithi* (Crustacea: Decapode: Sesarmidae). Marine Ecology Progress Series 33:147–155

Guest MA, Connolly RM (2004) Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. Aquatic Ecology 38:599–609

Guest MA, Connolly RM, Loneragan NR (2004) Carbon movement and assimilation by invertebrates in estuarine habitats at a scale of metres. Marine Ecology Progress Series 278:27–34

Guest MR, Connolly RM, Lee SY, Loneragan NR, Breitfuss NJ (2006) Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement. Oecologia 148:88–96

Imgraben S, Dittmann S (2009) Leaf litter dynamics and litter consumption in two temperate South Australian mangrove forests. Journal of Sea Research 59:83–93

Kwok PW, Lee SY (1995) The growth performances of two sesarmine crabs *Perisesarma bidens* and *Parasesarma plicata* under different diets. Hydrobiologia 295:141–148

Lee SY (1989) The importance of Sesarminae crabs Chiromanthes spp. and inundation frequency on mangrove (*Kandelia candel* (L.) Druce) leaf litter turnover in a Hong Kong tidal shrimp pond. Journal of Experimental Marine Biology and Ecology 131:23–43

Lee SY (1997) Potential trophic importance of the faecal material of the mangrove sesarmine crab *Sesarma messa*. Marine Ecology Progress Series 159:275–284

Lee SY (1998) Ecological role of grapsid crabs in mangrove ecosystems: a review. Marine and Freshwater Research 49 (4):335–343

Leh CMU, Sasekumar A (1985) The food of sesarmid crabs in Malaysian mangrove forests. Malaysian Nature Journal 39:135–145

Loneragan NR, Bunn SE, Kellaway DM (1997) Are mangroves and seagrass sources of organic carbon for penaeid prawns in a tropical estuary? A multiple Stable-isotope study. Marine Biology 130:289–300

Malley DF (1978) Degradation of mangrove leaf litter by the tropical sesarmid crab Chiromanthes onychophorum. Marine Biology 49:377–386

Mazumder D, Saintilan N (2003) A comparison of sampling techniques in the assessment of burrowing crab abundance in saltmarsh and mangrove in temperate Australia. Wetlands (Australia) 21:1–15

McGuinness KA (1997) Tests for artefacts in some methods used to study herbivory and predation in mangrove forests. Marine Ecology Progress Series 153:37–44

Melville JA, Connolly RM (2003) Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136:499–507

Micheli F (1993) Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. Journal of Experimental Marine Biology and Ecology 171:164–186

Neilson MJ, Giddens RL, Richards GN (1986) Effects of tannins on the palatability of mangrove leaves to the tropical sesarminid crab *Neosarmatium smithi*. Marine Ecology Progress Series 34:185–186

Nordhaus I, Wolff M, Diele K (2006) Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Estuarine, Coastal and Shelf Science 67:239–250

Olafsson E, Buchmayerm S, Skov MW (2002) The east African decapod crab *Neosarmatium meinerti* (de Man) sweeps mangrove floors clean of leaf litter. Ambio 31:569–573

Phillips DL (2001) Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia 27:166–170

Pinnegar JK, Polunin NVC (1999) Differential fractionation of d13C and d15N among fish tisues: implications for the study of trophic interactions. Functional Ecology 13:225–231

Polunin NV, Morales-Nin B, Pawsey WE, Carles JE, Pinnegar JK, Moranta J (2001) Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. Marine Ecology Progress Series 220:13–23

Poovachiranon S, Tantichodok P (1991) The role of sesarmid crabs in the mineralisation of leaf litter of *Rhizophora apiculata* in a mangrove, southern Thailand. Phuket Marine Biology Centre Research Bulletin 56:63–74

Robertson AI (1986) Leaf-burying crabs; their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. Journal of Experimental Marine Biology and Ecology 103:237–248

Robertson AI, Daniel PA (1989) The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. Oecologia 78:191–198

Rodelli MR, Gearing NJ, Gearning PJ, Marshall N, Sasekumar A (1984) Stable isotope ratio as a tracers as a mangrove carbon in Malaysian ecosystems. Oecologia 61:326–333

Rogers K, Saintilan N (2002) Monitoring the loss of saltmarsh in SE Australian estuary. Progress report to the Coasts & Clean Seas Initiative, Environment Australia. 73pp

Russell-Hunter WD (1970) Aquatic productivity: an introduction to some basic aspects of biological oceanography and limnology. Collier MacMillan, London

Saintilan N, Griffiths K, Jaafar W, Tibbey M (2000) A possible experimental artefact associated with leaf-tethering in crab herbivory experiments. Wetlands (Australia) 18(2):55–59

Salmon M, Hyatt GW (1983) Spatial and temporal aspects of reduction in North Carolina fiddler crabs (*Uca pugilator* Bosc.). Journal of Experimental Marine Biology and Ecology 70:21–43

Skov MW, Hartnoll RG (2002) Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? Oecologia 131:1–7

Smith TJ III, Daniel PA (1989) The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. Oecologia 78:191–198

Steinke TD, Rajh A, Holland AJ (1993) The feeding behaviour of the red mangrove crab Sesarma meinerti De Man, 1887 (Crustacea: Decapoda: Grapsidae) and its effect on the degradation of mangrove leaf litter. South African Journal of Marine Science 13:151–160

Vanderklift AM, Ponsard S (2003) Source of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. Oecologia 136:169–182

Wafar S, Untwale AG, Wafar M (1997) Litter fall and energy flux in a mangrove ecosystem. Estuarine Coastal and Shelf Science 44:111–124

CSIRO PUBLISHING

Marine and Freshwater Research, 2019, **70**, 1436–1444
https://doi.org/10.1071/MF18072

Equivalence of trophic structure between a tropical and temperate mangrove ecosystem in the Indo-Pacific

Debashish Mazumder[A,D], *Neil Saintilan*[B], *Fatimah M. Yusoff*[C] and *Jeffrey J. Kelleway*[B]

[A]Australian Nuclear Science and Technology Organisation, Locked Bag 2001, Kirrawee DC, NSW 2232, Australia.
[B]Department of Environmental Sciences, Macquarie University, Sydney, NSW 2109, Australia.
[C]Institute of Bioscience, Department of Aquaculture, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor Darul Ehsan, Malaysia.
[D]Corresponding author. Email: debashish.mazumder@ansto.gov.au

Abstract. In this study we compared ecosystem trophic structure between a tropical mangrove forest at Matang, Malaysia, and a temperate mangrove forest near mangrove poleward limits at Towra Point in south-east Australia. These forests are separated by 8500 km of ocean over 45° of latitude and are of contrasting size, productivity and diversity. However, we observed a marked degree of similarity in food chain length (approximately four trophic levels in both forests), the taxonomy of key intermediate members of the food chain and the isotope signature of primary carbon sources, suggesting a strong contribution of surface organic matter rather than mangrove detritus. Common families were represented among dominant grazing herbivores, zooplanktivorous fishes, decapod crustaceans and top predators. These similarities suggest that there is some consistency in trophic interactions within two mangroves on opposite sides of the Indo-Pacific, despite a degree of evolutionary divergence in the assemblage.

Additional keywords: food chain length, carbon isotope, coevolution, fisheries, phylogenetic.

Received 27 February 2018, accepted 7 March 2019, published online 22 May 2019

Introduction

Mangroves are tidally inundated forests located primarily along tropical shorelines in two major biogeographic provinces: the Indo-West Pacific and the Atlantic East Pacific (Duke *et al.* 1998). Both are secondary centres of radiation, sharing three common genera (*Avicennia*, *Rhizophora* and *Acrostichum*), but only one species (*Acrostichum aureum*; Duke 1992). Mangrove forests of the Indo-Western Pacific (IWP) form a phylogenetically consistent grouping with a centre of diversity (the highest globally) in tropical Malaysia and Indonesia (Duke *et al.* 1998) and radiating, with decreasing diversity, south to south-eastern Australia and north to Japan. Current mangrove floristic diversity decreases with increasing latitude and the most poleward mangroves in the IWP are found in south-east Australia, south to Corner Inlet (39°S), where only a single species, *Avicennia marina*, is found at the southern tip of the continent. Patterns in benthic faunal diversity mirror those of floristic diversity in mangroves: Ashton *et al.* (2003) sampled 31 crab and 44 molluscan species in Sarawak, compared with just 5 species of crabs and 2 mollusc species described by Mazumder (2009) in the mangroves of Towra Point, Sydney (34°S).

Throughout the Quaternary, glacial and interglacial cycles have caused the migration of mangrove ecosystems across shallow continental shelves while at the same time imposing and relaxing temperature constraints forcing the latitudinal expansion and contraction of species (Hashimoto *et al.* 2006). Although capable of long-distance oceanic dispersal, mangroves within estuarine compartments of the east Australian coastline show little genetic exchange, suggesting estuaries behaved like discrete islands over the Holocene as a result of restricted entrance conditions (Arnaud-Haond *et al.* 2006). Despite this apparent isolation in plant dispersal, the trophic structure of mangroves in subtropical and temperate Australia shows a high degree of consistency. Mangrove nekton species assemblages are similar between adjacent estuaries of Botany Bay and the Hawkesbury River in New South Wales, despite differences in geomorphic setting (Mazumder *et al.* 2006*a*), and with those of Moreton Bay, Queensland, 1000 km to the north (Laegdsgaard and Johnson 1995). Further, elements of trophic structure show marked regularity across these same locations, with crab larvae, released during spring tide inundation, offering an important dietary source to the numerically dominant fish within the estuaries, the glassfish (*Ambassis* spp.) and the mullet *Liza argentea*, among others (Hollingsworth and Connolly 2006; Mazumder *et al.* 2006*b*; McPhee *et al.* 2015).

These trophic interactions between elements of the south-east Australian mangroves were identified using gut content analysis, but can be clarified using stable isotopes, providing

Journal compilation © CSIRO 2019

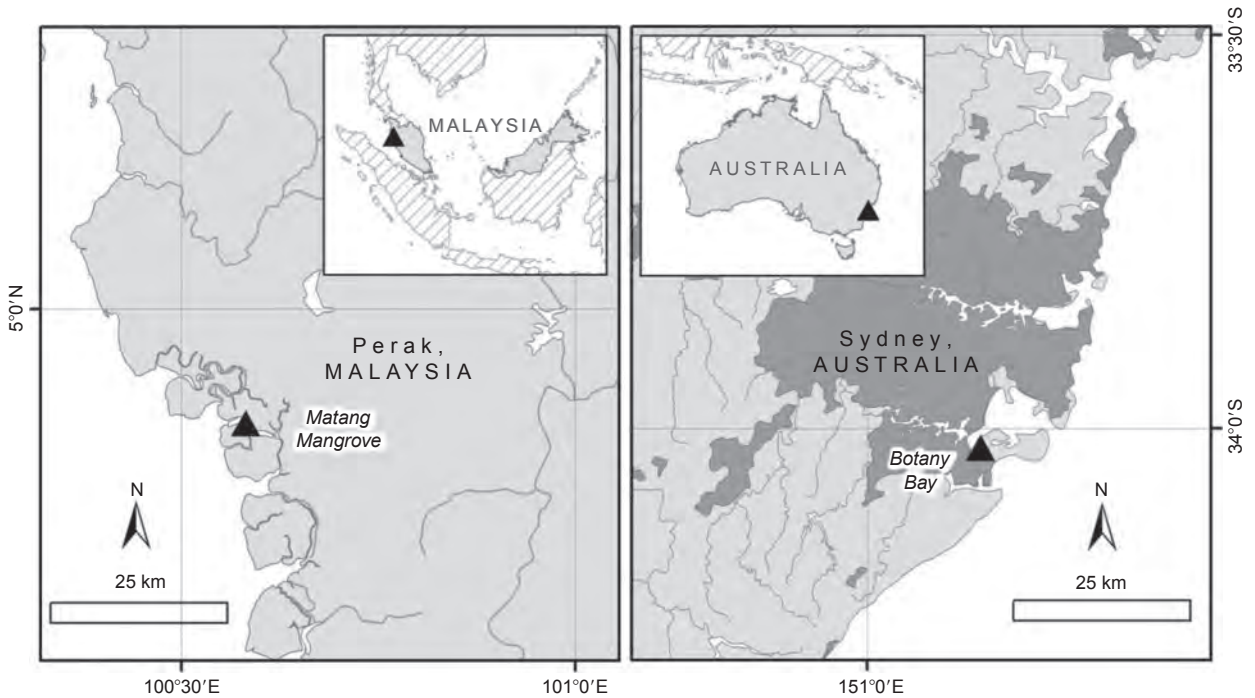


Fig. 1. Maps showing the location the tropical Matang mangrove, Malaysia, and the temperate Towra Point mangrove, in Botany Bay, New South Wales, Australia.

insight into trophic position and sources of autotrophic production contributing to ecosystem functions (Bouillon *et al.* 2002; Abrantes and Sheaves 2009). In a previous study, we used stable isotopes of nitrogen and carbon to describe trophic interactions within the mangrove forest at Towra Point, Sydney (fig. 1 in Mazumder *et al.* 2011). That study demonstrated the importance of benthic organic matter, derived from a range of autotrophs within and adjacent to the mangrove forest, contributing to a tightly linked trophic structure incorporating grapsid crab larvae, omnivorous and zooplanktivorous fishes and second-order carnivores of importance to commercial fisheries.

We repeated this approach in the Matang mangrove forest in tropical Malaysia (Fig. 1) with the intention of determining whether trophic structure and autotrophic dependencies differed substantially between tropical and temperate settings. The Matang mangrove forest is substantially larger (43 000 ha) than the mangrove forest at Towra Point (700 ha) and of higher standing biomass (30 kg m^{-2} at Matang, Gong and Ong 1990, compared with 15 kg m^{-2} at Towra, Kelleway *et al.* 2016). Larger ecosystems transverse a greater range and volume of basal resources (Schoener 1989), contain a greater number of species (Holt 1996) and thereby afford a greater potential for stable, higher-order trophic interactions (Cohen and Newman 1991), although the Matang forest is commercially harvested. Notwithstanding commercial logging, we would expect the Matang mangrove to support higher trophic levels than the Towra Point mangrove forest given the larger size and higher productivity. Where similarities exist in form and phylogenetic relationships, we postulate a similar trophic position, given the aforementioned evidence for niche conservatism at higher taxonomic levels. However, very few studies have explored similarity in trophic structure among analogous species in common habitats separated over large geographic ranges.

Specifically, in the present study we tested the following three hypotheses: (1) the Matang mangrove forest will support greater food chain length, as measured by the difference in nitrogen isotope ratios between top predators and autotrophs; (2) taxonomically similar species will be positioned in similar trophic niches, as evidenced by stables isotopes of carbon and nitrogen; and (3) carbon contributing to ecosystem components will reflect local sources of autotrophic production.

Materials and methods

Species sampled in the Towra Point and Matang forests are listed in Table 1. Five leaf specimens handpicked from the common macrophytes in each of the two forests were sampled: the mangroves *A. marina* and *Aegiceras corniculatum* at Towra Point, and *Rhizophora apiculata* and *Bruguiera parviflora* at Matang. Sediment scrapings were collected from the top 1 cm of surface sediment (Melville and Connolly 2003; Mazumder *et al.* 2011) at five locations in the vicinity of macrophyte and nekton sampling at Towra and Matang. Following a sensitivity analysis by Mazumder *et al.* (2008), five specimens of each target species were collected. Sampling focused on the most populous members of the ecosystems as determined by prior studies (Mazumder *et al.* 2005) and representing each trophic guild. At Towra Point, ovigerous females of the two crab species *Helograpsis haswellianus* and *Parasesarma erythrodactyla* were collected just before high spring tide using pit traps and kept in an aquarium. Within a few days, the crabs released their larvae. Newly hatched larvae were then collected and washed

Table 1. Common species sampled at Matang and Towra Point mangrove forests for stable isotope analysis, and their taxonomic associations ($n = 5$ in all cases)

Matang mangrove, Malaysia		Towra Point mangrove, Australia	
Finfish			
Sciaenidae	*Johnius belangerii* (adult and juvenile)	Sciaenidae	*Argyosomus japonicas*
Mugilidae	*Liza macrolepis*	Mugilidae	*Liza argentea*
Cyprinidae	*Parachela oxygastroides*	Ambassidae	*Ambassis jacksoniensis*
Plotosidae	*Plotosus canius*	Pseudomugilidae	*Pseudomogil signifer*
Polynemidae	*Leptomelanosoma indicum*	Sparidae	*Acanthopagrus australis*
Ariidae	*Hexanematichthys sagor*		
Ariidae	*Hexanematichthys maculatus*		
Lobotidae	*Lobotes surinamensis*		
Synodontidae	*Saurida tumbil*		
Synodontidae	*Synodus variegatus*		
Clupeidae	*Nematalosa come*		
Crustaceans			
Penaeidae	*Penaeus merguiensis*	Palaemonidae	*Macrobrachium intermedium*
Squillidae	*Miyakea nepa*		
Portunidae	*Scylla serrata*	Portunidae	*Scylla serrata*
Sesarmidae	*Parasesarma erythrodactyla*	Sesarmidae	*Parasesarma erythrodactyla*
		Grapsidae	*Helograpsus haswellianus*
Zooplankton			
Copepods (species not defined)		Copepods (species not defined)	
		Brachuryan larvae (*P. erythrodactyla* and *H. haswellianus*)	
Autotrophs			
Rhizophoraceae	*Rhizophora apiculata* leaf	Acanthaceae	*Avicennia marina* leaf
	Bruguiera parviflora leaf		*Avicennia marina* root
		Primulaceae	*Aegiceras corniculatum* leaf
		Zosteraceae	*Zostera capricorni* blade
Phytoplankton			
Sediment organic matter		Sediment organic matter	

with distilled water, dried and ground to fine powder for stable isotope analysis. Logistic constraints prevented this technique being used in the Matang forest and, for this reason, crab larvae were not obtained. The isotope signatures of these two larval species were pooled in the analysis. Copepods were collected using a 150-mm mesh plankton net. The plankton net was towed from a boat adjacent to the mangrove fringe. The catch was frozen immediately for laboratory processing. Fish and invertebrates at both sites were collected using fyke and seine nets and frozen immediately for laboratory processing.

Collection and preparation of Matang mangrove samples were conducted according to Malaysian research protocols. Collection of Towra Point samples was conducted under NSW Fisheries Scientific Research Permit F89/1598-3.0 and NSW Department of Environment, Climate Change and Water Scientific Licence S12527. Animal ethics approval was granted by the Director General's Animal Ethics Committee of the Department of Primary Industries (Project number 02/3477).

Sample processing

White muscle tissue was collected from the dorsal region of fish, because this tissue has been shown to be representative of overall stable isotope signatures in fish and to be less variable than other tissues (Hesslein *et al.* 1993; Pinnegar and Polunin 1999). Tail muscle tissues were collected from *Macrobrachium intermedium* and *Parachela oxygastroides*. For *P. erythrodactyla* and *Scylla serrata*, only muscle tissues were collected following the removal of the exoskeleton.

Benthic sediment samples were rinsed with Milli-Q water through a 0.25-mm mesh sieve and finest size fractions (<0.25 mm) were collected from the collection basin for isotope analysis. Acid washing of sediment samples was performed to remove inorganic fractionation for $\delta^{13}C$ (Mazumder *et al.* 2010); untreated sediment subsamples were analysed for $\delta^{15}N$. All samples were oven dried at ~60°C for 48 h and then ground to a fine powder with a mortar and pestle that had been cleaned with ethanol between samples to prevent cross-contamination.

Isotope analysis was performed at the Australian Nuclear Science and Technology Organisation (ANSTO) in Sydney (NSW, Australia). Powdered and homogenised tissue samples were loaded into tin capsules and analysed with a continuous flow isotope ratio mass spectrometer (CF-IRMS; Model Delta V Plus; Thermo Scientific, Waltham, MA, USA) interfaced with an elemental analyser (Thermo Fisher Flash 2000 HT EA; Thermo Electron, Waltham, MA, USA). Data are reported relative to International Atomic Energy Agency (IAEA) secondary standards certified relative to Vienna Pee Dee Belemnite (VPDB) for carbon and air for nitrogen. A two-point calibration was used to normalise the data, using standards that bracket the samples being analysed. Two quality control reference samples were also included in each run. Results are accurate to ±1% for both %C and %N and to ±0.3‰ for $\delta^{13}C$ and $\delta^{15}N$. Stable

isotope values are reported in delta (δ) units in parts per thousand (‰) relative to the international standard and determined as follows:

$$X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000$$

where X is $\delta^{13}C$ or $\delta^{15}N$ and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ respectively. Because the lipid content of tissue is related to the molar ratio of carbon to nitrogen (C : N), when C : N was >3.5 (e.g. high lipid content), the lipid content for muscle tissues was normalised using mathematical equations suggested by Post *et al.* (2007) as follows:

$$\delta^{13}C_{\text{normalised}} = \delta^{13}C_{\text{untreated}} - 3.32 + 0.99 \times C:N$$

The trophic position of species (TPS) was calculated using the formula reported by Post (2002):

$$TPS = \lambda + (\delta^{15}N_{\text{organism}} - \delta^{15}N_{\text{base}} \text{ of food web}) \div 3.4$$

where λ is the trophic level of the organism used to estimate $\delta^{15}N$ at the base of the food web. In the present study, sediment organic matter (SOM) from study sites was identified as the likely base trophic resource (i.e. trophic level = 1; Kelleway *et al.* 2010).

Mixing model

A multiple-source mixing model (Phillips and Gregg 2003) was used to estimate the possible contributions of the three potential diet sources (mangrove leaves, mangrove roots and SOM) to the isotopic makeup of the *P. erythrodactyla* which was common to both study sites and because a common herbivore is likely to be important in mediating the transfer of organic carbon into the food web. Prior to modelling, the mean isotope values of diet sources were adjusted by 1‰ enrichment fractionation for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$ (Carrasco *et al.* 2012). The model runs were performed with an increment of 1% and a tolerance of 0.01% to obtain feasible solutions. Because mangrove root material was not collected from the Matang forest, for the purposes of the mixing model root isotope values for Matang were estimated from leaves using a leaf to root fractionation value of 3.14‰ for $\delta^{13}C$ and −1.08‰ for $\delta^{15}N$. Although these fractionations were derived from *A. marina* in the Sydney region (Kelleway *et al.* 2018), leaf to root fractionation of a similar range (mean 2.4‰) was also observed in *R. apiculata* in Indonesia (Weiss *et al.* 2016).

Statistical analyses

To test the relationship between taxonomic similarity and trophic position, we measured taxonomic similarity for all heterotrophs by assigning each species to a taxonomic level using the following divisions: (1) Kingdom, (2) Superphylum, (3) Phylum, (4) Subphylum, (5) Class, (6) Subclass/Superorder, (7) Order, (8) Suborder/Superfamily, (9) Family and (10) Genus. Taxonomic similarity between species was measured as the value of the most precise common taxonomic level (e.g. 10 for two species of the same genus), divided by 1 plus the value of the most detailed level of any of both taxa (following Cattin *et al.* 2004). This measure is a surrogate for time of phylogenetic divergence between the two taxa (Bersier and Kehrli 2008). Phylogenetic information was derived from the Integrated Taxonomic Information System (www.itis.gov, accessed 11 October 2017).

Dietary similarity was measured using Euclidean distance between species in relation to their position in the carbon and nitrogen isotope biplots. In comparing trophic position of species between ecosystems, we standardised values to account for the small difference in basal SOM signature between the two locations of 0.61 for $\delta^{13}C$ and 0.28 for $\delta^{15}N$ (depleted and enriched respectively at Matang). We performed a Mantel test (Legendre and Legendre 2012) to compare the matrices of trophic and taxonomic similarity.

Results

Food chain length

The nektonic community in both mangrove forests showed consistent enrichment in $\delta^{13}C$ with enrichment in $\delta^{15}N$ as might be expected if species were trophically linked, and sourcing carbon ultimately from the same basal source, most probably SOM on the floor of the mangrove forest (Fig. 2). Although the Matang mangrove forest is more diverse than at Towra Point, few species collected appeared to be independent of this trophic transfer, an exception being *Saurida tumbil,* which is highly depleted in $\delta^{13}C$ with regard to similarly positioned species, although not mangrove leaves. There is little difference in food chain length between the two mangroves, assuming jewfish is the top predator and SOM the basal source. *Argyosomus japonicus* is positioned 4.1 trophic levels above basal carbon at Towra Point, and *Johnius belangerii* is positioned 3.9 trophic levels above basal carbon in the Matang mangrove forest.

Taxonomic and trophic relationships

Although only two species were sampled in common between the Towra Point and Matang forests (*S. serrata and P. erythrodactyla*), there are several common genera and families (Table 1). Similarity in trophic position was significantly correlated with similarity in phylogeny across all species (Mantel test $P = 0.05$), although the correlation was weak (0.21). Below we outline several common elements between the trophic structure of the Matang and Towra Point mangrove forests corresponding to taxonomic affinities (Fig. 3).

Crustacea

Shrimp in Towra Point and Matang have a very similar role in converting SOM to a form available to the first-order predatory fish (Fig. 2). They occur one trophic level above the SOM, and one trophic level below these predatory species. Copepods have a very similar $\delta^{13}C$ signature in both systems (ranging from −22 to −23‰) and are positioned at the base of a major trophic axis in Matang, but less so at Towra Point. Mixing models suggest a contribution of mangrove root material to the diet of Sesarmidae, particularly in the Matang mangrove (Table 2). *S. serrata* is positioned with the first-order carnivores in both systems, much higher than the smaller Sesarmidae.

Nekton

The two Mugilidae (*L. argentea* at Towra Point and *Liza macrolepis* at Matang) are one of the few congeneric

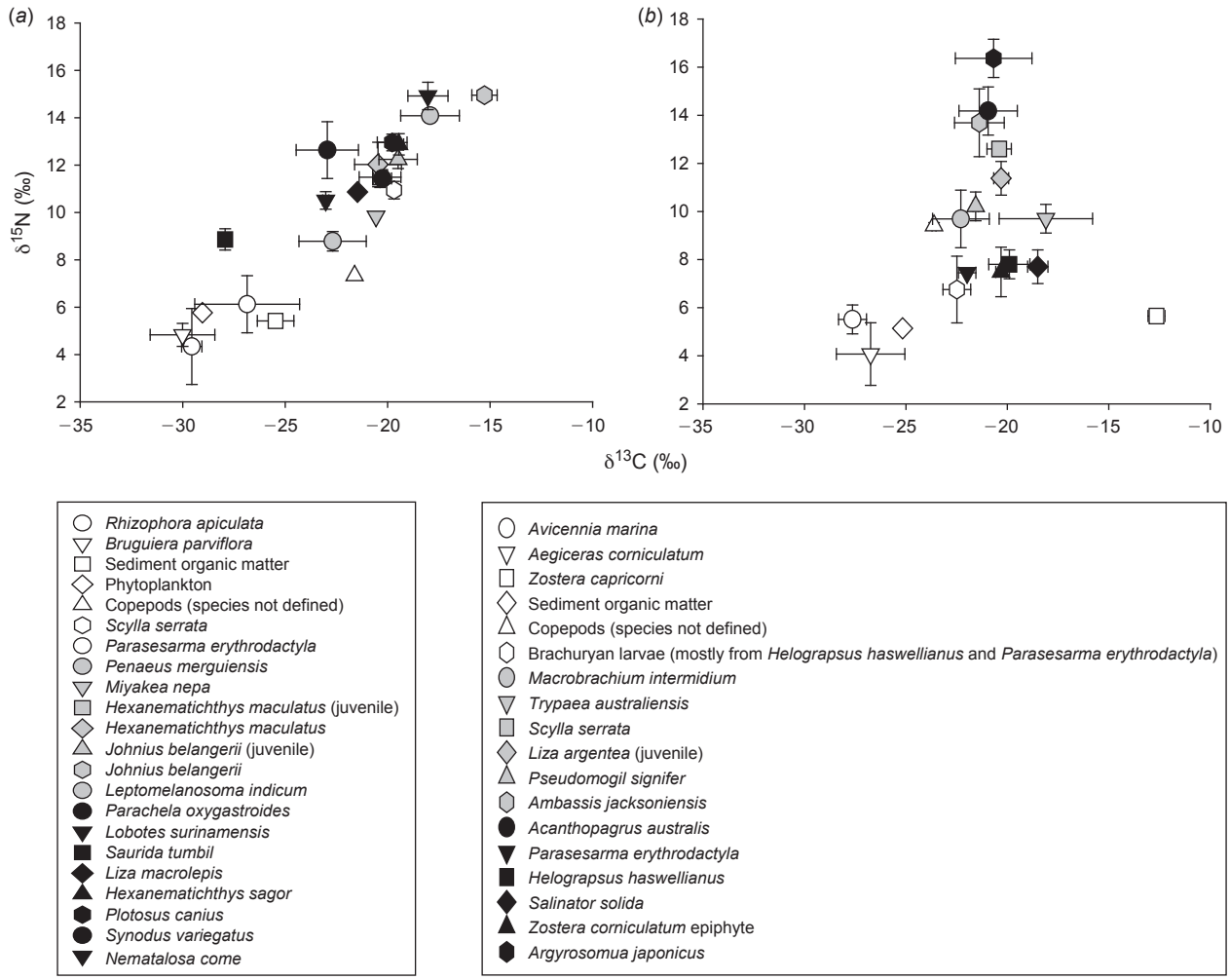


Fig. 2. Stable carbon and nitrogen biplot of mean (±s.d.) $\delta^{13}C$ and $\delta^{15}N$ values of food web components of (*a*) the tropical mangrove in Matang, Malaysia, and (*b*) the temperate mangrove at Towra Point, Australia. The temperate mangrove food web (*b*) has been modified from Mazumder *et al.* (2011).

comparisons between the two systems. These species occur at the same trophic level (~2.5 levels above the autotrophic producers), and their diet appears to be strongly linked to crustaceans, being enriched ~1‰ in $\delta^{13}C$ and ~3‰ in $\delta^{15}N$ in relation to the shrimp *M. intermedium* (Towra Point) and *Penaeus merguiensis* (Matang), consistent with predator–prey fractionation (DeNiro and Epstein 1981; Carrasco *et al.* 2012). Glassfish (*Ambassis jacksoniensis* at Towra Point and *P. oxygastroides* at Matang), although not closely related phylogenetically, are of similar morphology and occupy the same trophic position in both ecosystems, with $\delta^{13}C$ ranging from −21 to −22‰ and $\delta^{15}N$ ranging from 11 to 12‰ (Fig. 2). They are of a similar size at both locations (mean size 44 and 55 mm at Towra Point and Matang respectively). Both species of glassfish occur higher in the food chain than might be assumed from their small size (trophic position 3.0–3.5), although consistent with a zooplanktivorous rather than an omnivorous diet. The mulloway *A. japonicas* (Towra Point) and Belanger's jewfish *J. belangerii* (Matang) are the top predators sampled in each system, and both are members of the Family Sciaenidae.

Autotrophic sources of carbon

Major autotrophic sources were heavily depleted in both systems. Mangroves of the Rhizophoraceae (*R. apiculata* and *B. parviflora*) at Matang are more heavily depleted than *A. marina* and *A. corniculatum* at Towra Point, but these autotrophs are substantially depleted in $\delta^{13}C$ compared with the herbivores in both systems. At Towra Point, the saltmarsh *Sporobolus virginicus* and the seagrass *Zostera capricorni* are enriched compared with the herbivores, and Mazumder *et al.* (2011) suggested these are contributing to the SOM, yet these enriched autotrophic sources are absent from the Matang forest. Mangrove root systems are enriched in $\delta^{13}C$ compared with leaves of the same plant, with a difference of 3.1‰ at Towra Point for *A. marina* (Kelleway *et al.* 2018). In both cases, SOM is closer to mangrove root than leaf material, but could also be influenced

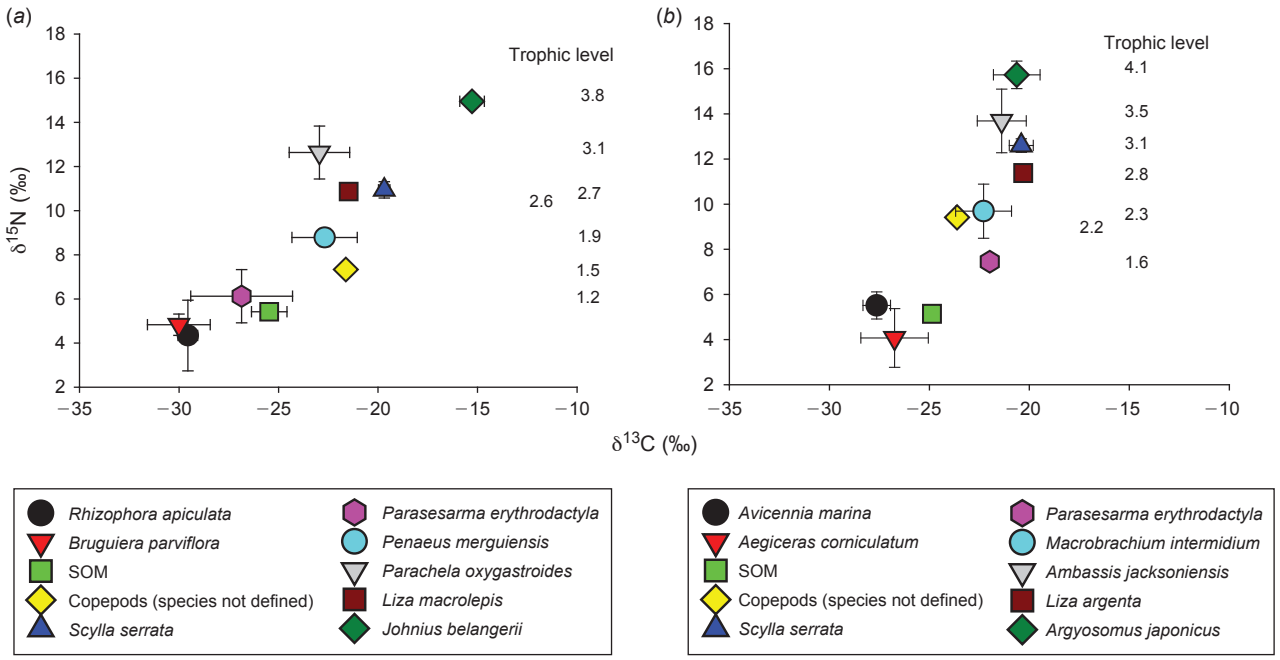


Fig. 3. Comparison of $\delta^{13}C$ and $\delta^{15}N$ biplots showing common elements of ecosystem structure between (*a*) the tropical mangrove in Matang, Malaysia, and (*b*) temperate mangrove at Towra Point, Australia. Data show the mean ± s.d. In (*a*) the trophic level values of 2.6 and 2.7 represent *L. macrolepis* and *S. serrata* respectively. In (*b*) the staggered trophic level values of 2.2 and 2.3 represent Copepods and *M. intermidium* respectively. SOM, sediment organic matter.

Table 2. Diet source mixing model results for Sesarmidae
Numbers represent the modelled percentage contribution to diet, and the probable range within one standard deviation

Diet source	*Parasesarma erythrodactyla*	
	Matang mangrove	Towra Point mangrove
Avicennia marina leaves		1.0 (0–3)
Avicennia marina root		4.8 (0–13)
Rhizophora apiculata leaves	24.4 (15–38)	
Rhizophora apiculata root	71.9 (61–84)	
Sediment organic matter	3.7 (0–10)	94.2 (87–100)

by the more enriched signal of marine benthic algae. The basal autotrophs have a similar $\delta^{15}N$ (4–5‰) in both systems.

Discussion

Comparison of trophic length and structure

We anticipated considerable differences between the temperate mangrove forest at Towra Point and the tropical mangrove forest at Matang to promote widely different trophic interactions. At Towra, a near monoculture of *A. marina* forms a fringing zone between a landward saltmarsh plain and a seaward seagrass meadow. At Matang, a floristically and structurally diverse mangrove forest of 40 151 ha, approximately double the biomass of Towra Point, produces an estimated 1×10^6 Mg of detritus annually (Gong and Ong 1990). The greater biomass, and higher floristic and nektonic diversity, may have been expected to yield starkly different ecosystem trophic structure, particularly when few if any species are common between the two locations.

Notwithstanding these differences, our stable isotope analyses suggest marked similarities in trophic structure between these ecosystems. The top sampled predators *J. belangerii* at Matang and *A. japonicas* at Towra Point belong to the Family Sciaenidae, the 'jewfish' or 'croaker'. These species occur at the same trophic position, approximately four trophic levels above the basal autotrophs, despite the higher productivity and size of the Matang mangrove ecosystem.

Nearly every species encountered at Towra Point finds a direct analogue in both form and function in the Matang ecosystem. In some cases, these are congeneric members; for example, species of the grapsid crab genera *Sesarma*, the mullet *Liza*, and the mud crab *Scylla*. In each case, the species occupy the same trophic position and often near-identical carbon and nitrogen isotope ratios. In some cases, species from different genera have very similar morphological and behavioural characteristics and are positioned in the same trophic position in both systems. The glassfish are a good example (*A. jacksoniensis* at Towra Point and *P. oxygastroides* at Matang). Similarly, the shrimp *M. intermedium* (Towra Point) and *P. merguiensis* (Matang) belong to different families but have precisely the same tropic position and stable isotope signatures in the two systems.

The idea that species can perform ecologically equivalent roles has a long history (Odum 1959; Bazzaz and Pickett 1980; Menge and Sutherland 1987) despite the overwhelming focus of research on interactions among small groups of species occupying unique niches in specific locations (Zamora 1999,

2000). Luczkovich *et al.* (2003) used the term 'regular equivalence' to describe species within an ecosystem playing the same structural roles, consuming the same class of prey (if not necessarily the same species) and being consumed by the same class of predator. Here, we propose a degree of regular equivalence to organisms across widely separated geographic locations, while pointing to a degree of taxonomic and morphological similarity. Where this occurs, ecosystem stability may be enhanced by the substitutability (and hence redundancy) of members (Resetarits and Chalcraft 2007). Such patterns of ecological or trophic organisation repeated by congeneric species (for example) across locations may provide insights into coevolution of morphological and behavioural traits (Thompson 1999).

Sources of dietary carbon

SOM is an important primary source of autotrophic carbon in both systems, and in both systems is strongly enriched in $\delta^{13}C$ relative to mangrove leaf samples. There are two potential explanations of this discrepancy between the dominant autotrophic source and the SOM signature: (1) that mangrove biomass contributions to SOM are dominated by roots not leaves, with mangrove root systems enriched compared with leaves of the same individuals (Kelleway *et al.* 2018), but the extent of the enrichment of roots compared to leaves only explains approximately half the enrichment in SOM $\delta^{13}C$; and (2) it is probable that benthic algae are also contributing to surface organic carbon.

Numerous studies of crab diet in tropical mangrove systems have identified grapsid crabs as processors of mangrove leaves (Robertson 1986; Micheli 1993). Ashton (2002) suggested that in Malaysia more than 30% of mangrove litterfall may be processed by crabs. However, Skov and Hartnoll (2002) pointed to the paradox that mangrove leaf material has a high tannin content and C : N ratio, suggesting this to be a unpalatable source of dietary carbon. Isotope studies have further pointed to a wide difference between mangrove leaf material and crab isotope signatures, particularly in temperate settings (Mazumder and Saintilan 2010). Our results suggest that *Sesarma* in Matang is more likely to be dependent upon mangrove biomass than in temperate Australia. If the enrichment in root material with regard to leaves is consistent with *R. apiculata* measured by Weiss *et al.* (2016) in nearby Indonesian sites ($\delta^{13}C$ −27.96‰ for roots *v.* −30.35‰ for leaves), fine mangrove roots are likely to be an important component of the crab diet here.

Rodelli *et al.* (1984) working in the Klang mangroves found the juvenile banana prawn *P. merguiensis* consumed ~65% mangrove-derived carbon, consistent with gut content analysis (Chong and Sasekumar 1981). Chong (2007) suggested that mangrove detritus could contribute up to 84% of shrimp diet in the Matang rivers. Our analysis suggests that at both Towra Point and Matang, shrimp are dependent upon surface organic matter, which is generally enriched compared with mangrove leaves. The position of shrimp is identical in both systems, as is the position of surface organic matter, despite differences in the degree of mangrove leaf enrichment between Matang and Towra Point. Although mangrove leaves may well contribute to SOM, other sources, such as mangrove root material and benthic algae, are likely to be as important.

Implications

The significance of mangroves to fisheries production has long been recognised in both settings. Malaysia's mangroves sustain more than 50% of annual fish landings of over 1×10^6 Mg year^{-1} (Chong 2007). Catches of shrimp (*Penaeus* sp.) are heavily weighted towards mangrove-fringed coastlines on Peninsular Malaysia (Sasekumar and Chong 1987). In South-east Australia, catches of several species of finfish and the mud crab *S. serrata* are closely linked to the area of intertidal wetland, including mangroves (Saintilan 2004). Clarification of the links between high-trophic order fishes, habitat resources and intermediate species contributing to the 'trophic relay' of resources from the wetland to the broader estuary or nearshore environment has strengthened the case for intertidal wetland management in support of fisheries values throughout the Indo-Pacific (Mazumder *et al.* 2006*b*; Qin *et al.* 2015).

We have identified a series of trophically analogous individuals between the Matang and Towra Point mangrove ecosystems. The observation that the most common and therefore trophically significant members of the Towra Point mangrove find direct analogues in the most common members of the Matang ecosystem suggests a common trophic organisation. This trophic similarity is remarkable given the distance between these sites, differences in resource base and non-overlap of species assemblage. Although occurring near the poleward limit of mangroves globally, the Towra Point mangrove has the essential elements giving expression to the same food chain length as Matang: herbivores processing mangrove and other intertidal autotrophic production, zooplankton assemblage including brachyuran larvae, zooplanktivores and omnivores taking advantage of periodic larval spawning (Mazumder *et al.* 2011; Ricardo *et al.* 2014) and carnivores targeting the relatively dense populations of fishes associated with tidal creeks within the mangrove (Nagelkerken *et al.* 2008). The taxonomic affinities at the genus and family levels may suggest evolutionary divergence across the geographic range over which these species interactions occur, without the loss of ecological function. Towra Point is less diverse, and the essential elements provide an insight into the positional redundancies within the Matang ecosystem. For example, there are several 'central species' providing intermediate trophic connections (Lai *et al.* 2012), which use similar resources to the *Penaeus* shrimps and mullet at Matang, but are unlikely to displace these given the geographic continuity of these elements. Greater competition for resources (e.g. the additional top predators of *Lobotes surinamensis* and *Leptomelanosoma indicum* in the Matang forest, and the more diverse first-order carnivore assemblage) is offset by the greater resource base. Matang forest is commercially harvested, including a practice of rotational clear felling in Kuala Sepetang North and South, two of the four forest management areas, and the effect of this practice on aquatic diversity and structure is poorly understood. This study suggests that whatever the impact of commercial operations on Matang mangrove ecological structure, important ecological associations have remained in place.

This study illustrates the energetic support mangroves provide to top-order predators of importance to fisheries in Malaysia and south-east Australia. Mangroves are inundated only periodically, and yet the species harvested from mangrove

creeks and other nearshore aquatic environments are tightly interconnected trophically, and clearly dependent upon surface organic material accumulating on the floor of the mangrove forest. These studies provide a strong argument for the continued protection of mangroves.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

The research in Matang was funded by Universiti Putra Malaysia, IPB Putra Grant.

Acknowledgements

The authors thank Siti Balqis and Fareha for their assistance in field sampling and sample processing. Thanks to Karthik Gopi for assistance with stable isotope sample preparation. The authors thank Stuart Hankin (ANSTO) for drawing Fig. 1 and Jagoda Crawford (ANSTO) for assistance with statistical analysis.

References

Abrantes, K., and Sheaves, M. (2009). Food web structure in a near-pristine mangrove area of the Australian Wet Tropics. *Estuarine, Coastal and Shelf Science* **82**(4), 597–607. doi:10.1016/J.ECSS.2009.02.021

Arnaud-Haond, S., Teixeira, S., Massa, S., Billot, C., Saenger, P., Coupland, G., Duarte, C., and Serrao, E. (2006). Genetic structure at range edge: low diversity and high inbreeding in Southeast Asian mangrove (*Avicennia marina*) populations. *Molecular Ecology* **15**(12), 3515–3525. doi:10.1111/J.1365-294X.2006.02997.X

Ashton, E. C. (2002). Mangrove sesarmid crab feeding experiments in Peninsular Malaysia. *Journal of Experimental Marine Biology and Ecology* **273**(1), 97–119. doi:10.1016/S0022-0981(02)00140-5

Ashton, E. C., Macintosh, D. J., and Hogarth, P. J. (2003). A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia. *Journal of Tropical Ecology* **19**(2), 127–142. doi:10.1017/S0266467403003158

Bazzaz, F., and Pickett, S. (1980). Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* **11**(1), 287–310. doi:10.1146/ANNUREV.ES.11.110180.001443

Bersier, L.-F., and Kehrli, P. (2008). The signature of phylogenetic constraints on food-web structure. *Ecological Complexity* **5**(2), 132–139. doi:10.1016/J.ECOCOM.2007.06.013

Bouillon, S., Raman, A., Dauby, P., and Dehairs, F. (2002). Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). *Estuarine, Coastal and Shelf Science* **54**(5), 901–913. doi:10.1006/ECSS.2001.0864

Carrasco, N. K., Perissinotto, R., and Nel, H. A. (2012). Diet of selected fish species in the freshwater-deprived St Lucia Estuary, South Africa, assessed using stable isotopes. *Marine Biology Research* **8**(8), 701–714. doi:10.1080/17451000.2012.678855

Cattin, M.-F., Bersier, L.-F., Banašek-Richter, C., Baltensperger, R., and Gabriel, J.-P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature* **427**(6977), 835–839. doi:10.1038/NATURE02327

Chong, V. (2007). Mangroves-fisheries linkages – the Malaysian perspective. *Bulletin of Marine Science* **80**(3), 755–772.

Chong, V., and Sasekumar, A. (1981). Food and feeding habits of the white prawn *Penaeus merguiensis*. *Marine Ecology Progress Series* **5**, 185–191. doi:10.3354/MEPS005185

Cohen, J. E., and Newman, C. M. (1991). Community area and food-chain length: theoretical predictions. *American Naturalist* **138**(6), 1542–1554. doi:10.1086/285299

DeNiro, M. J., and Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* **45**, 341–351. doi:10.1016/0016-7037(81)90244-1

Duke, N. C. (1992). Mangrove floristics and biogeography. *Tropical Mangrove Ecosystems* **41**, 63–100. doi:10.1029/CE041P0063

Duke, N., Ball, M., and Ellison, J. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters* **7**(1), 27–47. doi:10.2307/2997695

Gong, W.-K., and Ong, J.-E. (1990). Plant biomass and nutrient flux in a managed mangrove forest in Malaysia. *Estuarine, Coastal and Shelf Science* **31**(5), 519–530. doi:10.1016/0272-7714(90)90010-O

Hashimoto, T. R., Saintilan, N., and Haberle, S. G. (2006). Mid-Holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond River Estuary, New South Wales, Australia. *Geographical Research* **44**(1), 63–76. doi:10.1111/J.1745-5871.2006.00360.X

Hesslein, R. H., Hallard, K., and Ramlal, P. (1993). Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$. *Canadian Journal of Fisheries and Aquatic Sciences* **50**(10), 2071–2076. doi:10.1139/F93-230

Hollingsworth, A., and Connolly, R. M. (2006). Feeding by fish visiting inundated subtropical saltmarsh. *Journal of Experimental Marine Biology and Ecology* **336**(1), 88–98. doi:10.1016/J.JEMBE.2006.04.008

Holt, R. D. (1996). 'Food Webs; Integration of Patterns and Dynamics.' (Chapman and Hall: New York, NY, USA.)

Kelleway, J., Mazumder, D., Wilson, G. G., Saintilan, N., Knowles, L., Iles, J., and Kobayashi, T. (2010). Trophic structure of benthic resources and consumers varies across a regulated floodplain wetland. *Marine and Freshwater Research* **61**(4), 430–440. doi:10.1071/MF09113

Kelleway, J. J., Saintilan, N., Macreadie, P. I., Skilbeck, C. G., Zawadzki, A., and Ralph, P. J. (2016). Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Global Change Biology* **22**(3), 1097–1109. doi:10.1111/GCB.13158

Kelleway, J. J., Mazumder, D., Baldock, J. A., and Saintilan, N. (2018). Carbon isotope fractionation in the mangrove *Avicennia marina* has implications for food web and blue carbon research. *Estuarine, Coastal and Shelf Science* **205**, 68–74. doi:10.1016/J.ECSS.2018.03.011

Laegdsgaard, P., and Johnson, C. R. (1995). Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Marine Ecology Progress Series* **126**, 67–81. doi:10.3354/MEPS126067

Lai, S.-M., Liu, W.-C., and Jordán, F. (2012). On the centrality and uniqueness of species from the network perspective. *Biology Letters* **8**(4), 570–573. doi:10.1098/RSBL.2011.1167

Legendre, P., and Legendre, L. F. (2012). 'Numerical Ecology.' (Elsevier: Amsterdam, Netherlands.)

Luczkovich, J. J., Borgatti, S. P., Johnson, J. C., and Everett, M. G. (2003). Defining and measuring trophic role similarity in food webs using regular equivalence. *Journal of Theoretical Biology* **220**(3), 303–321. doi:10.1006/JTBI.2003.3147

Mazumder, D. (2009). 'Ecology of Burrowing Crabs in Temperate Saltmarsh of South-east Australia.' (CSIRO Publishing: Melbourne, Vic., Australia.)

Mazumder, D., and Saintilan, N. (2010). Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. *Wetlands* **30**(2), 375–380. doi:10.1007/S13157-010-0021-2

Mazumder, D., Saintilan, N., and Williams, R. J. (2005). Temporal variations in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. *Wetlands Ecology and Management* **13**(4), 457–467. doi:10.1007/S11273-004-0814-2

Mazumder, D., Saintilan, N., and Williams, R. J. (2006*a*). Fish assemblages in three tidal saltmarsh and mangrove flats in temperate NSW, Australia: a comparison based on species diversity and abundance. *Wetlands Ecology and Management* **14**(3), 201–209. doi:10.1007/S11273-005-7887-4

Mazumder, D., Saintilan, N., and Williams, R. J. (2006*b*). Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. *Marine and Freshwater Research* **57**(2), 193–199. doi:10.1071/MF05040

Mazumder, D., Williams, R. J., Reid, D., Saintilan, N., and Szymczak, R. (2008). Variability of stable isotope ratios of glassfish (*Ambassis jacksoniensis*) from mangrove/saltmarsh environments in southeast Australia and implications for choosing sample size. *Environmental Bioindicators* **3**(2), 114–123. doi:10.1080/15555270802266003

Mazumder, D., Iles, J., Kelleway, J., Kobayashi, T., Knowles, L., Saintilan, N., and Hollins, S. (2010). Effect of acidification on elemental and isotopic compositions of sediment organic matter and macroinvertebrate muscle tissues in food web research. *Rapid Communications in Mass Spectrometry* **24**(20), 2938–2942. doi:10.1002/RCM.4729

Mazumder, D., Saintilan, N., Williams, R. J., and Szymczak, R. (2011). Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. *Marine and Freshwater Research* **62**(1), 11–19. doi:10.1071/MF10076

McPhee, J. J., Freewater, P., Gladstone, W., Platell, M. E., and Schreider, M. J. (2015). Glassfish switch feeding from thalassinid larvae to crab zoeae after tidal inundation of saltmarsh. *Marine and Freshwater Research* **66**(11), 1037–1044. doi:10.1071/MF14202

Melville, A. J., and Connolly, R. (2003). Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. *Oecologia* **136**(4), 499–507. doi:10.1007/S00442-003-1302-8

Menge, B. A., and Sutherland, J. P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**(5), 730–757. doi:10.1086/284741

Micheli, F. (1993). Feeding ecology of mangrove crabs in north eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. *Journal of Experimental Marine Biology and Ecology* **171**(2), 165–186. doi:10.1016/0022-0981(93)90002-6

Nagelkerken, I., Blaber, S., Bouillon, S., Green, P., Haywood, M., Kirton, L., Meynecke, J.-O., Pawlik, J., Penrose, H., and Sasekumar, A. (2008). The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquatic Botany* **89**(2), 155–185. doi:10.1016/J.AQUABOT.2007.12.007

Odum, E. P. (1959). 'Fundamentals of Ecology.' (WB Saunders Company: Philadelphia, PA, USA.)

Phillips, D. L., and Gregg, J. W. (2003). Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136**(2), 261–269. doi:10.1007/S00442-003-1218-3

Pinnegar, J., and Polunin, N. (1999). Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implications for the study of trophic interactions. *Functional Ecology* **13**(2), 225–231. doi:10.1046/J.1365-2435.1999.00301.X

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**(3), 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., Montaña, C. G., and Rosenheim, J. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**(1), 179–189. doi:10.1007/S00442-006-0630-X

Qin, H., Sheng, Q., Chu, T., Wang, S., and Wu, J. (2015). Import and export fluxes of macrozooplankton are taxa- and season-dependent at Jiuduansha Marsh, Yangtze River estuary. *Estuarine, Coastal and Shelf Science* **163**, 254–264. doi:10.1016/J.ECSS.2014.11.024

Resetarits, W. J., and Chalcraft, D. R. (2007). Functional diversity within a morphologically conservative genus of predators: implications for functional equivalence and redundancy in ecological communities. *Functional Ecology* **21**(4), 793–804. doi:10.1111/J.1365-2435.2007.01282.X

Ricardo, G. F., Davis, A. R., Knott, N. A., and Minchinton, T. E. (2014). Diel and tidal cycles regulate larval dynamics in salt marshes and mangrove forests. *Marine Biology* **161**(4), 769–784. doi:10.1007/S00227-013-2376-4

Robertson, A. (1986). Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. *Journal of Experimental Marine Biology and Ecology* **102**(2–3), 237–248. doi:10.1016/0022-0981(86)90179-6

Rodelli, M. R., Gearing, J., Gearing, P., Marshall, N., and Sasekumar, A. (1984). Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia* **61**(3), 326–333. doi:10.1007/BF00379629

Saintilan, N. (2004). Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine, Coastal and Shelf Science* **61**(4), 591–601. doi:10.1016/J.ECSS.2004.07.002

Sasekumar, A., and Chong, V. C. (1987). 'Mangroves and Prawns: Further Perspectives.' (University of Malaya: Kuala Lumpur, Malaysia.)

Schoener, T. W. (1989). Food webs from the small to the large: the Robert H. MacArthur Award Lecture. *Ecology* **70**(6), 1559–1589. doi:10.2307/1938088

Skov, M. W., and Hartnoll, R. G. (2002). Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? *Oecologia* **131**(1), 1–7. doi:10.1007/S00442-001-0847-7

Thompson, J. N. (1999). Specific hypotheses on the geographic mosaic of coevolution. *American Naturalist* **153**, S1–S14. doi:10.1086/303208

Weiss, C., Weiss, J., Boy, J., Iskandar, I., Mikutta, R., and Guggenberger, G. (2016). Soil organic carbon stocks in estuarine and marine mangrove ecosystems are driven by nutrient colimitation of P and N. *Ecology and Evolution* **6**(14), 5043–5056. doi:10.1002/ECE3.2258

Zamora, R. (1999). Conditional outcomes of interactions: the pollinator–prey conflict of an insectivorous plant. *Ecology* **80**(3), 786–795.

Zamora, R. (2000). Functional equivalence in plant–animal interactions: ecological and evolutionary consequences. *Oikos* **88**(2), 442–447. doi:10.1034/J.1600-0706.2000.880222.X

Handling Editor: Max Finlayson

Hydrobiologia (2017) 803:239–250
DOI 10.1007/s10750-017-3150-2

MANGROVES IN CHANGING ENVIRONMENTS

Review Paper

Mass spawning of crabs: ecological implications in subtropical Australia

Neil Saintilan · Debashish Mazumder

Received: 28 September 2016 / Revised: 27 February 2017 / Accepted: 27 February 2017 / Published online: 22 March 2017
© Springer International Publishing Switzerland 2017

Abstract We review links between autotrophic production, crab herbivory and estuarine food chains in southeastern Australia, a region where mangrove and saltmarsh co-exist towards mangrove poleward limits. Studies in estuaries and embayments across the region have demonstrated a consistent and important role of crab larvae released in synchronised spawning during the spring tide in supplementing the diet of zooplanktivorous fishes. These numerically dominant fishes have been linked through isotopic studies to commercially important predator species. The role of macrophytic vegetation (mangrove and saltmarsh) in the diet of crabs remains controversial, though isotopic analysis has demonstrated the contribution of the C4 grass *Sporobolus virginicus* to crabs feeding in saltmarsh. Other dietary sources include microphytic algae, and potentially stranded zooplankton. The link between sediment organic matter, crab and zooplanktivore isotopic composition remained tightly coupled in spite of variation in anthropogenic N between estuaries and the isotopic signature of mangroves. Long-term threats to these trophic linkages include coastal squeeze associated with sea-level rise, and the fragmentation and disconnection of habitats.

Keywords Habitat · Diet · Stable isotope · Trophic relay · Saltmarsh · Mangrove

Guest editors: K. W. Krauss, I. C. Feller, D. A. Friess & R. R. Lewis III / Causes and Consequences of Mangrove Ecosystem Responses to an Ever-Changing Climate

N. Saintilan (✉) · D. Mazumder
Department of Environmental Sciences, Macquarie University, Sydney, NSW 2109, Australia
e-mail: neil.saintilan@mq.edu.au

D. Mazumder
Australian Nuclear Science and Technology Organisation, Locked Bag 2001, Kirrawee DC, NSW 2232, Australia

Introduction

Of the many ecological goods and services provided by intertidal mangrove and saltmarsh (Costanza et al., 2014), the provision of habitat for fisheries (including shell fisheries) is one of the more well documented and publically recognised (Nagelkerken et al., 2008). Mangroves and saltmarshes have long been associated with productive fisheries, a perception supported by regional-scale comparisons of fishery landing data (Meynecke et al., 2008; Saintilan et al., 2014). Aburto-Oropeza et al. (2008) analysed fish landing data from the Gulf of California in relation to climate, and the area of mangrove, seagrass and open-water lagoon habitat. They found that mangrove alone of the chosen variables predicted fish landings, and that 31.7% of the small-scale fisheries landings comprised fish and crab species dependent upon mangrove. In an analysis of fish landings from 55 estuaries subtropical and temperate Australia, Saintilan (2004) identified the importance of mangrove for long-finned eel *Anguilla*

reinhardtii (Steindachner, 1867), and the sand mullet *Myxus elongatus* (Günther, 1861), both important predators in mangrove creeks. Landings of the commercially important mud crab *Scylla serrata* (Forskål, 1775) were more accurately predicted by a combination of mangrove and saltmarsh rather than mangrove area alone.

At the site scale, mangroves and saltmarshes are documented as nursery sites, providing structural complexity and nutritional value important to juvenile fish (Robertson & Duke, 1987; Nordlie, 2003). However, the specific mechanisms whereby fish and other organisms gain nutritional benefit from mangroves and saltmarshes have been the cause of conjecture and controversy. Few species of fish can utilise mangrove and saltmarsh during low tide, and migration of species between adjacent habitats becomes has important implications for nutrient and energy transfer (Marcus, 2005). Stable isotope analysis has in some circumstances supported (Melville & Connolly, 2003), and other settings questioned (Loneragan et al., 1997; Lugendo et al., 2006) a strong link between vegetated habitats and fish dietary carbon in the wider estuarine or nearshore environments. A better understanding of the linkages between intertidal habitat, autotrophic carbon sources, and their trophic pathways is important for the protection of food chains vital to human wellbeing.

Research conducted in several locations across the Indo-Pacific region in recent decades has demonstrated that grapsid crabs are keystone species in the estuarine ecosystems of the region. The role of crabs in processing leaf litter in tropical mangroves in the Indo-Pacific has been extensively covered in earlier reviews (Lee, 1998; Cannicci et al., 2008; Kristensen et al., 2008). Here we focus on the contribution crabs make to the trophic ecology of estuaries, and whether these contributions are compromised by elevated Nitrogen levels. Intertidal crabs have been demonstrated to make substantial contributions to the zooplankton composition of estuarine waters across the Indo-Pacific, from the saltmarshes of the Yangzte (Qin et al., 2015) to the estuarine wetlands of SE Australia (Mazumder et al., 2011; Ricardo et al., 2014). Our review utilises as a case study the southeastern Australian east coast where, in common with many of the subtropical and temperate coastlines of the world, mangrove and saltmarsh compete for dominance, and rapid population growth has led to the alteration of nutrient and sediment inputs in estuaries. Throughout this region, the aerial extent of mangrove and saltmarsh has been impacted by reclamation, with widespread losses to industry and infrastructure, residential and recreational developments (Rogers et al., 2016). These anthropogenic pressures on saltmarsh extent have been exacerbated by climate change, and throughout the region, encroachment of mangrove into saltmarsh (Saintilan & Williams, 1999) is consistent with a global pattern of mangrove proliferation at poleward mangrove limits in cool climates (Saintilan et al., 2014), associated with sea-level rise and the relaxation of temperature constraints (Osland et al., 2013; Cavanaugh et al., 2014; Armitage et al., 2015; Giri & Long, 2016). We describe a now well-documented link between crab larval production and the feeding habits of zooplanktivorous fishes that provide a key link between wetland habitats and the diet of commercially important species.

Ecological significance of crabs

While portunid crabs (including the commercially important *S. serrata*) are found in the coastal wetlands of SE Australia, by far, the most common shore crabs belong to the Grapsidae and Ocypodidae families (Mazumder et al., 2006; Platell & Freewater, 2009). Of the Grapsidae, *Helograpsus haswellianus* (Whitelegge, 1889) is particularly common in saltmarsh, breeding mostly during the winter months. *Parasesarma erythrodactyla* (Hess, 1865) and *Paragrapsus laevis* (Dana, 1852), while found in saltmarsh, are more common in the mangrove forests, and *P. erythrodactyla* more commonly breeds during the summer months. *Heloecius cordiformis* (Milne Edwards, 1837) is the most common member of the Ocypodidae (Mazumder et al., 2006).

Coastal saltmarsh on the Australian east coast (Fig. 1) is inundated on consecutive spring tides, occurring at night during winter and during daylight hours in the summer. Both (Mazumder, 2004) in the Sydney region (34°S), and (Hollingsworth & Connolly, 2006) working over 1000 km to the north in SE Queensland (27°30′S), found crab larval release occurred from the second in a sequence of successive daily high tides during the monthly spring tide phase, concluding that the first tide inundation most probably acting as a trigger for spawning. The synchronised

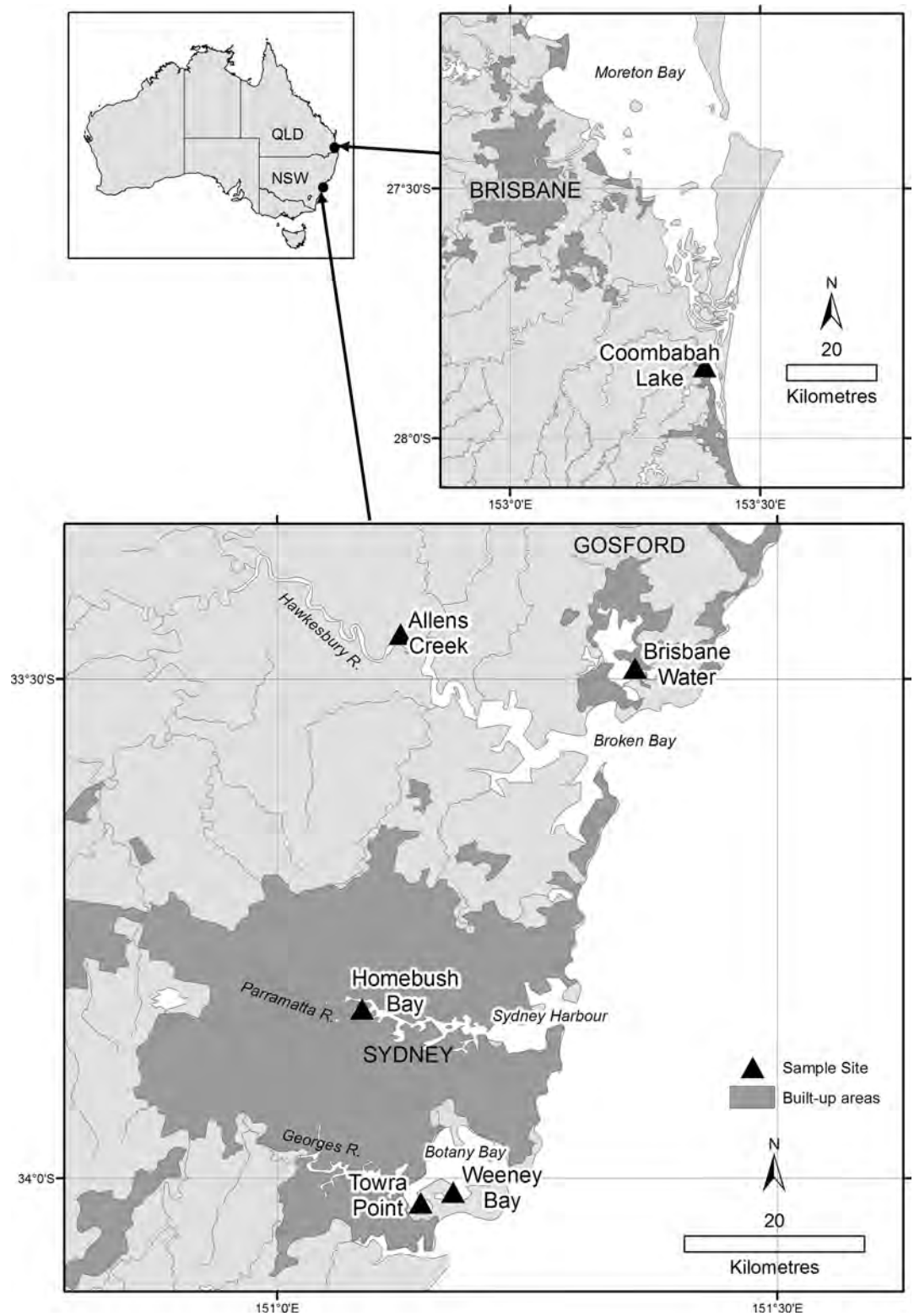


Fig. 1 Map of SE Australia showing the locations cited in the text

spawning of crabs in the intertidal environment is analogous to the mass spawning of corals (Harrison et al., 1984), which occurs in association with the full moon (Bouwmeester et al., 2015; Romero-Torresb et al., 2016). By spawning on mass, crabs are able to saturate predation capacity, providing a higher proportional survival rate. Crab zoaea are released predominantly into the highest tides of the year, both in spring and summer (Fig. 2), and are relatively strong swimmers (Epifanio & Cohen, 2016), maximising dispersal from the strongest tidal currents, thereby facilitating their movement to and incorporation into pelagic zooplankton communities.

The mass spawning of crabs in the estuaries of eastern Australia provides an important nutritional supplement to the estuarine ecosystems of the region. Crab and gastropod larvae in the saltmarsh during the spring tide cycle present the highest concentration of larvae available in estuarine environments (Mazumder et al., 2009), some four times greater density than adjacent mangrove and seagrass habitat. This is a remarkably efficient feeding opportunity, and the concentration of ambassids per unit volume of water is higher in the saltmarsh during the spring tide than in adjacent mangrove (Mazumder et al., 2009; Fig. 2). Sampling on the ebb tide (Mazumder et al., 2006) found high concentrations of crab larvae in the stomachs of the Port Jackson Glassfish (*Ambassis jacksoniensis*, Macleay, 1881), the Blue-eye (*Pseudomugil signifier*, Kner, 1867) and the Flat-tail Mullet (*Liza argentea*, Quoy & Gaimard, 1825), suggesting that itinerant fish visiting the saltmarsh during the high tide and feeding on crab larvae provided for the "trophic relay" of carbon from the saltmarsh to the estuary. Gastropod larvae, while also found in high abundance (Fig. 2), did not contribute substantially to the diet of Glassfish or Flat-tail Mullet (Mazumder, 2004). The study was the first to suggest the

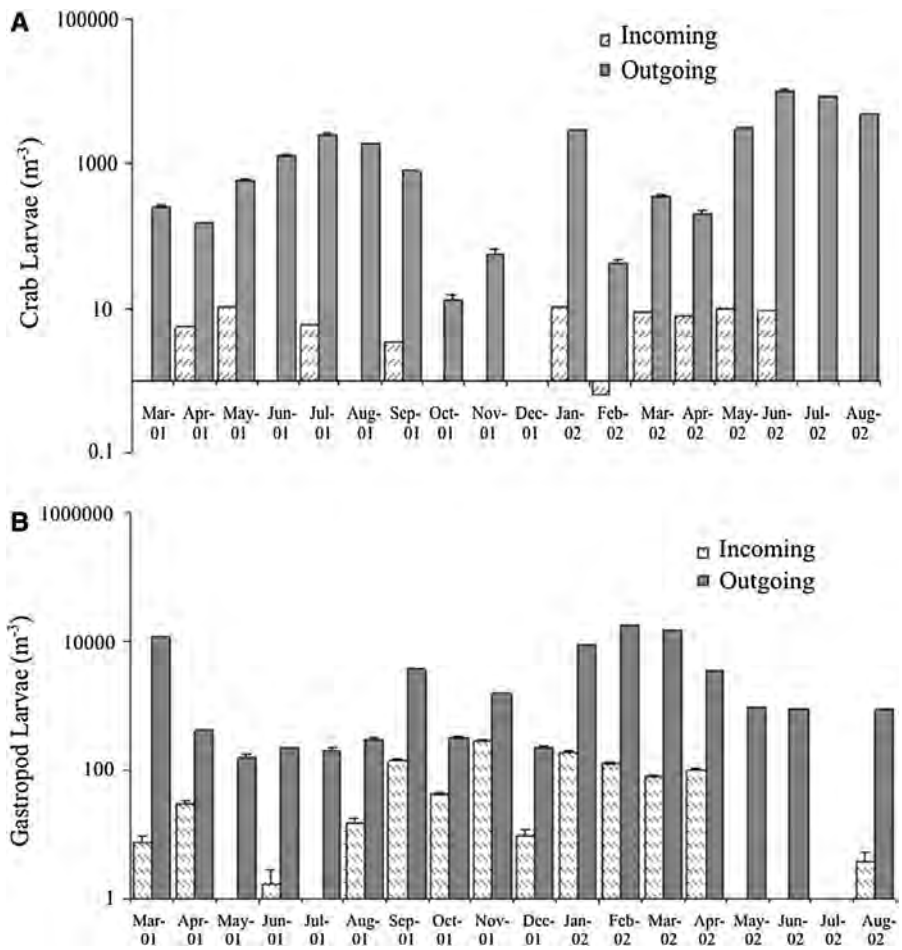


Fig. 2 Mean (±SE) abundance of crab larvae (**A**) and gastropod larvae (**B**) in in-flowing and out-flowing tidal waters of saltmarsh at Towra Point, 2001/02 during the spring tide phase. Logarithmic scale shown. Data sourced from Mazumder (2004, pp. 99, 100)

mechanism for a significant contribution of saltmarsh to fisheries in the region. A similar study in nearby Brisbane Waters (Platell & Freewater, 2009) found *A. jacksoniensis*, *Atherinosoma microstoma* (Günther, 1861) and *Redigobius macrostoma* (Günther, 1861) to be feeding almost exclusively on crab larvae released in saltmarsh during the spring tide.

The relative fullness of ambassid stomachs over different phases of the tide cycle (flood vs ebb; neap vs spring) was subsequently used in several studies to track the contribution of crab zoea to the diet of this numerically important species in the estuaries of eastern Australia. For example, McPhee et al. (2015b) working in Broken Bay on the central coast New South Wales, and Hollingsworth & Connolly (2006) working in Moreton Bay, SE Queensland, found the stomach content of *A. jacksoniensis* to be fuller on the ebb tide following saltmarsh inundation than at any other time, with a high proportional contribution of crab larvae. Rather than fasting between spring tide inundation events, the species was able to switch to other zooplankton sources, notably Thalassinid larvae (McPhee et al., 2015a). Isotope analysis of higher trophic levels of the estuarine ecosystem links commercially important species of fish (e.g. the bream *Acanthopagrus australis*, Günther, 1859), to omnivorous and zooplanktivorous fish feeding on crab zoea derived from wetland environments (Mazumder et al., 2011).

Primary sources of carbon

Wetland macrophytes are an obvious potential source of nutrition for crabs when feeding in wetlands. Observations of crab feeding behaviours in Queensland have demonstrated crabs will not forage far from their burrows, with most feeding across a range of only a few square metres, during low tide (Guest et al., 2004). The highly localised habit of crab foraging has made possible observational studies of crab emergence (Nobbs & McGuinness, 1999), difference in density of species between habitats (Mazumder, 2004) and probable sources of diet (Guest & Connolly, 2005; Alderson et al., 2013).

Several studies in tropical mangroves of eastern Australia have stressed the importance of fallen mangrove leaves as a nutritional source for crabs (Robertson, 1986; Micheli, 1993). Leaf tethering experiments have been used to demonstrate the burial of leaves by crabs (Robertson, 1986; McIvor & Smith, 1995), and their incorporation into the walls of burrows (Ólafsson et al., 2002), presumably to promote decomposition and ease of consumption. However, several authors have pointed to the paradox that, notwithstanding the volume of evidence in favour of leaf shredding and consumption by tropical sesarmids, the nutritional value of mangroves leaves is low (Skov & Hartnoll, 2002), and the carbon isotope values of crabs do not seem to reflect those of bulk leaf samples (Guest et al., 2004; Mazumder & Saintilan, 2010). The C:N ratio of mangrove leaves typically exceeds 17 and the leaves are high in tannins, suggesting a highly unpalatable source of nutrition (Skov & Hartnoll, 2002). Furthermore, mangrove crabs are typically enriched in $\delta^{13}C$ some 7–8‰ in comparison to mangrove leaves sampled in the same location (Mazumder & Saintilan, 2010), well beyond the 1‰ fractionation typical between trophic levels.

Laboratory studies exploring the influence of leaf material on crab isotopic composition have suggested that while crabs do consume leaves, bulk leaf material may not be the most appropriate method for determining leaf contributions to crab nutrition (Herbon & Nordhaus, 2013; Bui & Lee, 2014). Crabs appear to be highly selective in the components of leaves consumed, and compound-specific isotope analysis may be a more accurate way of linking crab isotopic composition to leaf material. For this reason, it may have been premature to discard the importance of mangrove detritus to estuarine and nearshore ecosystems, given the degree of compound-specific selection and apparent fractionation by consumers providing an important mediatory link to higher ecosystem levels.

In wild populations, several other potential sources of carbon may be important for crabs. Mangrove fine root material is enriched in $\delta^{13}C$ compared to leaves (Saintilan et al., 2013) and closer to crab isotopic composition. It is unknown whether crabs consume fine root material during high tide or during burrow excavation. Surface organic matter may also provide important nutritional subsidies, and in temperate mangrove environments, this source appears to dominate mangrove crab diet (Mazumder et al., 2011). Microphytobenthos has received the most attention as the predominant source of carbon in surficial sediments utilised by crabs in mangrove (Guest et al., 2004), though stranded zooplankton may also make an

important contribution. Mazumder et al. (2009) sampled zooplankton concentration in tidal waters entering and leaving the saltmarsh on a monthly basis for 18 months at the Towra Point wetland, Sydney, and found that in every month, the density of Amphipods and Copepods was higher in the flood-tide water than the ebb-tide water. These differences amounted to approx. 400 individuals stranded per square metre of the wetland with each tide. Similar results were found in the adjacent estuaries of Sydney Harbour and the Hawkesbury Rivers (Fig. 3).

Sporobolus virginicus (L.) Kunth) utilises the C4 photosynthetic pathway, and is heavily depleted in $\delta^{13}C$ compared to other widely available sources of carbon in the wetland, such as mangrove (−28), phytoplankton (ca. −20) and microphytobenthos (−23.7: Guest & Connolly (2006). The presence of the grass *S. virginicus* with its distinctive isotope signature has facilitated the testing of hypothesis concerning the contribution of plant material to the diet of grazing herbivores. The plant is the dominant saltmarsh species in the tropical and subtropical east Australian coast (Saintilan, 2009), and is co-dominant with the chenopod *Sarcocornia quinqueflora* (Bunge ex Ung.-Sternb.) throughout NSW (Fig. 4). However, it is less extensive in the more floristically diverse saltmarshes of the southern shores of the continent (Saintilan, 2009).

Given the small feeding range of crabs and the high likelihood of local assimilation of carbon, patches of *S. virginicus* can be used to test the hypothesis that crabs derive carbon from local plant material. Guest & Connolly (2006) found the carbon isotope signatures of crabs collected from *S. virginicus* patches to be significantly enriched in $\delta^{13}C$ compared to crabs collected from the mangrove, reflecting the more enriched signature of the grass. Similarly, Saintilan & Mazumder (2010) and Alderson et al. (2013) sampled between patches of *S. virginicus* and *S. quinqueflora* in patch mosaics at Towra Point, Sydney, and the nearby Brisbane Waters estuary, respectively, finding $\delta^{13}C$ values of crabs enriched in *S. virginicus* compared to

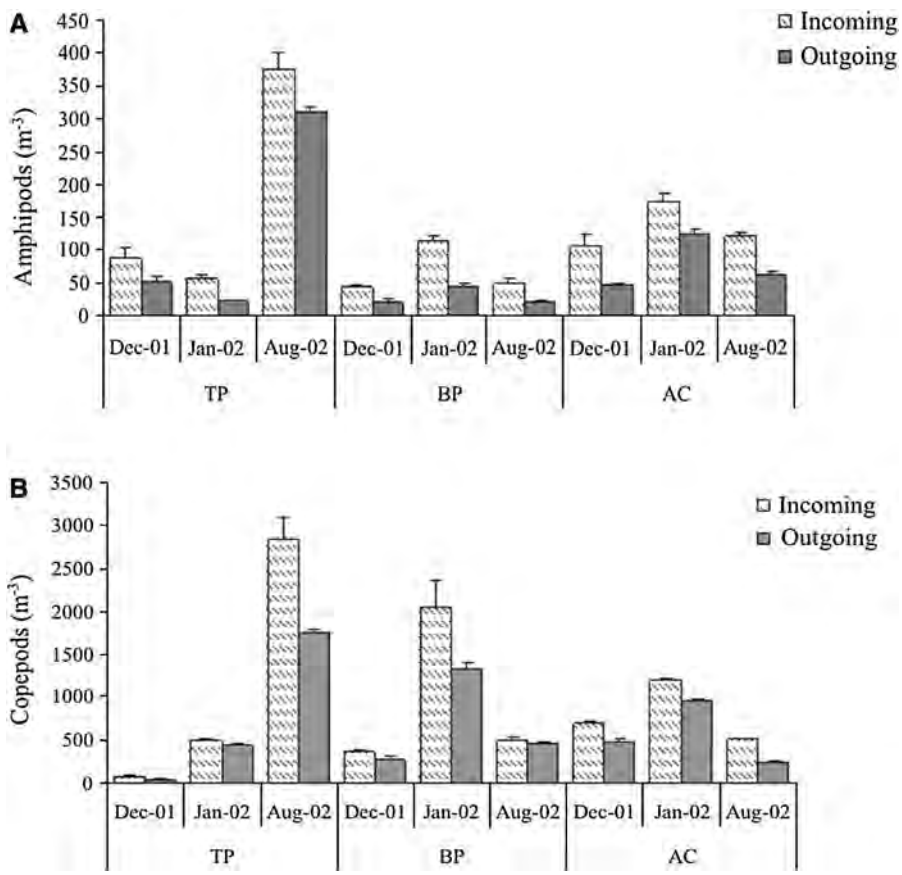


Fig. 3 Mean (±SE) abundance of amphipod (**A**) and copepod (**B**) in inflowing and out-flowing tidal waters of Towra Point (TP), Bicentennial Park (BP) and Allens Creek (AC) in December 01, January 02 and August 02. Data sourced from Mazumder (2004, p. 110, 111)

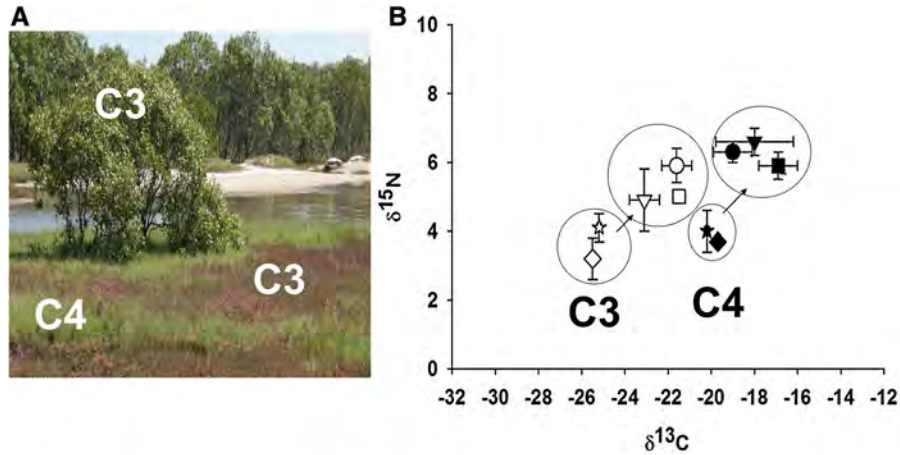


Fig. 4 **A** Mosaic of dominant species occupying the upper intertidal environment in SE Australia and their photosynthetic pathway, including the mangrove *Avicennia marina* ((Forssk.) (C3), the saltmarsh grass *S. virginicus* (C4) and the saltmarsh chenopod *S. quinqueflora*. **B** In the saltmarsh dominant plant habitats (C3 *S. quinqueflora* open symbols; *S. virginicus* closed symbols), surface organic matter (FBOM: fine benthic organic matter ☆; CBOM: coarse benthic organic matter ◇) influence carbon isotope ratios (±SE) of grazing invertebrates including the crabs *P. erythrodactyla* ▽, *H. haswellianus* ○, and the snail *L. luteola* □. Data sourced from Saintilan & Mazumder (2010, p. 618)

those feeding in *S. quinqueflora*. Figure 3 shows this association for two species of crabs (*P. erythrodactyla* and *H. haswellianus*) and the gastropod *Littoraria luteola* (Quoy & Gaimard, 1833), also an important contributor to larval export from the saltmarsh. However, in both studies, the application of mixing models testing the relative contributions of leaves, detritus and benthic algae suggested a dominant contribution of microphytobenthos, a carbon source also enriched within *S. virginicus* patches. Alderson et al. (2013) concluded that dissolved inorganic carbon may be transferred from saltmarsh to algal sources, complicating the direct attribution of dietary carbon in the wetland.

Will anthropogenic N disrupt trophic interactions?

The introduction of anthropogenic sources of Nitrogen in the world's estuaries has been recognised as a globally significant problem (Rabalais, 2002), with the potential to disrupt coastal ecosystems of high importance to human populations (Lotze et al., 2006). Adjacent to our study site of Towra Point, Macreadie et al. (2012) noted a shift in C:N ratios of organic carbon in cores retrieved from open-water habitat, Sydney suggesting a shift from macrophytic to algal autotrophic production as the dominant contributor to carbon accumulation. This occurred in a period corresponding to European colonisation and urbanisation of the catchment. Given that isotopic analyses of crab diet suggest a mix of algal and detrital contributions, alterations to the availability of one or the other source driven by alterations in N levels have the potential to profoundly influence estuarine trophic interactions.

The capacity of isotope studies to document and trace the effects of anthropogenic N in ecosystems is enhanced by the tendency for $\delta^{15}N$ to be enriched in anthropogenic sources. Human wastewater is enriched in $\delta^{15}N$ as a result of denitrification and volatilisation of ammonia (Kendall et al., 2007). The enriched $\delta^{15}N$ is then transferred from autotrophs to herbivores and their consumers, along with the 3–4‰ fractionation typical of each trophic transfer. Mazumder et al. (2015) tested the consistency of the trophic links between sediment organic matter (SOM), crabs and ambassids across estuaries with a range of anthropogenic N input in the Sydney region (Fig. 5). Brisbane Waters, Sydney Harbour and the Georges River/Botany Bay had increased total N inputs of 200, 400 and 800%, respectively, on modelled pre-European levels (Mazumder et al., 2015). Consistently higher $\delta^{15}N$ values are found in the heavily developed Sydney Harbour and Botany Bay mangrove forests compared to Brisbane Waters (Fig. 4), though the

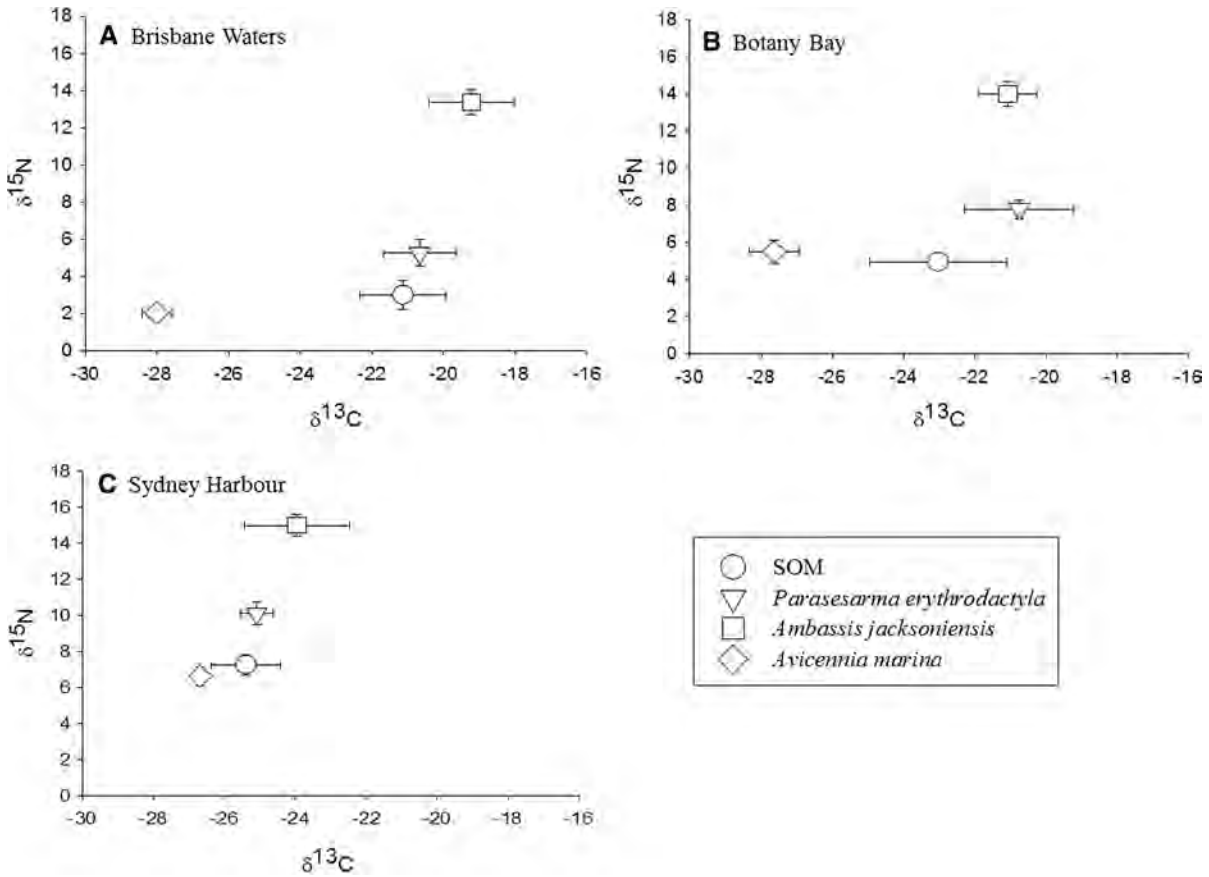


Fig. 5 Variation in fish, crab and primary organic matter $\delta^{13}C$ and $\delta^{15}N$ across three estuaries of varying levels of N input. Links between SOM, crabs and fish are tightly coupled, in spite of variability in the levels of $\delta^{15}N$, and the position of the dominant mangrove *Avicennia marina*. After Mazumder et al. (2015, p. 220)

relative position of crabs relation to SOM is similar across estuaries. Crab $\delta^{15}N$ and $\delta^{13}C$ is tightly coupled with SOM, as these vary between sites, though not with mangrove leaves.

On this basis, Mazumder et al. (2015) concluded that elevated N in heavily developed estuaries on the NSW coast was not disrupting the key trophic exchanges at the base of estuarine ecosystems, and that in the mangrove, algal carbon was most probably a dominant carbon source across the gradient of estuary development. However, they noted that trophic length was lower in the more heavily developed estuaries, and that ambassids were most probably accessing a greater range of zooplankton, at higher trophic levels, than in the heavily impacted estuaries of Sydney Harbour and Botany Bay. This is unlikely to be the result of fishing pressure, as the developed estuaries had closed their commercial fisheries, associated with an increase in the population of ambassids (Saintilan et al., 2008).

Conclusions

Grapsid crabs of east-coast Australian intertidal wetlands play an important role in supporting the dietary requirements of estuarine fish. Crabs feed on a range of organic carbon sources on the saltmarsh and mangrove flats at low tide, most probably a combination of algal material and plant detritus. The production of larvae, time with the lunar cycle, provides a mechanism for trophic relay (Kneib, 1997), whereby carbon is exported from the intertidal environment and incorporated into the estuarine food chain, with zooplanktivorous ambassids, the numerically dominant fish of the estuaries, playing a key role. Observations of fish

species abundance in seagrass adjacent to saltmarsh have shown that while seagrass specialists show little change in numbers between neap and spring tide phases, *A. jacksoniensis* shows marked declines during the spring tide phase, co-incident with their arrival in the saltmarsh (Saintilan et al., 2007). In this way, the transfer of crab zoaea through the outwelling tide, and the feeding migration of fish from saltmarsh to estuary, provide an exemplar of transfers and linkages within the coastal ecosystem mosaic, interlinking coastal, estuarine, wetland and freshwater habitats in the gradient from ocean to land (Sheaves, 2009).

The strength of this transfer seems not to be interrupted by the addition of anthropogenic Nitrogen to the estuary. Of the plant sources sampled, only the grass *S. virginicus* unequivocally contributed to the diet of grazing crabs and gastropods. One potential impact of elevated atmospheric CO_2 is to increase the growth rate of C3 plants over C4, given that C4 photosynthesis is saturated with regards to CO_2 uptake at lower levels than ambient concentrations (Morgan et al., 2007). The implications for the long-term competitive ability of *S. virginicus* over other mangrove and other saltmarsh species are unclear, but an important area of research given the trophic significance of this species to invertebrate, and possibly mammalian (Spencer et al., 2009) herbivores in the saltmarsh.

The monthly release of crab and gastropod larvae from the saltmarsh into the spring tide provides for the highest density of meroplankton in the water column (Ricardo et al., 2014), and a unique feeding opportunity for itinerant fish. The extent to which sea-level rise threatens this ecosystem service will largely be determined by management decisions. Under natural circumstances, wetlands may adjust to sea-level rise through vertical accretion or, if the rate of sea-level rise exceeds vertical adjustment, through landward retreat (Rogers et al., 2016). In SE Australia, measures of marsh vertical adjustment have demonstrated that while mangroves accrete at rates comparable to local sea-level rise, saltmarshes do not and this may explain the widespread encroachment of mangrove (Rogers et al., 2013, 2014). Sea-level rise is likely to be facilitating a transition from saltmarsh to mangrove with corresponding changes to crab species assemblage and the timing of zooplankton release. Over time, the imposition of barriers to migration, commonly termed "coastal squeeze", will particularly impact on the high-density provision of zooplankton unique to the upper intertidal environment.

While the press effects of elevated CO_2, temperature and sea-level are already impacting the world's coastal ecosystems (McKee et al., 2012; Saintilan et al., 2014), these impacts are dwarfed in many locations by reclamation of wetlands for alternative land use (Pendleton et al., 2012). The extents of historical losses in eastern Australia are poorly documented, and have largely been arrested by the introduction of protective legislation and policy several decades ago (Rogers et al., 2016). However, the legacy of habitat fragmentation remains, and patch scale is an important determinant of the contribution of detritus to crab isotopic signatures (Guest & Connolly, 2006), as well as edge effects associated with feeding behaviour of aquatic (Sheaves et al., 2012) and aerial (Gonsalves et al., 2012) feeders. The influence of patch size and the location of habitat patches in the context of the broader mosaic of habitats of the estuary remains an important field for further investigation.

Acknowledgements The authors would like to thank Stuart Hankin (ANSTO) for drawing location map of Australia (Fig. 1). Research in SE Australia was conducted with funding assistance from the Australian Research Council and supported by the NSW Office of Environment and Heritage.

References

Aburto-Oropeza, O., E. Ezcurra, G. Danemann, V. Valdez, J. Murray & E. Sala, 2008. Mangroves in the Gulf of California increase fishery yields. Proceedings of the National Academy of Sciences of the United States of America 105(30): 10456–10459.

Alderson, B., D. Mazumder, N. Saintilan, K. Zimmerman & P. Mulry, 2013. Application of isotope mixing models to discriminate dietary sources over small-scale patches in saltmarsh. Marine Ecology Progress Series 487: 113–122.

Armitage, A. R., W. E. Highfield, S. D. Brody & P. Louchouarn, 2015. The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. PLoS ONE 10(5): e0125404.

Bouwmeester, J., A. H. Baird, C. J. Chen, J. R. Guest, K. C. Vicentuan & M. L. Berumen, 2015. Multi-species spawning synchrony within scleractinian coral assemblages in the Red Sea. Coral Reefs 34(1): 65–77.

Bui, T. H. H. & S. Y. Lee, 2014. Does 'you are what you eat' apply to mangrove grapsid crabs? PLoS ONE 9(2): e89074.

Cannicci, S., D. Burrows, S. Fratini, T. J. Smith Iii, J. Offenberg & F. Dahdouh-Guebas, 2008. Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. Aquatic Botany 89(2): 186–200.

Cavanaugh, K. C., J. R. Kellner, A. J. Forde, D. S. Gruner, J. D. Parker, W. Rodriguez & I. C. Feller, 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proceedings of the National Academy of Sciences of the United States of America 111(2): 723–727.

Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S. J. Anderson, I. Kubiszewski, S. Farber & R. K. Turner, 2014. Changes in the global value of ecosystem services. Global Environmental Change 26: 152–158.

Epifanio, C. E. & J. H. Cohen, 2016. Behavioral adaptations in larvae of brachyuran crabs: a review. Journal of Experimental Marine Biology and Ecology 482: 85–105.

Giri, C. & J. Long, 2016. Is the geographic range of mangrove forests in the conterminous United States really expanding? Sensors 16(12): 2010.

Gonsalves, L., B. Law, C. Webb & V. Monamy, 2012. Are vegetation interfaces important to foraging insectivorous bats in endangered coastal saltmarsh on the Central Coast of New South Wales? Pacific Conservation Biology 18(4): 282–292.

Guest, M. & R. Connolly, 2005. Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. Aquatic Ecology 38(4): 599–609.

Guest, M. A. & R. M. Connolly, 2006. Movement of carbon among estuarine habitats: the influence of saltmarsh patch size. Marine Ecology Progress Series 310: 15–24.

Guest, M. A., R. M. Connolly & N. R. Loneragan, 2004. Carbon movement and assimilation by invertebrates in estuarine habitats at a scale of metres. Marine Ecology Progress Series 278: 27–34.

Harrison, P. L., R. C. Babcock, G. D. Bull, J. K. Oliver, C. C. Wallace & B. L. Willis, 1984. Mass spawning in tropical reef corals. Science 223(4641): 1186–1189.

Herbon, C. M. & I. Nordhaus, 2013. Experimental determination of stable carbon and nitrogen isotope fractionation between mangrove leaves and crabs. Marine Ecology Progress Series 490: 91–105.

Hollingsworth, A. & R. M. Connolly, 2006. Feeding by fish visiting inundated subtropical saltmarsh. Journal of Experimental Marine Biology and Ecology 336(1): 88–98.

Kendall, C., E. M. Elliott & S. D. Wankel, 2007. Tracing anthropogenic inputs of nitrogen to ecosystems, 2nd ed. Blackwell Publishing, London.

Kneib, R. T., 1997. The role of tidal marshes in the ecology of estuarine nekton. Oceanography and Marine Biology 35: 163–220.

Kristensen, E., S. Bouillon, T. Dittmar & C. Marchand, 2008. Organic carbon dynamics in mangrove ecosystems: a review. Aquatic Botany 89(2): 201–219.

Lee, S., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Marine and Freshwater Research 49(4): 335–343.

Loneragan, N. R., S. E. Bunn & D. M. Kellaway, 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Marine Biology 130(2): 289–300.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson & J. B. C. Jackson, 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312(5781): 1806–1809.

Lugendo, B. R., I. Nagelkerken, G. Van Der Velde & Y. D. Mgaya, 2006. The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas for juvenile fishes in Chwaka Bay, Zanzibar: gut content and stable isotope analyses. Journal of Fish Biology 69(6): 1639–1661.

Romero-Torresb, M., A. Acosta & E. A. Treml, 2016. The regional structure of spawning phenology and the potential consequences for connectivity of coral assemblages across the Eastern Tropical Pacific. ICES Journal of Marine Science. doi:10.1093/icesjms/fsw218.

Macreadie, P. I., K. Allen, B. P. Kelaher, P. J. Ralph & C. G. Skilbeck, 2012. Paleoreconstruction of estuarine sediments reveal human-induced weakening of coastal carbon sinks. Global Change Biology 18(3): 891–901.

Marcus, S., 2005. Nature and consequences of biological connectivity in mangrove systems. Marine Ecology Progress Series 302: 293–305.

Mazumder, D., 2004. Contribution of saltmarsh to temperate estuarine fish in southeast Australia, Australian Catholic University.

Mazumder, D. & N. Saintilan, 2010. Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. Wetlands 30(2): 375–380.

Mazumder, D., N. Saintilan & R. J. Williams, 2006. Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. Marine and Freshwater Research 57(2): 193–199.

Mazumder, D., N. Saintilan & R. J. Williams, 2009. Zooplankton inputs and outputs in the saltmarsh at Towra Point. Australia. Wetlands Ecol Manage 17(3): 225–230.

Mazumder, D., N. Saintilan, R. J. Williams & R. Szymczak, 2011. Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. Marine and Freshwater Research 62(1): 11–19.

Mazumder, D., N. Saintilan, B. Alderson & S. Hollins, 2015. Inputs of anthropogenic nitrogen influence isotopic composition and trophic structure in SE Australian estuaries. Marine Pollution Bulletin 100(1): 217–223.

McIvor, C. C. & T. J. Smith, 1995. Differences in the crab fauna of mangrove areas at a Southwest Florida and a Northeast Australia location: implications for leaf litter processing. Estuaries 18(4): 591–597.

McKee, K., K. Rogers & N. Saintilan, 2012. Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In Middleton, A. B. (ed), Global Change and the Function and Distribution of Wetlands. Springer, Dordrecht: 63–96.

McPhee, J. J., P. Freewater, W. Gladstone, M. E. Platell & M. J. Schreider, 2015a. Glassfish switch feeding from thalassinid larvae to crab zoeae after tidal inundation of saltmarsh. Marine and Freshwater Research 66(11): 1037–1044.

McPhee, J. J., M. E. Platell & M. J. Schreider, 2015b. Trophic relay and prey switching–A stomach contents and calorimetric investigation of an ambassid fish and their

saltmarsh prey. Estuarine, Coastal and Shelf Science 167: 67–74.
Melville, A. & R. Connolly, 2003. Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136(4): 499–507.
Meynecke, J. O., S. Y. Lee & N. C. Duke, 2008. Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. Biological Conservation 141(4): 981–996.
Micheli, F., 1993. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. Journal of Experimental Marine Biology and Ecology 171(2): 165–186.
Morgan, J. A., D. G. Milchunas, D. R. LeCain, M. West & A. R. Mosier, 2007. Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. Proceedings of the National Academy of Sciences of the United States of America 104(37): 14724–14729.
Nagelkerken, I., S. J. M. Blaber, S. Bouillon, P. Green, M. Haywood, L. G. Kirton, J. O. Meynecke, J. Pawlik, H. M. Penrose, A. Sasekumar & P. J. Somerfield, 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. Aquatic Botany 89(2): 155–185.
Nobbs, M. & K. A. McGuinness, 1999. Developing methods for quantifying the apparent abundance of fiddler crabs (Ocypodidae: Uca) in mangrove habitats. Australian Journal of Ecology 24(1): 43–49.
Nordlie, F. G., 2003. Fish communities of estuarine salt marshes of eastern North America, and comparisons with temperate estuaries of other continents. Reviews in Fish Biology and Fisheries 13(3): 281–325.
Ólafsson, E., S. Buchmayer & M. W. Skov, 2002. The East African decapod crab *Neosarmatium meinerti* (de Man) sweeps mangrove floors clean of leaf litter. AMBIO: A Journal of the Human Environment 31(7): 569–573.
Osland, M. J., N. Enwright, R. H. Day & T. W. Doyle, 2013. Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. Global Change Biology 19(5): 1482–1494.
Pendleton, L., D. C. Donato, B. C. Murray, S. Crooks, W. A. Jenkins, S. Sifleet, C. Craft, J. W. Fourqurean, J. B. Kauffman, N. Marbà, P. Megonigal, E. Pidgeon, D. Herr, D. Gordon & A. Baldera, 2012. Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. PLoS ONE 7(9): e43542.
Platell, M. E. & P. Freewater, 2009. Importance of saltmarsh to fish species of a large south-eastern Australian estuary during a spring tide cycle. Marine and Freshwater Research 60(9): 936–941.
Qin, H., Q. Sheng, T. Chu, S. Wang & J. Wu, 2015. Import and export fluxes of macrozooplankton are taxa- and season-dependent at Jiuduansha marsh, Yangtze River estuary. Estuarine, Coastal and Shelf Science 163B: 254–264.
Rabalais, N. N., 2002. Nitrogen in aquatic ecosystems. AMBIO: A Journal of the Human Environment 31(2): 102–112.
Ricardo, G. F., A. R. Davis, N. A. Knott & T. E. Minchinton, 2014. Diel and tidal cycles regulate larval dynamics in salt marshes and mangrove forests. Marine Biology 161(4): 769–784.
Robertson, A. I., 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. Journal of Experimental Marine Biology and Ecology 102(2–3): 237–248.
Robertson, A. & N. Duke, 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Marine Biology 96(2): 193–205.
Rogers, K., N. Saintilan, A. J. Howe & J. F. Rodríguez, 2013. Sedimentation, elevation and marsh evolution in a southeastern Australian estuary during changing climatic conditions. Estuarine, Coastal and Shelf Science 133: 172–181.
Rogers, K., N. Saintilan & C. D. Woodroffe, 2014. Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: implications for coastal wetland response to climate change. Estuarine, Coastal and Shelf Science 149: 46–56.
Rogers, K., P. I. Boon, S. Branigan, N. C. Duke, C. D. Field, J. A. Fitzsimons, H. Kirkman, J. R. Mackenzie & N. Saintilan, 2016. The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. Marine Policy 72: 139–155.
Saintilan, N., 2004. Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. Estuarine, Coastal and Shelf Science 61(4): 591–601.
Saintilan, N., 2009. Biogeography of Australian saltmarsh plants. Austral Ecology 34(8): 929–937.
Saintilan, N. & D. Mazumder, 2010. Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. Marine and Freshwater Research 61(5): 615–620.
Saintilan, N. & R. J. Williams, 1999. Mangrove transgression into saltmarsh environments in south-east Australia. Global Ecology and Biogeography 8(2): 117–124.
Saintilan, N., K. Hossain & D. Mazumder, 2007. Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary. New South Wales. Wetlands Ecol Manage 15(4): 277–286.
Saintilan, N., D. Mazumder & K. Cranney, 2008. Changes to fish assemblages visiting estuarine wetlands following the closure of commercial fishing in Botany Bay. Australia. Aquatic Ecosystem Health & Management 11(4): 441–449.
Saintilan, N., K. Rogers, D. Mazumder & C. Woodroffe, 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuarine, Coastal and Shelf Science 128: 84–92.
Saintilan, N., N. C. Wilson, K. Rogers, A. Rajkaran & K. W. Krauss, 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Global change biology 20(1): 147–157.
Sheaves, M., 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. Marine Ecology Progress Series 391: 107–115.
Sheaves, M., R. Johnston, R. M. Connolly & R. Baker, 2012. Importance of estuarine mangroves to juvenile banana

prawns. Estuarine, Coastal and Shelf Science 114: 208–219.
Skov, M. W. & R. G. Hartnoll, 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? Oecologia 131(1): 1–7.
Spencer, J., V. Monamy & M. Breitfuss, 2009. Saltmarsh as habitat for birds and other vertebrates. In Saintilan, N. (ed), Australian Saltmarsh Ecology. CSIRO, Melbourne: 149–165.

Wetlands Ecol Manage (2007) 15:277–286
DOI 10.1007/s11273-006-9028-0

ORIGINAL PAPER

Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales

Neil Saintilan · Kamal Hossain · Debashish Mazumder

Received: 1 December 2006 / Accepted: 8 December 2006 / Published online: 3 February 2007
© Springer Science+Business Media B.V. 2007

Abstract Shallow-water vegetated estuarine habitats, notably seagrass, mangrove and saltmarsh, are known to be important habitats for many species of small or juvenile fish in temperate Australia. However, the movement of fish between these habitats is poorly understood, and yet critical to the management of the estuarine fisheries resource. We installed a series of buoyant pop nets in adjacent stands of seagrass, mangrove and saltmarsh in order to determine how relative abundance of fishes varied through lunar cycles. Nets were released in all habitats at the peak of the monthly spring tide for 12 months, and in the seagrass habitat at the peak of the neap tide also. The assemblage of fish in each habitat differed during the spring tides. The seagrass assemblage differed between spring and neap tide, with the neap tide assemblage showing greater abundances of fish, particularly those species which visited the adjacent habitats when inundated during spring tides. The result supports the hypothesis that fish move from the seagrass to the adjacent mangrove and saltmarsh during spring tides, taking advantage of high abundances of zooplankton, and use seagrass as a refuge during lower tides. The restoration and preservation of mangrove and saltmarsh utility as fish habitat may in some situations be linked to the proximity of available seagrass.

Keywords Seagrass · Mangrove · Saltmarsh · Fish · Habitat

N. Saintilan (✉)
Rivers and Wetlands Unit, Department of Environment and Conservation, NSW, PO Box A290, Sydney South, NSW 1232, Australia
e-mail: neil.saintilan@environment.nsw.gov.au

K. Hossain
Macquarie University, Sydney, Australia

D. Mazumder
Institute for Nuclear Geophysiology, Australian Nuclear Science and Technology Organisation (ANSTO), Menai, NSW, Australia

Introduction

The importance of shallow-water estuarine habitats for juvenile fish has been well demonstrated in temperate (Loneragan et al. 1986; Hannan and Williams 1998) and tropical (Parrish 1989) systems. These habitats provide a refuge from predators due to high structural complexity (Robertson and Blaber 1992; Blaber et al. 1995; Beyst et al. 2002; Nagelkerken et al. 2000) and higher turbidity than marine waters (Blaber and Blaber 1980; Robertson and Blaber 1992). The same habitats may also provide significant sources of prey for fish (Dexter 1984; Du Preez et al. 1990; Jaraillo and McLachlan 1993; Haynes and Quinn

1995). Recent work in temperate and subtropical Australia has demonstrated the utilization of mangroves and saltmarshes for fish during spring high tides (Thomas and Connolly 2001; Crinall and Hindell 2004, Mazumder et al. 2005a), and the importance of saltmarsh as a source of zooplankton for the diet of several species (Mazumder et al. 2006a, Hollingsworth and Connolly 2006).

However, some temperate Australian studies have demonstrated that the assemblage of fish visiting mangroves may differ with geomorphic setting (Mazumder et al. 2006b), and between mangrove stands within bays (Clynick and Chapman 2002). Factors controlling the variation in fish community structure in vegetated estuarine habitats are poorly understood. One important factor which may be influencing variation in fish utilization of flooded vegetated habitats is the proximity of heterogeneous habitat types (Irlandi and Crawford 1997, Skilleter et al. 2005). Within estuaries, seagrass, mangrove and saltmarsh may be distributed over spatial scales of hundreds of meters, and provide opportunities for fish to move between habitats over tidal cycles, or life stages. The study of habitats as discrete entities limits our understanding of interaction between the mosaics of habitats which occur in these environments (Meyer et al. 1993; Fonseca et al. 1994) at scales relevant to the management of these systems.

Several northern hemisphere studies have recently illustrated the importance of habitat mosaics for juvenile fish. Irlandi and Crawford (1997) demonstrated that pinfish (*Lagodon rhomboides*) was more likely to move from saltmarsh to adjacent subtidal habitat if the subtidal habitat was vegetated. In the Caribbean, seagrass beds supported higher densities of small fish if adjacent to mangroves (Nagelkerken et al. 2001), in spite of the negligible contribution of mangrove plant material to fish diet.

In temperate Australia, Mazumder et al. (2006b) demonstrated a higher diversity and abundance of fish in mangrove and saltmarsh with large adjacent seagrass beds than at sites with no adjacent seagrass. Jelbert et al (2006) found the corollary to be true, demonstrating a higher density of fish in seagrass beds close to mangrove than those further away. One hypothesis explaining this observation is that fish utilize seagrass habitats during low tides when mangrove and saltmarsh are not flooded. At high tide, and in particular spring tides, when both mangrove and saltmarsh are flooded, fish may move from the seagrass to mangrove and saltmarsh to take advantage of structural protection from predators and/or the high availability of zooplankton, particularly brachyuran larvae (see Mazumder et al. 2006a). In support of this hypothesis, Jelbart et al (2006) showed that in seagrass close to mangrove had greater numbers of those fish found utilizing mangrove at high tide.

This paper employs a common methodology (buoyant pop nets) to examine fish community structure in adjacent mangrove, saltmarsh and seagrass at Towra Point, Botany Bay. By comparing the seagrass fish community during spring and neap tidal cycles over the course of a year, we were able to test the hypothesis that the seagrass fish assemblage will change as adjacent intertidal habitats become available. Further, the design allowed us to test whether these changes were explicable in terms of the subsequent appearance of the same species in the adjacent mangrove and saltmarsh flooded by the same spring tides.

Methods

Study site

The Towra Point Nature Reserve is situated in Botany Bay, New South Wales (Fig. 1). The eastern shore of Woolooware Bay has been the location of numerous ecological investigations (Clarke and Hannon 1967; Mitchell and Adam 1989; Hunt 1989; McGuiness 1990; Roach 1998; Roach and Lim 2000; Mazumder and Saintilan 2003; Mazumder et al. 2005a, b; 2006a, b) and the ecological characteristics of the estuarine wetlands are described in Mazumder et al. (2005a).

The seagrass community within Woolooware Bay is dominated by *Zostera capricorni*. The biomass is low and distribution patchy compared with seagrass communities in similar geomorphic situations elsewhere in NSW (Hossain 2005). The mangrove community is a low woodland

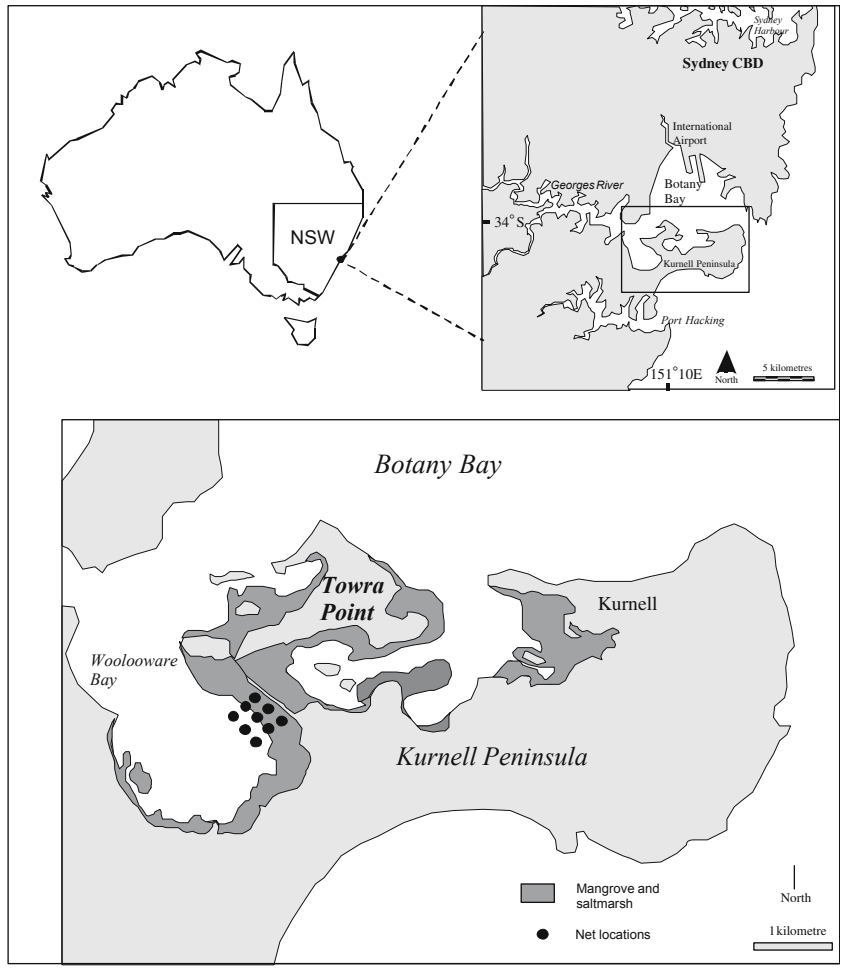


Fig. 1 Location of Towra Point and the configuration of pop nets in the estuarine wetlands

dominated by *Avicennia marina*, though *Aegiceras corniculatum* occurs in patches, primarily as a landward fringe. The saltmarsh community supports a number of floristic associations, the one chosen for this study being an assemblage consisting *Sarcocornia quinqueflora*, *Sporobolus virginicus*, *Sueada australis* and *Triglochin striata*. The seagrass, mangrove and saltmarsh zones are extensive, situated as shore-normal bands at least 100 m wide throughout the study area.

Fish collection

Bouyant pop nets are an effective means of sampling fish populations in shallow-water habitats (Michael et al. 1989; Connolly 1994; Mazumder et al. 2005a, 2006b), particularly where densities are to be compared between sites (Mazumder et al. 2005b). The aim of this experiment was to compare fish diversity and abundance between three distinct habitats; seagrass, saltmarsh and mangrove. To this end, three buoyant pop nets were deployed in each habitat as fixed sampling points for the duration of the experiment. Nets within habitats were placed at 70 m intervals parallel to the shore, and the width of each habitat allowed nets to be placed approximately 50 m apart along a shore-normal transect. The nets were 5.5 m^2, elevating to a maximum height of 1.5 m in the mangrove and saltmarsh, and 2.0 m in the seagrass. The nets consisted of a nylon mesh of 0.6 mm, attached at the top to a 20 mm diameter PVC pipe, sealed for floatation. The base of the net was secured tightly to the marsh surface using tent pegs, with nets hidden prior to release inside shallow trenches. Nets were weighted down with four concrete blocks attached with nylon rope

to a remote point approximately 30 m from the nets. The nets were released from this remote point during the peak of the tide.

In the mangrove and saltmarsh habitats, fish samples were collected monthly during the spring tide, when the entire marsh was inundated with tidal water. At these times, inundation depths were approximately 1.8 m in the seagrass, 1.5 m in the mangrove and 0.5 m in the saltmarsh. In the seagrass, fish samples were collected fortnightly, during both spring and neap high tides. During the neap high tides, the saltmarsh remained dry and only the seaward sections of the mangrove were inundated. Seagrass was the only vegetated habitat inundated.

Statistical methods

Differences in assemblages of fish between seagrass, saltmarsh and mangrove were examined using Bray-Curtis measures of dissimilarity (Bray and Curtis 1957) with square-root transformed data. Non-metric multidimensional scaling plots were also used to demonstrate the intra and inter-habitat similarity in assemblages. The multivariate technique ANOSIM (Analysis of Similarities: Clarke and Warwick 2001) was used to test for statistically significant differences between fish assemblages in the three habitat types. The contribution made by individual species to differences in assemblages determined by ANOSIM was explored using SIMPER (similarity percentages-species contribution: Clarke and Warwick 2001). These procedures were also used to compare neap and spring-tide assemblages in the seagrass. All procedures were accessed using Primer Version 5 (Clarke and Warwick 2001). Univariate analysis (ANOVA) was used to test for significant differences in the abundance of individual species between the three habitat types.

Results

Differences in assemblages between habitats

Twenty-eight species of fish were encountered in the estuarine wetlands of Towra Point during the survey, representing 19 families (Table 1). Consistent differences in fish assemblages were found between each habitat, when months were grouped into four seasons (Fig. 2). ANOSIM tests demonstrated significant differences between habitats at a significant level of $P = 0.001$ in all four seasons.

The consistent differences between seagrass and the intertidal (mangrove and saltmarsh) assemblages is largely explained by higher numbers of crustaceans (*M. macleayi*, *M. intermedium* and *A. edwardsi*) in the seagrass, along with the trumpeter *P. quadrilineatus* (Table 2). In contrast, the glassfish *A. jacksoniensis* was found at consistently higher numbers in the mangrove and saltmarsh, and saltmarsh in particular. The mangrove goby *M. paludis* was found in consistently higher numbers in mangrove, and was absent from seagrass. The statistical significance of abundance comparisons for individual species across the three habitats is represented in Table 3.

Differences between spring and neap-tide seagrass assemblages

Differences were found in the assemblages of fish in seagrass between spring and neap high tides (ANOSIM $P = 0.03$). These differences were primarily due to lower numbers of many species during spring high tides, particularly glassfish *A. jacksoniensis* (Table 4, Fig. 3), *A. edwardsi*, *P. olorum*, *A. bifrenatus*, *L. argenta*, and *A. australis*. Of these, *A. jacksoniensis* and *A. australis* differed significantly between neap and spring tide abundances in univariate analyses. All these species were found in the adjacent mangrove and saltmarsh during the same spring tides.

Discussion

The results support the hypothesis that fish move from seagrass to the adjacent mangrove and saltmarsh during spring high tides. The comparison of spring and neap tide fish assemblages in seagrass showed a consistent decline in numbers of fish within the seagrass during spring tides, in

Table 1 Fish per net by species in the seagrass, mangrove and saltmarsh habitats at Towra Point 2001–2002

Family	Scientific name	Common name	Seagrass	SD	Mangrove	SD	Saltmarsh	SD
Poeciliidae	*Gambusia holbrooki*	Mosquito fish	0.00	0.00	0.00	0.00	0.02	0.14
Gobiidae	*Mugilogobius paludis*	Mangrove goby	0.00	0.00	4.54	9.75	0.29	0.85
Gobiidae	*Mugilogobius stigmaticus*	Checkered mangrove goby	0.00	0.00	1.27	2.57	0.21	0.65
Gobiidae	*Taeniodes mordax*	Snake head goby	0.00	0.00	1.52	5.81	0.00	0.00
Gobiidae	*Pseudogobius olorum*	Blue spot goby	3.19	2.63	1.02	3.78	1.02	4.59
Gobiidae	*Redigobius macrostoma*	Large mouth goby	0.00	0.00	0.15	0.65	0.00	0.00
Gobiidae	*Arenigobius bifrenatus*	Bridled goby	3.20	2.34	0.15	0.62	0.00	0.00
Gobiidae	*Gobiopterus semivestitus*	Glass goby	0.00	0.00	1.19	4.49	3.19	5.45
Chandidae	*Ambassis jacksoniensis*	Glassfish	3.44	2.90	6.35	28.11	7.33	18.58
Tetraodontidae	*Tetractenos hamiltoni*	Common toad	1.48	1.22	0.13	0.44	0.13	0.53
Atherinidae	*Psuedomugil signifer*	Blue eye	0.00	0.00	0.54	2.77	1.58	4.19
Mugilidae	*Liza argenta*	Flat tail mullet	1.37	1.71	0.56	1.65	0.10	0.52
Mugilidae	*Myxus elongates*	Sand mullet	0.00	0.00	0.02	0.14	0.10	0.42
Mugilidae	*Mugil cephalus*	Sea mullet	0.00	0.00	0.04	0.29	0.06	0.43
Gerreidae	*Gerres subfasciatus*	Silver biddy	0.00	0.00	2.35	4.95	1.13	2.10
Sparidae	*Acanthopagrus australis*	Yellow fin bream	1.20	1.70	1.29	2.00	0.44	1.11
Sparidae	*Rhabdosargus sarba*	Tarwhine	0.00	0.00	0.15	0.55	0.00	0.00
Platycephalidae	*Platycephalus fuscus*	Dusky flathead	0.00	0.00	0.19	0.61	0.19	0.57
Teraponidae	*Pelates quadrilineatus*	Trumpeter	4.73	2.95	0.29	1.03	0.00	0.00
Sillaginidae	*Sillago cilliata*	Sand whiting	0.00	0.00	0.00	0.00	0.00	0.00
Bothidae	*Ammotretis rostratus*	Large toothed flounder	0.00	0.00	0.38	1.30	0.00	0.00
Girellidae	*Girella tricuspidata*	Luderick	0.00	0.00	0.27	0.92	0.00	0.00
Atyidae	*Macrobrachium intermedium*	Grass shrimp	6.61	3.98	0.10	0.52	0.94	2.68
Alpheidae	*Alpheus edwardsi*	Pistol shrimp	6.24	4.49	0.52	1.69	0.15	0.58
Penaeidae	*Metapenaeus macleayi*	School prawn	8.43	4.02	0.00	0.00	0.00	0.00
Eleotridae	*Gobiumorphus autralis*	Striped gudgeon	0.00	0.00	0.13	0.87	0.00	0.00
Anguillidae	*Anguilla reinhardtii*	Long-finned eel	0.00	0.00	0.07	0.28	0.00	0.00
Ophichthidae	*Ophisurus serpens*	Serpent eel	1.01	1.05	0.00	0.00	0.00	0.00

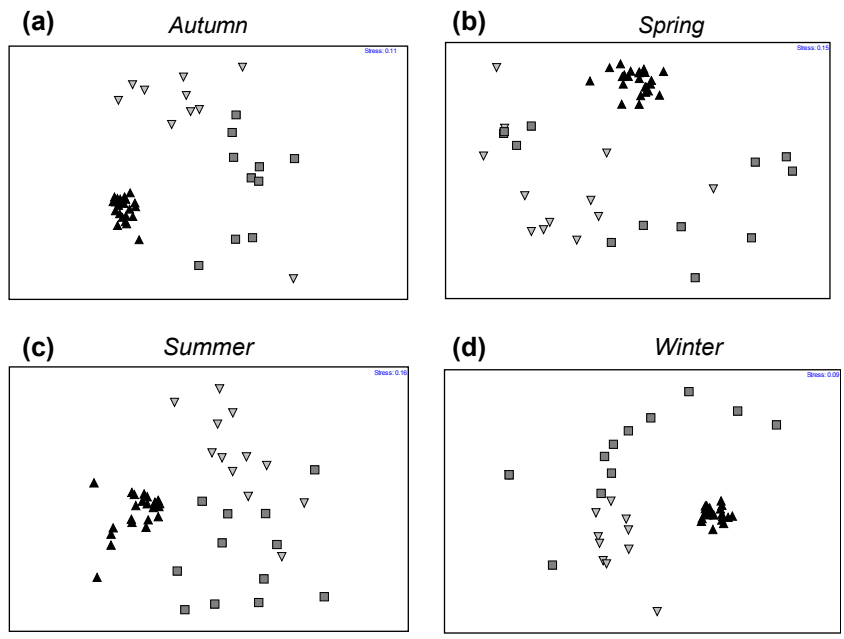


Fig. 2 nMDS plots representing similarity of fish assemblages in seagrass ▲, saltmarsh ▽ and mangrove □ at Towra Point in autumn 2001, spring 2001, summer 2001–2002 and winter, 2001 at Towra Point. Stress values range from 0.11 (autumn) to 0.16 (summer)

Table 2 Species contributing primarily to dissimilarity between assemblages

Species	Seagrass vs. saltmarsh			Seagrass vs. mangrove			Saltmarsh vs. mangrove		
	Abundance seagrass	Abundance saltmarsh	% Contribution	Abundance seagrass	Abundance mangrove	% Contribution	Abundance saltmarsh	Abundance mangrove	% Contribution
M. macleayi	8.43	0.00	14.45	8.43	0.00	13.47			
M. intermedium	6.61	0.94	10.98	6.61	0.10	10.81			
A. edwardsi	6.24	0.15	10.68	6.24	0.52	9.58			
P. quadrilineatus	4.73	0.00	10.04	4.73	0.29	8.91			
A. jacksoniensis	3.44	7.40	7.97	3.44	6.35	7.72	7.40	6.35	19.79
A. bifrenatus	3.20	0.00	7.75	3.20	0.15	7.05			
M. paludis				0.00	4.54	5.72	0.29	4.54	10.11
G. semivestitus	0.00	3.23	5.83				3.23	1.25	11.98

Average abundance per pop net is compared, and the contribution of the species to overall dissimilarity between assemblages is generated from SIMPER. Species are included only if they contribute more then 5% to overall dissimilarity

spite of the greater volume of water at these times. The same fish species were caught at the same time in the flooded mangrove and saltmarsh. The only species showing no consistent decline with the onset of spring tide conditions were those infrequently found in the intertidal wetlands: *Pelates quadrilineatus* and *Ophisurus serpens*.

The species with the largest and most consistent proportional decline in abundance in the seagrass during spring tides was the species found in greatest numbers in the mangrove and saltmarsh; the glassfish *Ambassis jacksoniensis*. This species is known to consume brachyuran larvae in the saltmarsh during spring tides (Mazumder et al. 2006a, Hollingsworth and Connolly 2006). Indeed, the gut content analysis by Mazumder et al. (2006a) utilized fish collected during this survey, and supported the view that several species feed on items available in the saltmarsh, primarily crab larvae (important for *L. argenta*, *A. jacksoniensis*) but also mature crab and small fish (found in the stomach of *A. australis* and *M. paludis*). The visitation of the infrequently inundated saltmarsh by itinerant fish provides an thereby provides and important conduit for the movement of secondary production from the saltmarsh to the rest of the estuary, and complements the available diet of fish occupying subtidal vegetated habitats for most of the time.

The three habitats supported different fish communities during all four seasons. Though considerable numbers of fish move to the intertidal wetland communities during the spring tide, they are not evenly dispersed, and some species occupy the mangrove but not the saltmarsh (*R. macrostoma*, *A. bifrenatus*; see also Mazumder et al. 2005a). Similarly, during neap tide phases, some species when saltmarsh and much of the mangrove is not flooded, some species do not appear in the seagrass community (primarily Gobiidae; e.g. *M. paludis*, *M. stigmaticus* and *T. mordax*), and may occupy tidal creeks within the mangrove, or other unvegetated habitats.

The evidence of this paper supports the view that the utility of mangrove and saltmarsh as a habitat for fish is likely to be enhanced by the availability of adjacent seagrass, though the

Table 3 Significant differences in abundance of species between habitats

Scientific name	Seagrass neap vs. seagrass spring	Seagrass vs. mangrove	Seagrass vs. saltmarsh	Saltmarsh vs. mangrove
Gambusia holbrooki				
Mugilogobius paludis		***	**	
Mugilogobius stigmaticus		**	**	***
Taeniodes mordax				**
Pseudogobius olorum				***
Redigobius macrostoma		***		*
Arenigobius bifrenatus		***		***
Gobiopterus semivestitus		***		**
Ambassis jacksoniensis	*			
Tetractenos hamiltoni	*	***		***
Psuedomugil signifer		***		*
Liza argenta		***		**
Myxus elongates		*		*
Mugil cephalus				
Gerres subfasciatus		***		***
Acanthopagrus australis	*	*	**	*
Rhabdosargus sarba		**		**
Platycephalus fuscus		***	*	***
Pelates quadrilineatus				
Sillago cilliata			*	
Ammotretis rostratus			*	
Girella tricuspidata		***	*	***
Macrobrachium intermedium		***		***
Alpheus edwardsi		***		***
Metapenaeus macleayi				
Gobiumorphus autralis				
Anguilla reinhardtii				
Hyporhamphus australis		***		***

(ANOVA: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$)

question of the relative utilization of seagrass and bare mudflat was not addressed in this study. Within the region, most evidence suggests a higher diversity of fish in *Zostera* seagrass than unvegetated habitats (Bell and Pollard 1989; Ferrell and Bell 1991; West and King 1996; Gray et al. 1996). *Zostera* seagrass beds appear to provide a refuge for juvenile and other small fish when the intertidal wetlands are not flooded, with the density of seagrass less important than

Table 4 Differences in catch in seagrass between spring and neap tide inundations, and the contribution of species to the dissimilarity between assemblages

Numbers represent average fish per net release (n = 36) and standard deviation

Species	Spring tide	SD	Neap tide	SD	Contribution to dissimilarity (%)
A. jacksoniensis	2.79	2.72	4.06	2.94	11.65
A. edwardsi	6.10	4.06	6.48	4.65	11.44
P. olorum	3.08	2.78	3.56	2.57	10.28
M.intermedium	6.65	3.98	6.60	3.70	9.71
A. bifrenatus	3.02	2.25	3.13	2.47	9.46
L. argenta	1.00	1.47	1.81	1.95	8.75
P. quadrilineatus	4.85	3.04	4.69	2.87	8.67
A. australis	0.73	1.02	1.67	1.45	8.58
M. macleayi	7.73	4.01	9.48	3.79	7.83
T. hamiltoni	1.65	1.31	1.27	1.14	6.88

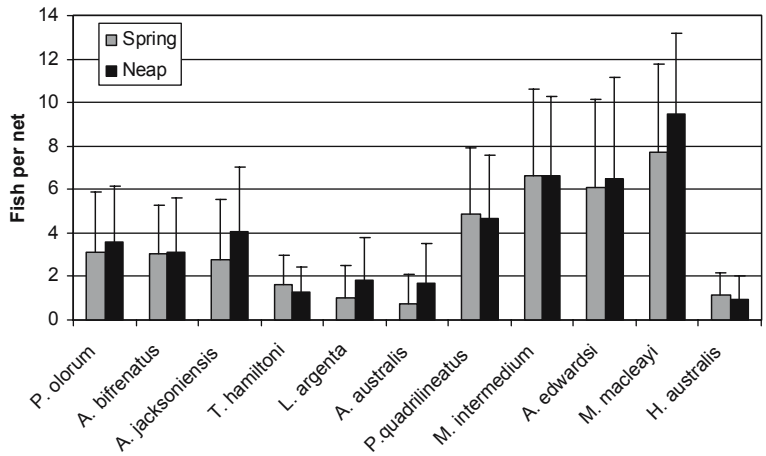


Fig. 3 Average fish per net (and standard deviation) in pop nets released during the spring and neap high tides, monthly from March 2001 to February 2002

the presence or absence of seagrass (Bell and Westoby 1986; Worthington and Westoby 1991). Fish habitats should be therefore viewed as mosaics, with fish moving between compartments over the tidal cycle, both diurnal and lunar. With the decline and fragmentation of seagrass and saltmarsh habitat in southeast Australia (Bowen et al. 1995) increasing attention is being given to the restoration of these habitats or to the compensation of habitat when loss is inevitable. To optimize outcomes for fish habitat, mangrove and saltmarsh restoration projects should either be prioritized to locations where available seagrass exists, or should have seagrass restoration incorporated as an objective (Irlandi and Crawford 1997). Further study is required however, to understand the effect of patch size on the movement of fish between adjacent shallow-water habitats, and the relative importance of these habitats to the diet of fish and other nekton.

Acknowledgements This study was supported by APAI scholarships from the Australian Research Council to M. K. Hossain and D. Mazumder, and contributions from the Department of Natural Resources, and the Department of Primary Industries. Rob Williams is thanked for contributions to logistics and fish identification. The authors also acknowledge the assistance of several field volunteers especially Kerrylee Rogers, Abdul Halim Miah, and Rifat.

References

Bell JD, Pollard DA (1989) Ecology of fish assemblages and fisheries associated with seagrasses. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of the seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, pp 565–609

Bell JD, Westoby M (1986) Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. J Exp Mar Biol Ecol 104:275–295

Beyst B, Hostens K, Mees J (2002) Factors influencing the spatial variation in fish and macrocrustacean communities in the surf zone of sandy beaches in Belguim. J Mar Biol Assoc UK 82:181–187

Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. J Fish Biol 17:143–162

Blaber SJM, Brewer DT, Salini JP (1995) Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. Estuar Coast Shelf S 40:176–193

Bowen R, Stephens N, Donnelly P (1995) SEPP 14: wetland protection and the role of mitigation. Wetlands 14:6–12

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Clarke LD, Hannon NJ (1967) The mangrove and salt marsh communities of the Sydney district I. Vegetation, soils and climate. J Ecol 55:753–771

Clarke KR, Warwick RM (2001) Changes in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E; Plymouth, United Kingdom

Clynick B, Chapman MG (2002) Assemblages of small fish in patchy mangrove forest in Sydney Harbour. Mar Freshwater Res 53:669–677

Connolly MR (1994) Comparison of fish catches from a buoyant pop net and beach seine net in a shallow seagrass habitat. Mar Ecol Prog Ser 109:305–309

Crinall SM, Hindell JS (2004) Assessing the use of saltmarsh flats by fish in a temperate Australian embayment. Estuaries 27:728–739

Dexter DM (1984) Temporal and spatial variability in the community structure of the fauna of four sandy beaches in South-eastern New South Wales. Aust J Mar Freshwater Res 35:663–672

Du Preez HH, McLachlan A, Marais JFK, Cockcrfoft AC (1990) Bioenergetics of fishes in a high-energy surf zone. Mar Biol 106:1–12

Fenseca MS, Thayer GW, Meyer DL, Thayer VG (1994) Effect of habitat heterogeneity in planted saltmarsh and seagrass on system linkages and faunal development. Report 1, prepared for U.S. Army Corp of Engineers and monitored by Environmental Laboratory, U.S. Army Engineer Waterways Experimental Station, Vicksburg MS

Ferrell DJ, Bell JD (1991) Differences among assemblages of fish associated with Zostera capricorni and bare sand over a large spatial scale. Mar Ecol Prog Ser 72:15–24

Gray CA, McElligott DJ, Chick RC (1996) Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. Mar Freshwater Res 47:723–735

Hannan JC, Williams RJ (1998) Recruitment of juvenile marine fishes to seagrass habitat in a temperate Australian estuary. Estuaries 21:29–51

Haynes D, Quinn GP (1995) Temporal and spatial variability in community structure of a sandy intertidal beach, Cape Paterson, Victoria. Mar Freshwater Res 46:931–942

Hollingsworth A, Connolly RM (2006) Feeding by fish visiting inundated tropical saltmarsh. J Exp Mar Biol Ecol 336:88–98

Hossain MK (2005) An examination of seagrass monitoring protocols as applied to two New South Wales estuarine settings. M.Phil. Thesis, Australian Catholic University, 70 pp

Hunt A (1989) Carbon flow through populations of the pulmonate gastropods *Salinator solida* and *Ophicardelus ornatus* at Towra Point, NSW. M.Sc. Thesis, University of Technology, Sydney

Irlandi EA, Crawford MK (1997) Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of estuarine fish. Oecologia 110:222–230

Jaraillo E, McLachlan A (1993) Community and population responses of the macrofauna to physical factors over a range of exposed sandy beaches in South-central Chile. Estuar Coast Shelf S 37:615–624

Jelbart JE, Ross PM, Connolly RM (2006) Fish assemblages in seagrass beds are influenced by the proximity of mangrove forests. Mar Biol (in press)

Longeragan NR, Potter IC, Lenanton RCJ, Caputi N (1986) Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. Mar Biol 92:575–586

Mazumder D, Saintilan N (2003) A comparison of sampling techniques in the assessment of burrowing crab abundance in saltmarsh and mangrove environments. Wetlands (Aust.) 21:1–15

Mazumder D, Saintilan N, Williams R (2005a) Temporal variation in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. Wetl Ecol Manag 13(4):457–467

Mazumder D, Saintilan N, Williams R (2005b) Comparison of fish catches using fyke nets and buoyant pop nets in a vegetated shallow water saltmarsh flat at Towra Point, NSW. Wetlands (Aust) 23(1):37–45

Mazumder D, Saintilan N, Williams R (2006a) Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. Mar Freshwater Res 57:193–199

Mazumder D, Saintilan N, Williams R (2006b) Fish assemblages in three tidal saltmarsh and mangrove flats in temperate NSW, Australia: a comparison based on species diversity and abundance. Wetl Ecol Manag 14(3):201–209

McGuiness KA (1990) Effects of oil spills on macroinvertebrates of saltmarsh and mangrove forests in Botany Bay, New South Wales, Australia. J Mar Biol Ecol 142:131–135

Meyer DL, Fonseca MS, Colby DR, Kenworthy WJ, Thayer GW (1993) An examination of created marsh and seagrass utilization by living marine resources. In: Coastal Zone '93. Proceedings of the Seventh Symposium on Coastal Ocean Management, 9–13 July, New Orleans, LA, American Society of Civil Engineers, New York

Mitchell ML, Adam P (1989) The relationship between mangrove and saltmarsh communities in the Sydney region. Wetlands (Aust) 9:37–46

Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, vant Hof T, den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reefs as a nursery for importance coral reef fishes, using a visual census techniques. Estuar Coast Shelf S 51:31–44

Nagelkerken I, Kleijnen S, Klop T, van den Brand RACJ, Cocheret de la Moriniere E, van der Velde G (2001). Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Mar Ecol Prog Ser 214:225–235

Parish JD (1989) Fish communities of interacting shallow-water habitats in tropical oceanic regions. Mar Ecol Prog Ser 58:143–160

Roach AC (1998) Effects of predation on the size structure of the gastropod Salinator solida (Martens) populations at Towra Point, NSW, Australia. Mar Freshwater Res 49:779–784

Roach AC, Lim RP (2000) Variation in the population dynamics of the intertidal pulmonate gastropod Salinator solida Martens (Gastropoda: Amphibolidae) at Towra Point, NSW, Australia. Wetl Ecol Manag 8:53–69

Robertson AI, Blaber SJM (1992) Plankton, epibenthos and fish communities. Coast Estuar Stud 41:173–224

Skilleter GA, Loneragan NR, Olds A, Zharikov Y (2005) The value of patches of intertidal seagrass to prawns depends on the proximity of patches to mangroves. Mar Biol 147:353–365

Thomas EB, Connolly RM (2001) Fish use of subtropical saltmarsh in Queensland, Australia: relationships with vegetation, water depth and distance onto the marsh. Mar Ecol Prog Ser 209:275–288

West RJ, King RJ (1996) Marine, brackish and freshwater fish communities in the vegetated and bare shallows of an Australian coastal river. Estuaries 19:31–41

Worthington DG, Westoby M (1991) Fish larvae settling in seagrass: effects of leaf density and an epiphytic alga. Aust J Ecol 16:289–293

Marine Pollution Bulletin 100 (2015) 217–223

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Inputs of anthropogenic nitrogen influence isotopic composition and trophic structure in SE Australian estuaries

Debashish Mazumder [a,*], Neil Saintilan [b], Brendan Alderson [c], Suzanne Hollins [a]

[a] Australian Nuclear Science and Technology Organisation, Locked Bag 2001 Kirrawee DC, NSW 2232, Australia
[b] Department of Environmental Sciences, Macquarie University, Sydney, NSW 2109, Australia
[c] Cardno, PO Box 19, St Leonards, NSW 1590, Australia

ARTICLE INFO

Article history:
Received 2 April 2015
Received in revised form 31 August 2015
Accepted 31 August 2015
Available online 12 September 2015

Keywords:
Estuaries
Anthropogenic N
Trophic linkages
Stable isotopes

ABSTRACT

Urban development in coastal settings has increased the input of nitrogen into estuaries globally, in many cases changing the composition of estuarine ecosystems. By focussing on three adjacent estuaries with a gradient of anthropogenic N loadings, we used stable isotopes of N and C to test for changes due to increased anthropogenic N input on the structure of some key trophic linkages in estuaries. We found a consistent enrichment in $\delta^{15}N$ corresponding to increased anthropogenic N at the three ecosystem levels studied: fine benthic organic matter, grazing invertebrate, and planktivorous fish. The degree of enrichment in $\delta^{15}N$ between fine benthic organic matter and the grapsid crab *Parasesarma erythrodactyla* was identical across the three sites. The glassfish *Ambassis jacksoniensis* showed lower levels of enrichment compared to basal food sources at the higher N-loaded sites, suggesting a possible effect of anthropogenic N in decreasing food-chain length in these estuaries.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Anthropogenic influences on nutrient inputs into estuaries, in particular the elevation of nitrogen levels, have the potential to alter the structure and function of estuarine ecosystems. The accumulation of biomass in most coastal systems is nitrogen (N) limited (Rabalais, 2002). The nitrogen enrichment in the coastal water is increasing as a result of increasing anthropogenic activities (Fry et al., 2003) and globally several large estuarine and nearshore systems have been subject to eutrophication and hypoxia (Rabalais, 2002). In a global review, Leavitt et al. (2006) report a continued trend in the period following 1950 of increases in N and P leading to oxygen depletion and alterations to primary productivity, as a direct result of point and nonpoint pollution.

One effect of elevated N in estuarine waters is a shifting of the production base from macrophytes to microphytic algae. Macreadie et al. (2012) demonstrated a shift in C to N ratios of organic carbon, consistent with a transition from macrophyte to algal carbon sources in estuarine cores from Botany Bay, Australia. The period of transition corresponded to catchment development and alterations to nutrient concentrations following European colonisation and catchment development. Such changes have the potential to alter the diet of benthic and intertidal herbivores, and Macreadie et al. (2012) called for further work to determine how increases in microalgae in Botany Bay have affected food web dynamics and ecosystem function within the Bay.

The trophic structure of benthic communities in Botany Bay has been extensively studied using stable isotopes of carbon and nitrogen (Mazumder et al., 2011; Saintilan and Mazumder, 2010). Generally crabs graze within narrowly defined feeding ranges (Guest et al., 2004), which allows the contrasting carbon isotope signatures of C_3 and C_4 saltmarsh plants, growing in mosaics, to be used to identify the relative contribution of macrophyte carbon in crab diets (Guest and Connolly, 2005). These studies have demonstrated a mixture of microphytobenthos and macrophyte detritus contributing to the diet of grapsid crabs, both at Botany Bay (Saintilan and Mazumder, 2010), and at nearby Brisbane Water (Alderson et al., 2013). Grapsid crabs play a keystone role in estuarine ecosystems in SE Australia, releasing larvae into the ebbing spring tide waters which provides an important source of nutrition for small fish (Mazumder et al., 2006) with a trophic relay traceable to commercially important predatory species (Mazumder et al., 2011). Shifts in the productivity base are therefore likely to show flow-on effects through the entire ecosystem.

Stable nitrogen isotope analysis has emerged as an effective way of exploring the uptake of anthropogenic N in estuarine ecosystems. Inputs of nitrogen in catchments increase the amount of N cycling in soils, a process that results in enrichment of the heavier ^{15}N isotope (Fry et al., 2003). Nitrate from human wastewater is also enriched in ^{15}N as a result of de-nitrification and volatilization of ammonia (Kendall et al., 2007), with $\delta^{15}N$ values typically in the range of +10‰ to +20‰ (Hoffman et al., 2012). Surface and groundwater bearing atmospherically derived N typically support background $\delta^{15}N$ signatures of +2‰ to +8‰ (McClelland et al., 1997).

* Corresponding author.
E-mail address: debashish.mazumder@ansto.gov.au (D. Mazumder).

http://dx.doi.org/10.1016/j.marpolbul.2015.08.047
0025-326X/© 2015 Elsevier Ltd. All rights reserved.

This alteration to the $\delta^{15}N$ signatures resulting from anthropogenic nitrogen inputs has been detected in an extensive range of ecosystem components. The nitrogen isotope ratios of primary producers reflect that of their nitrogen source, though fractionated (differential use of ^{15}N and ^{14}N) during uptake. Consumers typically show a +3‰ to +5‰ enrichment in $\delta^{15}N$ with respect to their diet (De Niro and Epstein, 1981; Minagawa and Wada, 1984). Elevated levels of $\delta^{15}N$ have been identified in sediment and suspended particulate organic matter (Kohzu et al., 2009); macroalgae and macrophytes (Cole et al., 2004; Kaldy, 2011); bivalves (Oczkowski et al., 2008); macroinvertebrates and zooplankton (Peterson et al., 2007), and fish (Bannon and Roman, 2008; Hoffman et al., 2012). The $\delta^{15}N$ values of nitrogen from animal waste, agricultural fertilisers and urban effluent sources are isotopically distinct from each other (Peterson, 1999; Costanzo et al., 2001, 2003), therefore the use of $\delta^{15}N$ provides the advantage of integrating, through the relatively long absorption time (3–5 weeks) water quality fluctuations occurring over the short term. However, the approach may not detect very high ammonium inputs from sewage (Fry et al., 2003).

Multi-estuary comparisons using gradients of N input have demonstrated the utility of $\delta^{15}N$ as a potential indicator of N loading. McClelland et al. (1997) sampled a range of trophic levels in a series of estuaries in Cape Cod (USA) in which nitrogen loads varied from 2 to 467 kg N $ha^{-1}yr^{-1}$, and found that anthropogenic N was detectable even at relatively low loadings. Hoffman et al. (2012) compared larval fish $\delta^{15}N$ across three watersheds spanning a large population density gradient in Lake Superior (USA), finding that $\delta^{15}N$ increased with N concentration, reflecting higher anthropogenic inputs. Fry et al. (2003), compared N loading with $\delta^{15}N$ in components of the estuarine biota in four West-Coast American systems, none low impact in respect to nitrogen loading, finding that macroalgae provided a good indicator of anthropogenic N.

Several issues remain unresolved in relation to the impacts of nitrogen loading in the estuarine environment. Although numerous studies have demonstrated significant uptake of anthropogenic N in tissues of estuarine organisms, it is unclear in many cases whether this amounts to an environmental problem such that ecosystem structure and function are disrupted, and if so, at what thresholds of N loading these changes occur (Rabalais, 2002). The exploration of ecosystem-level effects of elevated anthropogenic N requires consideration of trophic linkages using multiple stable isotope tracers across impact gradients.

In this study, we use stable isotopes of C and N in three estuarine settings that span a range of N loadings to explore the effect of elevated anthropogenic N on ecosystem trophic structure. Because $\delta^{15}N$ is fractionated between consumer and prey by predictable amounts the measure can be used to determine trophic position, where the signature of basal $\delta^{15}N$ is known. The dietary source is identified using $\delta^{13}C$, which has a lower degree of fractionation between diet and consumer (De Niro and Epstein, 1978). We utilise a well-studied trophic link between benthic detrital sources of carbon and nitrogen, and the dietary carbon source and trophic position of grazing crabs of the species *Parasesarma erythrodactyla*, and the glassfish *Ambassis jacksoniensis*, known to predate on the larvae of *P. erythrodactyla*, amongst other zooplankton sources. Three adjacent estuaries in the Sydney region, SE Australia, provide contrasting levels of anthropogenic N input while supporting common species and habitats. Our hypothesis is that the gradient of anthropogenic nitrogen input will correspond with a gradient of $\delta^{15}N$ values at all trophic levels, but that the trophic position and dependencies of organisms will be otherwise unchanged.

2. Methods

2.1. Site selection

Samples were collected from the three SE Australian estuaries with variable anthropogenic nitrogen inputs (Fig. 1). Brisbane Water is situated on the northern entrance of Broken Bay, and the intertidal wetlands form on flood-tidal deltaic sands. The primary hydrological input is oceanic tidal water with no major rivers contributing sediment or water. This site is the least disturbed of the three chosen, with the lowest level of catchment clearance, lowest population density, and lowest percentage increase in anthropogenic N against estimated pre-development levels (Table 1). The mangrove community at the site is dominated by *Avicennia marina*, fronted at the seaward edge by Zostera seagrass meadows.

Botany Bay represents an intermediate level of anthropogenic modification amongst the three sites, in percentage clearance, and population density. Though current N inputs are lower than Brisbane Water, the Bay receives inputs from the Georges River, the major tributary, which contains a relatively high level of anthropogenic N (Table 1). Water clarity at the sampling site of Towra Point, Botany Bay is sufficient to support the seagrasses *Posidonia australis* and other species in the families Zosteraceae and Hydrocharitaceae. The mangrove community is dominated by *A. marina*, and the wetland consists of a diverse saltmarsh assemblage in the upper intertidal zone. In the late 1970s Towra Point was declared a nature reserve and in the mid-1980s its adjacent waters were declared an aquatic reserve.

Homebush Bay, within the Parramatta River estuary, is the site of highest anthropogenic disturbance with the highest population density, highest level of clearance and highest levels of local anthropogenic nitrogen input of the three sites. The wetlands are situated on estuarine silts approximately 20 km from the ocean. From the late 1920s until the mid-1980s, the eastern shore of Homebush Bay was the site of various industrial facilities at which timber preservatives, tar-based products, herbicides, pesticides, chlorine gas and plastics were produced (Alexander, 2002). Some of the by-product material was disposed of on site, and contaminated spoil was used to reclaim land for the expansion of adjacent industrial facilities (Birch et al., 2007). A National Dioxin Study identified the highest dioxin and furan concentrations in Australia to be from Homebush Bay (Mueller et al., 2004). The industrial sites on the east side of the bay have been progressively replaced with residential apartments, with conditions of approval requiring the dredging, removal and treatment of contaminated soil. In the upper portion of the bay, brickworks and an abattoir operated for many decades but were replaced in the late 1990s to provide the site for the Sydney 2000 Olympics. Two small creeks, channelized and hence vastly modified from their natural condition, enter Homebush Bay from the south. Mangrove (*A. marina*) and saltmarsh are present, but seagrass is not, presumably due to reduced water clarity at this location. There were no sewage treatment facilities in the vicinity of any of the three sampling sites.

2.2. Sampling and analytical methods

Three components of the food chain: sediment organic matter (SOM), burrowing crabs (*P. erythrodactyla*) and estuarine glassfish (*A. jacksoniensis*) were collected from saltmarsh and mangrove habitats of the three estuaries. Sample replication was determined using the prior power analysis of Mazumder et al. (2008).

Sediment organic matter is the likely base of the food chain, and was collected from saltmarsh/mangrove habitats of the three estuarine ecosystems ($n = 9–17$). Sediment organic matter includes variety of living and non-living sources including microalgae (Nils, 2003). Sediment scrapings were collected from the top 1 cm of surface sediment (Melville and Connolly, 2003) and the samples were washed through 4-mm, 1-mm, 0.5-mm, and 0.25-mm sieves following the method of (Loneragan et al., 1997). Material elutriated from the finest size-fractions (<0.25 mm) were analysed for isotopic values. As stable isotopes used in trophic ecology rely on C fixed in the organic form (Mateo et al., 2008), acid-washing of sediment samples was performed prior to analysis. To avoid bias introduced by inorganic C, a small volume of 1 M hydrochloric acid was added to sediment sub-samples and left

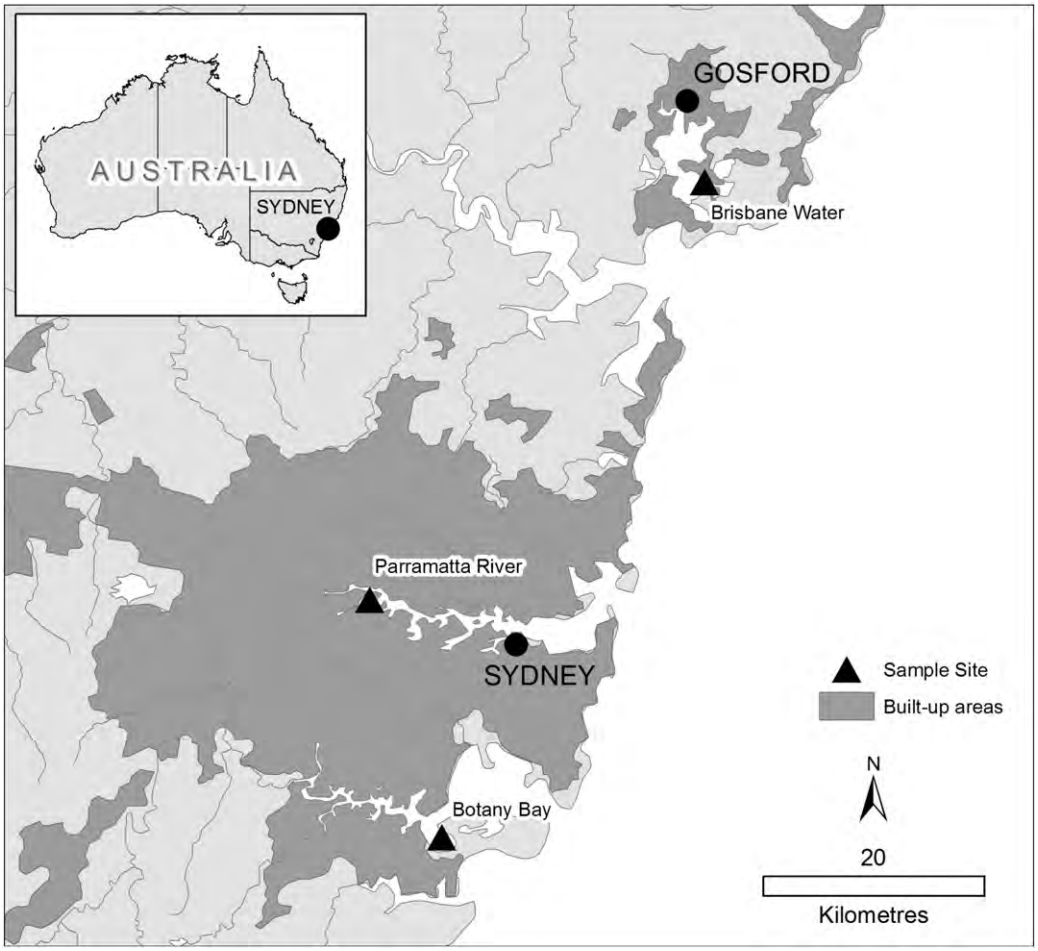


Fig. 1. Sampling sites from the three SE Australian estuaries with variable anthropogenic nitrogen inputs indicated by triangles.

for 3 h to remove the inorganic carbon present in the sediment (Polunin et al., 2001). The samples were then rinsed with distilled water, dried and ground to a fine powder. Since this acid-washing process results in enrichment of $\delta^{15}N$ (Pinnegar and Polunin, 1999), untreated sediment sub-samples were analysed for $\delta^{15}N$.

The dominant shore crab species *P. erythrodactyla* is a benthic grazer with a diet consisting of fine benthic material on the sediment surface (Guest and Connolly, 2005; Saintilan and Mazumder, 2010). Adult *P. erythrodactyla* were collected by hand from mangrove habitats at the three sites and frozen immediately for laboratory processing. White muscle tissue from crabs was sampled following the removal of exoskeleton.

Glassfish (*A. jacksoniensis*) is a small fish (adult length ranges 43–44 mm; Mazumder et al., 2011) that is common to estuaries along the southeast coast and on the basis of limited evidence (SPCC, 1981), appears to be consumed by a number of higher order predators. In turn, *A. jacksoniensis* is a carnivore, preying on crab larvae (Mazumder et al., 2006, 2011). Adult glassfish were collected from the saltmarsh and mangrove habitats using fyke nets and frozen instantly for laboratory processing. White muscle tissue from the dorsal region of glassfish was collected for isotopic analysis.

Lipid extractions were not undertaken as delipidation from muscle tissue appears to lead to only small (<1‰) isotope shifts in $\delta^{13}C$ and $\delta^{15}N$ values (Sotiropoulos et al., 2004). Muscle tissue samples were dried at 60 °C for 72 h and then ground to a fine powder with mortar and pestle. After processing, samples were loaded in tin capsules and were analysed with a continuous flow isotope ratio mass spectrometer (CF-IRMS), model Delta V Plus (Thermo Scientific Corporation, U.S.A.), interfaced with an elemental analyser (Thermo Fisher Flash 2000 HT EA, Thermo Electron Corporation, U.S.A.). The data are reported relative to IAEA secondary standards that have been certified relative to VPDB for carbon and air for nitrogen. A two point calibration is employed to normalise the data, utilising standards that bracket the samples being analysed. Two quality control references were also included in each run. Results are accurate to 1% for both C% and N% and ±0.3 per mill for $\delta^{13}C$ and $\delta^{15}N$. Stable isotope values were reported in delta (δ) units in parts per thousand (‰) relative to the international standard and determined as follows:

$$X(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

where $X = \delta^{13}C$ or $\delta^{15}N$, and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$, respectively.

Table 1
Anthropogenic modification metrics for each study site, including Total Nitrogen (TN) loading in 2012. Georges River drains into Botany Bay and nitrogen loading at the point of sampling is likely to be influenced by this source.
Source: NSW Office of Environment and Heritage, Australia (http://www.environment.nsw.gov.au).

	Georges River	Botany Bay	Parramatta River	Brisbane Water
Catchment area (km^2)	450,940	18,566	67,918	39,025
% catchment cleared	59	61.5	86.1	52.1
Population	851,544	110,990	652,176	100,969
Population density (no/km^2)	900.3	1210.5	2460	644.4
TN (t yr^{-1})	450,940	18,466	67,918	39,025
% increase TN on pre-development	870.6	824.7	397	188
Flushing time (days)	62.5	39.9	17.3	24.6

2.3. Statistical methods

Multifactorial permutational analysis of variance (PERMANOVA, Anderson et al. (2008) was used to investigate the difference between estuaries for $\delta^{13}C$ and $\delta^{15}N$ values of food chain components (i.e., SOM, crab and glassfish). The analyses were univariate and were based on Euclidean distance matrices calculated by PRIMER v6 for Windows (PRIMER-E Ltd., Plymouth, UK) using untransformed data. The food chain components analysed included $\delta^{13}C$ and $\delta^{15}N$ for SOM (sediment organic matter), *P. erythrodactyla* and *A. jacksoniensis*. The advantages of PERMANOVA approach over traditional ANOVA are that there is no assumption that the data are normally distributed and the test is not affected by unbalanced designs (Anderson et al., 2008). For the factor site, pairwise comparisons of disturbance levels (low impact, moderate and high nitrogen input sites) were performed to test whether significant differences between sites for isotopic values of food chain components were apparent. Trophic position of species was calculated using the formula reported by (Post, 2002):

$$TPO = \lambda + \left(\delta^{15}N_{organism} - \delta^{15}N_{base\ of\ food\ web}\right)/3.4$$

where λ is the trophic level of the organism used to estimate $\delta^{15}N_{base\ of\ food\ web}$. In this study, sediment organic matter (SOM) from study sites were identified as the likely base trophic resource (i.e. trophic level = 1, Kelleway et al. (2010). We applied commonly used trophic enrichment factor 3.4‰ (Post, 2002) to estimate trophic position.

3. Results

Similar patterns of food chain structure were found in all three sites. The $\delta^{13}C$ values of crabs were close to the SOM signature, suggesting this to be the common source of crab dietary carbon at all sites. The $\delta^{15}N$ enrichment between SOM and *P. erythrodactyla* was 2.2‰ to 2.8‰ across the three sites, positioning crabs less than one trophic level above SOM in all cases (Fig. 2). If the standard enrichment of 3.4‰ is to be applied, suggesting either additional, depleted food sources or an uncommonly low level of enrichment for this trophic link. The small carnivorous fish *A. jacksoniensis* was consistently placed above the herbivorous crabs in food-chain structure all three sites. The $\delta^{15}N$ enrichment between *P. erythrodactyla* and *A. jacksoniensis* though smaller for Parramatta River (4.9‰) and Botany Bay (6.2‰), was somewhat higher (8.1‰) at Brisbane Water. Trophic positions of *P. erythrodactyla* were similar across sites, ranging from 1.6 to 1.8, whereas trophic positions of *A. jacksoniensis* were similar at Botany Bay and Parramatta River sites and slightly higher (~0.6) in the Brisbane Water site (Fig. 2). The $\delta^{15}N$ values of all components increased with increasing N loading, with a 1.9‰ increase in $\delta^{15}N$ between Brisbane Water and Botany Bay for SOM, and a 4.2‰ increase between Brisbane Water and Parramatta River for SOM. These differences were promulgated through the ecosystems. $\delta^{15}N$ values of *P. erythrodactyla* and *A. jacksoniensis* increased 2.5‰ and 0.7‰ respectively from Brisbane Water to Botany Bay and 4.9‰ and 1.6‰ respectively from Brisbane Water to Sydney Harbour.

Carbon stable isotope ratios confirm the importance of sediment organic matter as the basal carbon source to the dominant herbivores (*P. erythrodactyla*) and carnivores (*A. jacksoniensis*) at all sites. While

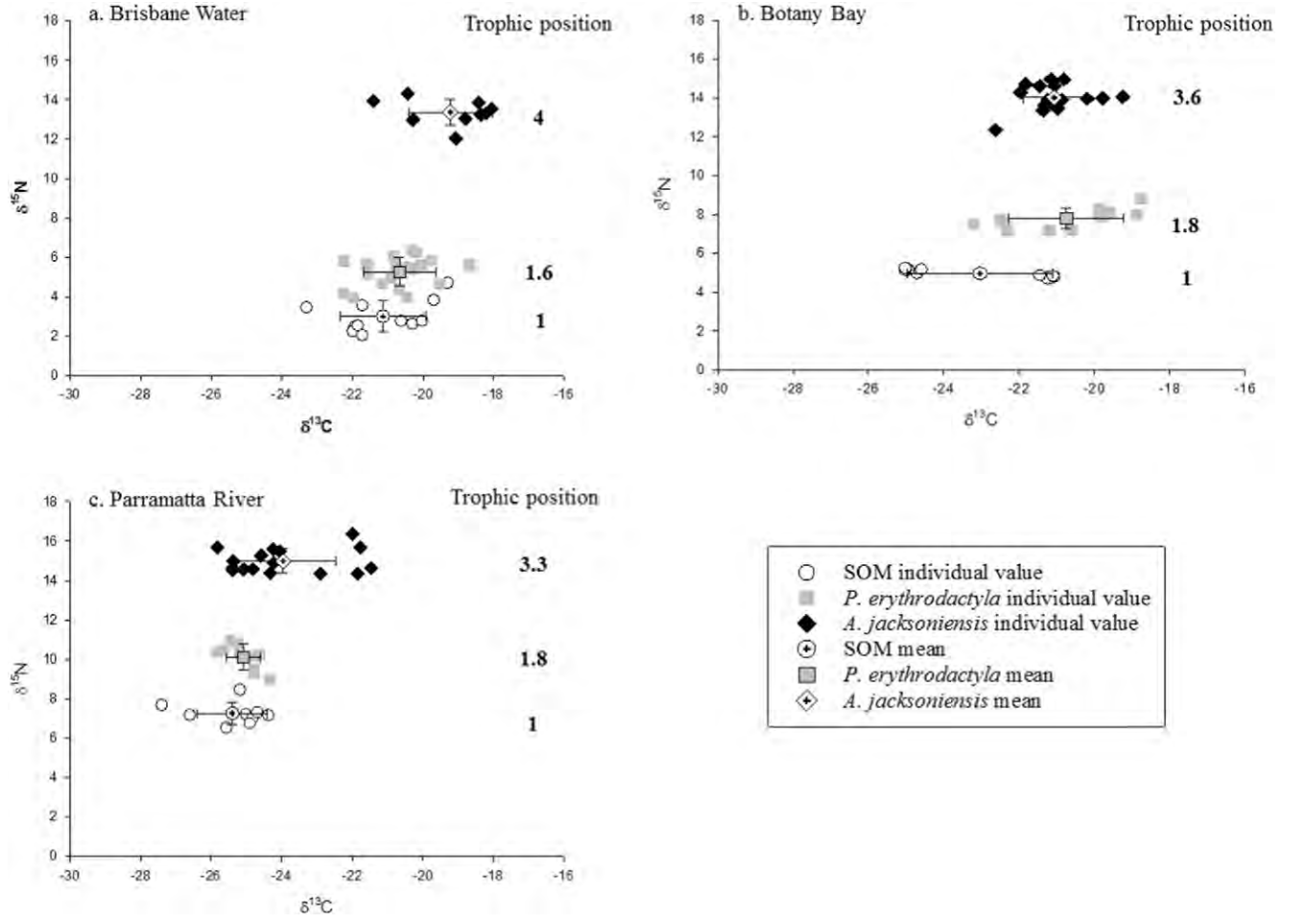


Fig. 2. Stable carbon and nitrogen bi-plots showing food chain connectivity amongst three ecosystem level samples in the three studied sites with variable anthropogenic N inputs. a) Brisbane Water = low impact site, b) Botany Bay = moderate site and c) Parramatta River = high impacted site. Individual and mean values ± sd of samples were shown in the figures.

$\delta^{13}C$ values varied between sites (being more depleted at the Parramatta River site), this positioning of consumer $\delta^{13}C$ in relation to SOM $\delta^{13}C$ did not change, being slightly fractionated between trophic levels, as would be expected (0 to +1‰ fractionation between levels for $\delta^{13}C$; De Niro and Epstein, 1978; Peterson and Fry, 1987).

PERMANOVA results found that sites were significantly different ($P < 0.05$) for both isotopes in SOM, *P. erythrodactyla* and *A. jacksoniensis* (Table 2). Comparison of the isotopic ($\delta^{13}C$ and $\delta^{15}N$) values of samples between sites generally showed a significant difference ($P < 0.05$) in both isotopes in all samples types at all sites; the exceptions were the $\delta^{13}C$ values of *P. erythrodactyla* samples from Brisbane Water (low impact) and Botany Bay (moderate) for which no difference was found (Table 3).

Table 3
Pairwise comparisons between levels (i.e., Brisbane Water: low impacted site, Botany Bay: moderately impacted site and Parramatta River: high impacted site) based on $\delta^{13}C$ and $\delta^{15}N$ isotope values of three food chain components. Significant differences between sites are determined by $P < 0.05$.

		$\delta^{13}C$		$\delta^{15}N$	
Samples	Groups	*t*	*P* (Perm)	*t*	*P* (Perm)
SOM	Low, moderate	2.7364	0.0136	7.61	0.0001
	Low, high	8.4502	0.0001	13.5	0.0001
	Moderate, high	3.2972	0.0076	12.1	0.0002
P. erythrodactyla	Low, moderate	0.20807	0.8377	10.8	0.0001
	Low, high	13.03	0.0001	18	0.0001
	Moderate, High	8.6201	0.0001	9.42	0.0001
A. jacksoniensis	Low, moderate	4.6139	0.0001	2.37	0.0257
	Low, high	8.2161	0.0001	6.25	0.0001
	Moderate, high	6.8352	0.0001	4.24	0.0001

4. Discussion

Degradation in the water quality of estuaries is a global trend (Smith et al., 1997), and commonly moves through two phases: firstly a pulse of sediment and nutrient resulting from deforestation and altered land use, and then the ongoing elevation of nitrogen and phosphorus loading from point and non-point sources (Lotze et al., 2006). Elevated N levels in estuarine waters promotes the growth of algae, potentially shifting the production base of estuarine food webs from macrophytic to microalgal sources (Elliot and Quintino, 2007). This is either because of the prevalence of microalgae or the replacement of seagrass due to poor water quality (Cole et al., 2004). The increase in N loading in estuaries globally has occurred primarily in the last half-century (Lotze et al., 2006), and is strongly associated with human population pressure.

In temperate Australia, estuaries in their natural state are characterised by low levels of nitrogen, resulting from the character of soil vegetation and traditional land-use in the catchment (Specht and Specht, 1999). As a result, settlement and population growth following European colonisation and the introduction of fertilisers have led to profound alterations to the nutrient dynamics of Australian estuaries (Roy et al., 2001). Focussing seagrass habitat adjacent to one of our sampling sites, Macreadie et al. (2012) demonstrated a shift in C:N ratio of organic material within Botany Bay coincident with industrial and residential development within the catchment. They suggested that a trend towards algal rather than macrophyte sources might have flow-on effects in estuarine food chains. We tested this hypothesis across a gradient of N-impacted estuaries in the Sydney region, utilising stable isotopes of carbon and nitrogen in a well-documented trophic link between sediment organic material, grazing crabs and ambassids, the numerically dominant zooplanktivorous fish in the region. The Ambassids we analysed migrate between the seagrass beds and the adjacent mangrove and saltmarsh over the tidal cycle, as do several other fish species (Saintilan et al., 2007), feeding primarily on material exported from the mangrove and saltmarsh (Mazumder et al., 2006). This model of trophic association between brachuryan larvae, and feeding by Ambassids on lunar cycles finds common application across multiple estuaries in eastern Australia (Hollingsworth and Connolly, 2006; Platell and Freewater, 2009). Given the numerical importance of Ambassids in the estuarine environment, we expect that any changes in the trophic position or function of the species would be propagated through the estuarine ecosystem.

Our findings concord with previous studies have shown that fine benthic organic material, comprising plant detritus and microphytobenthos, is the primary source of nutrition for grazing crabs in the region (Saintilan and Mazumder, 2010; Alderson et al., 2013). Trends in the $\delta^{15}N$ values of fine benthic organic material, the dominant source of dietary carbon to grazing invertebrates, closely followed the trends in the level of anthropogenic N input across the three estuaries studied. These were reflected in the $\delta^{15}N$ signatures of the grazing grapsid crab *P. erythrodactyla*, which were fractionated by 2.2–2.8‰ at each site. This level of $\delta^{15}N$ fractionation falls within reported ranges between 0.7‰ to 5.2‰ for invertebrates (Caut et al., 2009). Crab $\delta^{13}C$ signatures also followed differences in SOM $\delta^{13}C$ between estuaries. Crabs appear tightly coupled with SOM and the link is unaffected by elevated levels of anthropogenic N inputs between sites.

The $\delta^{15}N$ of muscle tissue of the glassfish *A. jacksoniensis* was enriched approximately 5.5‰ compared to *P. erythrodactyla* at the Botany Bay and Parramatta River sites, and 8.1‰ at the Brisbane Water site. The estimated trophic position of the species changed in association with the gradient in anthropogenic N inputs between estuaries, being 3.3 at the most heavily impacted site, 3.6 at the site of intermediate impact, and 4.0 at the least impacted site. *A. jacksoniensis* is a small carnivore, not directly preying upon adult *P. erythrodactyla* but preying on zooplankton including *P. erythrodactyla* larvae (Mazumder et al., 2006, 2011), but also caridean decapods, amphipods, sergestid decapods and algae (McPhee et al., 2015a,2015b). The species can shift between diet sources depending on availability, and has been demonstrated to do so over a spring tidal cycle (McPhee et al., 2015a,b). We postulate that differences in trophic position of the species in relation to basal food sources may relate to the availability of decapod

Table 2
Univariate PERMANOVA results for $\delta^{13}C$ and $\delta^{15}N$ values of three food chain components sampled from three sites (i.e., Brisbane Water, Botany Bay and Parramatta River) in NSW, Australia. Significant differences amongst sites for isotopic values are determined by $P < 0.05$.

Samples	$\delta^{13}C$						$\delta^{15}N$					
	Source of variation	df	SS	MS	Pseudo-*F*	*P* (Perm)	Source of variation	df	SS	MS	Pseudo-*F*	*P* (Perm)
SOM	Site	2	90	44.977	21.667	0.0001	Site	2	89.884	44.942	132.29	0.0001
	Residual	27	56	2.0759			Residual	27	9.1727	0.33973		
	Total	29	146				Total	29	99.056			
P. erythrodactyla	Site	2	148	74.099	61.447	0.0001	Site	2	168.23	84.116	198.07	0.0001
	Residual	40	48.2	1.2059			Residual	40	16.988	0.42469		
	Total	42	196				Total	42	185.22			
A. jacksoniensis	Site	2	142	71.151	50.183	0.0001	Site	2	16.843	8.4214	19.888	0.0001
	Residual	38	53.9	1.4178			Residual	38	16.091	0.42344		
	Total	40	196				Total	40	32.934			

and algal food sources between sites, with the elevated $\delta^{15}N$ signatures of the larval zooplankton counterbalanced by a higher availability of algae at the N enriched sites. Further research on variation in the diet of this species along N pollution gradients would help elucidate this.

We found no evidence to support the contention that elevated N shifted the source of dietary carbon of grazing crabs from benthic macrophyte-derived sources to microphytos. We found microphytobenthos was the dominant source of dietary carbon for crabs grazing beneath mangrove at the least impacted site, as documented in Alderson et al. (2013). The $\delta^{13}C$ value of microalgae in Brisbane Water has previously been measured as approximately −22‰ (Alderson et al., 2013) and the $\delta^{13}C$ values of macrophytes in Botany Bay have been found to range from approximately −15‰ (*Sporobolus virginicus* saltmarsh) to −27‰ (Mazumder et al., 2011). The more depleted $\delta^{13}C$ values at the Parramatta River site, the most impacted of the three, suggests a higher contribution of macrophyte carbon. This is the site most heavily impacted by N pollution, though the results may reflect the relatively greater distance from the estuary entrance, and presumably lower concentrations of marine diatoms. Crabs seem to feed on fine detrital material of macrophyte or algal origin depending on availability within their narrow feeding range, and make an important contribution to the diet of glassfish, most probably through the export of larvae (Mazumder et al., 2011).

Our results provide further evidence of the utility of stable N isotopes in monitoring the uptake of anthropogenic N in estuarine ecosystems. The organisms chosen are easily sampled, and suitable statistical power is provided by a modest number of replicates in most settings (Mazumder et al., 2008). The stable N isotope ratios of tissues collected across the three sites reflected the degree of anthropogenic modification and nitrogen pollution in the estuaries, and corresponded to population density within the catchments, in common with North American studies (Bannon and Roman, 2008; Cole et al., 2004).

Acknowledgements

Samples were collected under scientific license SL100432. Barbora Neklapilova (ANSTO) and Scott Allchin (ANSTO) assisted with sample preparation and analysis. Stuart Hankin (ANSTO) for drawing Fig. 1. Dr Swapan Paul (SOPA) is thanked for assisting in the collection of samples from Homebush Bay. Office of Environment and Heritage, NSW provided access to the Towra Point sites, and data on N loadings and anthropogenic modification to the estuaries. Comments from anonymous reviewers allowed us to improve the quality of the completed manuscript. Animal ethics approval was granted by the Director General's Animal Ethics Committee of the Department of Primary Industries, project number 02/3477 and samples collected from Brisbane Water were collected under NSW Scientific Collection Permit P07/0122-2.0.

References

Alderson, B., Mazumder, D., Saintilan, N., Zimmerman, K., Mulry, P., 2013. Application of isotope mixing models to discriminate dietary sources over small-scale patches in saltmarsh. Mar. Ecol. Prog. Ser. 487, 113–122.

Alexander, M., 2002. Environmental Impact Statement; the Remediation of the Lednez site, Rhodes Peninsula and Homebush Bay—Summary. Parsons Brincherhoff, Australia.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods. Plymouth, UK.

Bannon, R.O., Roman, C.T., 2008. Using stable isotopes to monitor anthropogenic nitrogen inputs to estuaries. Ecol. Appl. 18, 22–30.

Birch, G.F., Harrington, C., Symons, R.K., Hunt, J.W., 2007. The source and distribution of polychlorinated dibenzo-p-dioxin and polychlorinated dibenzofurans in sediments of Port Jackson, Australia. Mar. Pollut. Bull. 54, 295–308.

Caut, S., Angulo, E., Courchamp, F., 2009. Variation in discrimination factors (Δ15N and Δ13C): the effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. 46, 443–453.

Cole, M.L., Valiela, I., Kroeger, K.D., Tomasky, G.L., Cebrian, J., Wigand, C., McKinney, R.A., Grady, S.P., Carvalho da Silva, M.H., 2004. Assessment of a $\delta^{15}N$ isotopic method to indicate anthropogenic eutrophication in aquatic ecosystems. J. Environ. Qual. 33, 124–132.

Costanzo, S.D., O'Donohue, M.J., Dennison, W.C., 2003. Assessing the seasonal influence of sewage and agricultural nutrient inputs in a subtropical river estuary. Estuaries 26, 857–865.

Costanzo, S.D., O'Donohue, M.J., Dennison, W.C., Loneragan, N.R., Thomas, M., 2001. A new approach for detecting and mapping sewage impacts. Mar. Pollut. Bull. 42, 149–156.

De Niro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta 42, 495–506.

De Niro, M.J., Epstein, S., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta 45, 341–351.

Elliot, M., Quintino, V., 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar. Pollut. Bull. 54, 640–645.

Fry, B., Gace, A., McClelland, J.W., 2003. Chemical indicators of anthropogenic nitrogen loading in four Pacific estuaries. Pac. Sci. 57, 77–101.

Guest, M., Connolly, R., 2005. Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. Aquat. Ecol. 38, 599–609.

Guest, M.A., Connolly, R.M., Loneragan, N.R., 2004. Carbon movement and assimilation by invertebrates in estuarine habitats at a scale of metres. Mar. Ecol. Prog. Ser. 278, 27–34.

Hoffman, J., Kelly, J., Peterson, G., Cotter, A., Starry, M., Sierszen, M., 2012. Using $\delta^{15}N$ in fish larvae as an indicator of watershed sources of anthropogenic nitrogen: response at multiple spatial scales. Estuar. Coasts 35, 1453–1467.

Hollingsworth, A., Connolly, R.M., 2006. Feeding by fish visiting inundated subtropical saltmarsh. J. Exp. Mar. Biol. Ecol. 336, 88–98.

Kaldy, J., 2011. Using a macroalgal $\delta^{15}N$ bioassay to detect cruise ship waste water effluent inputs. Mar. Pollut. Bull. 62, 1762–1771.

Kelleway, J., Mazumder, D., Wilson, G., Kobayashi, T., 2010. Using Isotopic Techniques to Assess Trophic Structure in Northern Murray-Darling Basin Wetlands. CSIRO Publishing, Melbourne.

Kendall, C., Elliott, E.M., Wankel, S.D., 2007. Tracing Anthropogenic Inputs of Nitrogen to Ecosystems. 2nd edition ed. Blackwell Publishing.

Kohzu, A., Tayasu, I., Yoshimizu, C., Maruyama, A., Kohmatsu, Y., Hyodo, F., Onoda, Y., Igeta, A., Matsui, K., Nakano, T., Wada, E., Nagata, T., Takemon, Y., 2009. Nitrogen-stable isotopic signatures of basal food items, primary consumers and omnivores in rivers with different levels of human impact. Ecol. Res. 24, 127–136.

Leavitt, P.R., Brock, C.S., Ebel, C., Patoine, A., 2006. Landscape-scale effects of urban nitrogen on a chain of freshwater lakes in central North America. Limnol. Oceanogr. 51, 2262–2277.

Loneragan, N.R., Bunn, S.E., Kellaway, D.M., 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Mar. Biol. 130, 289–300.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312, 1806–1809.

Macreadie, P.I., Allen, K., Kelaher, B.P., Ralph, P.J., Skilbeck, C.G., 2012. Paleoreconstruction of estuarine sediments reveal human-induced weakening of coastal carbon sinks. Glob. Chang. Biol. 18, 891–901.

Mateo, M., Serrano, O., Serrano, L., Michener, R., 2008. Effects of sample preparation on stable isotope ratios of carbon and nitrogen in marine invertebrates: implications for food web studies using stable isotopes. Oecologia 157, 105–115.

Mazumder, D., Saintilan, N., Williams, R.J., 2006. Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. Mar. Freshw. Res. 57, 193–199.

Mazumder, D., Saintilan, N., Williams, R.J., Szymczak, R., 2011. Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. Mar. Freshw. Res. 62, 11–19.

Mazumder, D., Williams, R.J., Reid, D., Saintilan, N., Szymczak, R., 2008. Variability of stable isotope ratios of glassfish (*Ambassis jacksoniensis*) from mangrove/saltmarsh environments in southeast Australia and implications for choosing sample size. Environ. Bioindic. 3, 114–123.

McClelland, J.W., Valiela, I., Michener, R.H., 1997. Nitrogen-stable isotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. Limnol. Oceanogr. 42, 930–937.

McPhee, J.J., Freewater, P., Gladstone, W., Platell, M.E., Schreider, M.J., 2015a. Glassfish switch feeding from thalassinid larvae to crab zoeae after tidal inundation of saltmarsh. Mar. Freshw. Res. 66, 1–8.

McPhee, J.J., Platell, M.E., Schreider, M.J., 2015b. Trophic relay and prey switching — a stomach contents and calorimetric investigation of an ambassid fish and their saltmarsh prey. Estuar. Coast. Shelf Sci. http://dx.doi.org/10.1016/j.ecss.2015.07.008 (in press).

Melville, A., Connolly, R., 2003. Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136, 499–507.

Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta 48, 1135–1140.

Mueller, J., Muller, R., Goudkamp, K., Shaw, M., Mortimer, M., Haynes, D., Paxman, D., Hyne, R., McTaggart, A., Burniston, D., Symons, R., Moore, M., 2004. Dioxins in aquatic environments in Australia. National Dioxins Program Technical Report No. 6. Australian Government Department of the Environment and Heritage, Canberra.

Nils, R.-P., 2003. Coupled nitrification–denitrification in autotrophic and heterotrophic estuarine sediments: on the influence of benthic microalgae. Limnol. Oceanogr. 48, 93–105.

Oczkowski, A., Nixon, S., Henry, K., DiMilla, P., Pilson, M., Granger, S., Buckley, B., Thornber, C., McKinney, R., Chaves, J., 2008. Distribution and trophic importance of anthropogenic nitrogen in Narragansett Bay: an assessment using stable isotopes. Estuar. Coasts 31, 53–69.

Peterson, B.J., Fry, B., 1987. Stable Isotopes in Ecosystem Studies. Annu. Rev. Ecol. Syst. 18, 293–320.
Peterson, B.J., 1999. Stable isotopes as tracers of organic matter input and transfer in benthic food webs: a review. Acta Oecol. 20, 479–487.
Peterson, G.S., Sierszen, M.E., Yurista, P.M., Kelly, J.R., 2007. Stable nitrogen isotopes of plankton and benthos reflect a landscape-level influence on Great Lakes coastal ecosystems. J. Great Lakes Res. 33 (Supplement 3), 27–41.
Pinnegar, J.K., Polunin, N.V.C., 1999. Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implications for the study of trophic interactions. Funct. Ecol. 13, 225–231.
Platell, M.E., Freewater, P., 2009. Importance of saltmarsh to fish species of a large south-eastern Australian estuary during a spring tide cycle. Mar. Freshw. Res. 60, 936–941.
Polunin, N.V.C., Morales-Nin, B., Pawsey, W.E., Cartes, J.E., Pinnegar, J.K., Moranta, J., 2001. Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. Mar. Ecol. Prog. Ser. 220, 13–23.
Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.
Rabalais, N.N., 2002. Nitrogen in aquatic ecosystems. Ambio 31, 102–112.
Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of South-east Australian estuaries. Estuar. Coast. Shelf Sci. 53, 351–384.
Saintilan, N., Hossain, K., Mazumder, D., 2007. Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. Wetl. Ecol. Manag. 15, 277–286.
Saintilan, N., Mazumder, D., 2010. Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. Mar. Freshw. Res. 61, 615–620.
Smith, R.A., Schwarz, G.E., Alexander, R.B., 1997. Regional interpretation of water-quality monitoring data. Water Resour. Res. 33, 2781–2798.
Sotiropoulos, M.A., Tonn, W.M., Wassenaar, L.I., 2004. Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. Ecol. Freshw. Fish 13, 155–160.
SPCC, 1981. The ecology of fish in Botany Bay — biology of commercially and recreationally valuable species. Environmental Control Study of Botany Bay. State Pollution Control Commission, Sydney, Australia, p. 287.
Specht, R.L., Specht, A., 1999. Australian Plant Communities: Dynamics of Structure, Growth and Biodiversity. Oxford University Press, Melbourne.

Received: 21 December 2016 | Accepted: 21 February 2017

DOI: 10.1111/gcb.13727

REVIEW

WILEY Global Change Biology

Review of the ecosystem service implications of mangrove encroachment into salt marshes

Jeffrey J. Kelleway[1] | Kyle Cavanaugh[2] | Kerrylee Rogers[3] | Ilka C. Feller[4] | Emilie Ens[1] | Cheryl Doughty[2] | Neil Saintilan[1]

[1]Department of Environmental Sciences, Macquarie University, Sydney, NSW, Australia

[2]Department of Geography, University of California, Los Angeles, CA, USA

[3]School of Earth and Environmental Science, University of Wollongong, Wollongong, NSW, Australia

[4]Smithsonian Environmental Research Center, Edgewater, MD, USA

Correspondence
Jeffrey J. Kelleway, Department of Environmental Sciences, Macquarie University, Sydney, NSW, Australia.
Email: jeffrey.kelleway@mq.edu.au

Abstract

Salt marsh and mangrove have been recognized as being among the most valuable ecosystem types globally in terms of their supply of ecosystem services and support for human livelihoods. These coastal ecosystems are also susceptible to the impacts of climate change and rising sea levels, with evidence of global shifts in the distribution of mangroves, including encroachment into salt marshes. The encroachment of woody mangrove shrubs and trees into herbaceous salt marshes may represent a substantial change in ecosystem structure, although resulting impacts on ecosystem functions and service provisions are largely unknown. In this review, we assess changes in ecosystem services associated with mangrove encroachment. While there is quantitative evidence to suggest that mangrove encroachment may enhance carbon storage and the capacity of a wetland to increase surface elevation in response to sea-level rise, for most services there has been no direct assessment of encroachment impact. On the basis of current understanding of ecosystem structure and function, we theorize that mangrove encroachment may increase nutrient storage and improve storm protection, but cause declines in habitat availability for fauna requiring open vegetation structure (such as migratory birds and foraging bats) as well as the recreational and cultural activities associated with this fauna (e.g., bird-watching and/or hunting). Changes to provisional services such as fisheries productivity and cultural services are likely to be site specific and dependent on the species involved. We discuss the need for explicit experimental testing of the effects of encroachment on ecosystem services in order to address key knowledge gaps, and present an overview of the options available to coastal resource managers during a time of environmental change.

KEYWORDS

blue carbon, climate change, coastal protection, cultural values, habitat function, mangrove expansion, nutrient cycling, salt marsh, sea-level rise, threatened species

1 | INTRODUCTION

1.1 | Ecosystem services of coastal wetlands

Global climate change is altering the distribution, abundance, and phenology of species and ecosystems worldwide. Temperate and tropical plants and animals, for example, are moving poleward in response to global warming (e.g., Habary, Johansen, Nay, Steffensen, & Rummer, 2016; Walther et al., 2002), displacing native species, altering biodiversity patterns, and likely impacting ecosystem structure and function. Climate-related impacts to foundation species, that is, those that provide food and habitat for entire ecological

 © 2017 John Wiley & Sons Ltd

communities, are especially significant due to the critical influence these species have on ecosystem structure and function (Ellison et al., 2005). Recent expansion of woody mangroves into herbaceous salt marshes is a prime example of this phenomenon (Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). These changes will likely have large impacts on the structure, function, and service provisioning of coastal wetlands; however, there is a great deal of uncertainty regarding the direction and magnitude of these changes.

In terms of ecosystem services, coastal intertidal wetlands (mangrove and tidal marsh) are among the most valuable of all ecosystems globally, with their annual supply of services estimated at (2007) US$24.8 trillion (Costanza et al., 2014; De Groot et al., 2012). These services include providing nursery habitat for fisheries, filtering of nutrients and other pollutants, carbon sequestration and storage, elevation maintenance, and a variety of recreational and cultural uses. While there have been numerous efforts to identify the ecosystem services provided by mangroves (e.g., Friess, 2016; Lee et al., 2014) and salt marshes (e.g., Craft et al., 2009), little comparative analysis has been undertaken between these ecosystems, especially in regard to the global changes to mangrove and salt marsh dynamics.

1.2 | Global mangrove and salt marsh dynamics

Salt marshes and mangroves generally share a similar landscape position in the intertidal zone of low-energy coastlines (Figure 1).

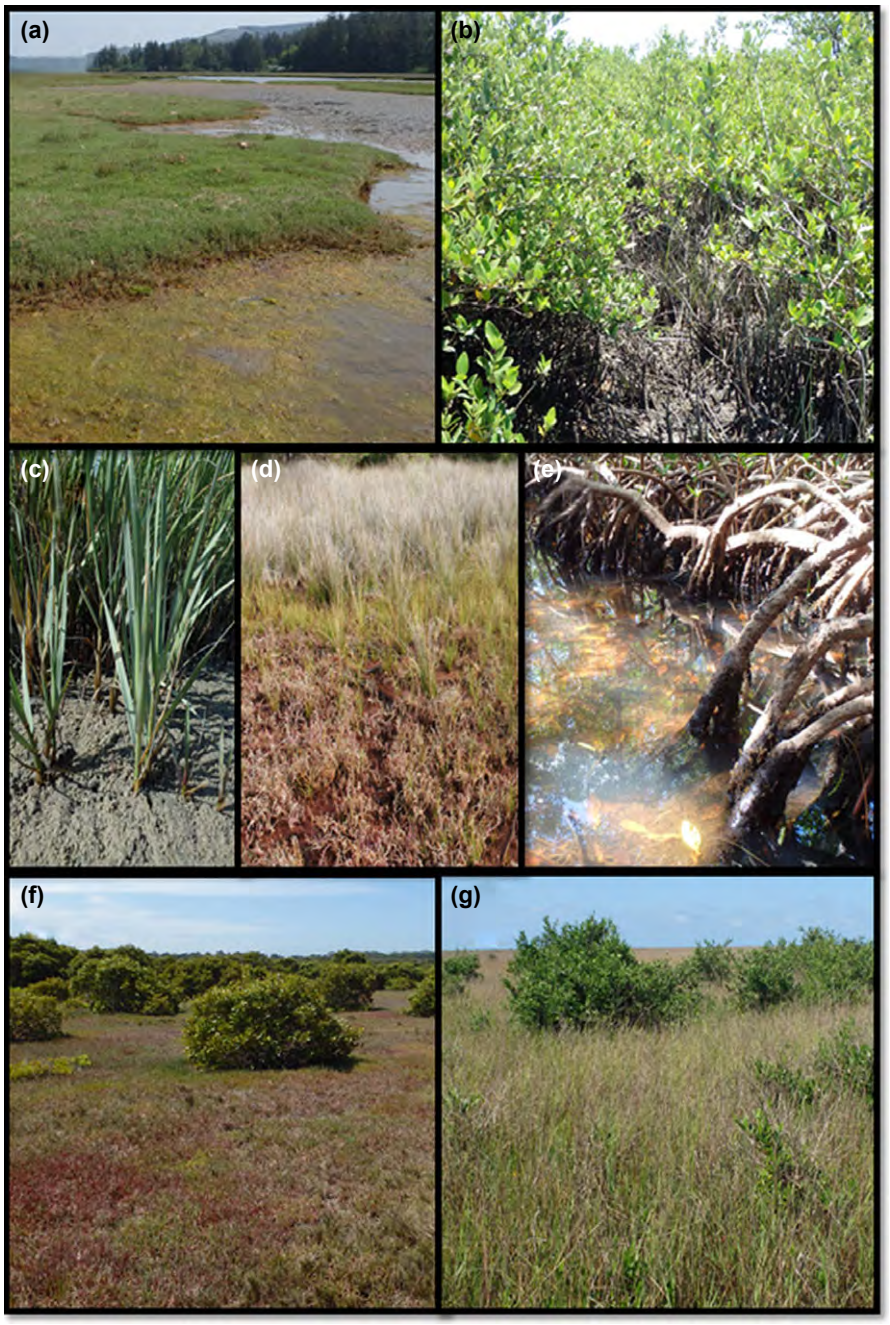


FIGURE 1 Open salt marsh habitat outside of mangrove range (Oregon, USA) (a); dense growth of *Avicennia germinans* with pneumatophores near its poleward limit (Florida, USA) (b); variation in aboveground vegetation structure of *Spartina alterniflora* (c), *Sarcocornia quinqueflora* (foreground) and *Juncus kraussii* (background) (d), and aerial roots of the mangrove *Rhizophora mangle* (e); examples of encroachment of *Avicennia marina* into *Sarcocornia-Sporobolus* salt marsh in SE Australia (f); and encroachment of *Avicennia germinans* into *Spartina alterniflora* salt marsh in southern USA (g) [Colour figure can be viewed at wileyonlinelibrary.com]

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Mangrove distribution is constrained primarily by latitude, temperature, and to a lesser extent, aridity with most species confined to tropical or subtropical regions (Duke, Ball, & Ellison, 1998; Friess et al., 2012; Saintilan, Rogers, & McKee, 2009). Salt marshes, by contrast, are found from tropical to arctic climates, although their areal extent and species diversity are often greater in higher latitudes, where mangroves are absent (Adam, 1993). Where salt marsh and mangrove distributions do overlap, they may form adjacent and/or ecotonal communities in the intertidal zone (Osland, Enwright, Day, & Doyle, 2013; Rogers, Battley, Piersma, Van Gils, & Rogers, 2006; Rogers, Wilton, & Saintilan, 2006) (Figure 1f, g).

The nature and location of the mangrove–salt marsh interface is currently undergoing rapid, global change. In recent years, an expansion of mangrove extent at or near to poleward limits has been reported on each of the continents that mangroves and salt marshes co-occur—Asia, Africa, Australia/New Zealand, North America, and South America (Cavanaugh et al., 2014; Giri & Long, 2016; Godoy & Lacerda, 2015; Saintilan et al., 2014). This poleward proliferation is concurrent with a "within-range" (i.e., lower-latitude) encroachment of mangroves into salt marshes, and expansion of mangroves into unvegetated tidal flats and other coastal fringe vegetation (e.g., *Melaleuca* wetlands in Australia). "Within-range" encroachment has been documented in eastern Australia (Saintilan & Williams, 1999), New Zealand (Swales, Bentley, & Lovelock, 2015), South Africa (Adams, Colloty, & Bate, 2004), South America (Godoy & Lacerda, 2015), and western North America (López-Medellín et al., 2011). Despite these local expansions in mangrove extent, it is important to note that on a global scale mangrove coverage is undergoing net global decline (Spalding, 2010), primarily due to deforestation and habitat conversion in the tropics (Valiela, Bowen, & York, 2001).

Near the poleward limits of mangroves in North America, declines in the occurrence of extreme winter temperature events have been identified as a primary driver of mangrove survival and expansion in recent decades (Cavanaugh et al., 2014; Stevens, Fox, & Montague, 2006). Biotic interactions between mangrove and marsh species, plus positive biological feedbacks (such as increased resilience to frost damage with mangrove age), may also influence the distribution and rate of mangrove expansion and salt marsh loss, beyond what would be predicted from temperature changes alone (Guo, Zhang, Lan, & Pennings, 2013; Howard et al., 2015; Osland et al., 2015; Peterson & Bell, 2015). The drivers of within-range mangrove expansion are less clear and may include rises in relative sea level (whereby mangroves migrate upslope into salt marshes) (Kelleway et al., 2016; Raabe, Roy, & McIvor, 2012; Rogers, Battley, et al., 2006, Rogers, Wilton, & Saintilan, 2006); changing rainfall patterns (Eslami-Andargoli, Dale, Sipe, & Chaseling, 2009); increasing atmospheric CO_2 concentration and soil nutrients (McKee, Rogers, & Saintilan, 2012; McKee & Rooth, 2008); sedimentation and geomorphic change associated with catchment land use (Swales et al., 2015); changes in tidal influence and freshwater inflow (Howard et al., 2016), among other factors (Saintilan & Williams, 1999).

Herbaceous salt marsh and woody mangroves differ in their above- and belowground biomass and architecture (Figures 1 and 2), their rates of nutrient and carbon cycling, and their ability to trap

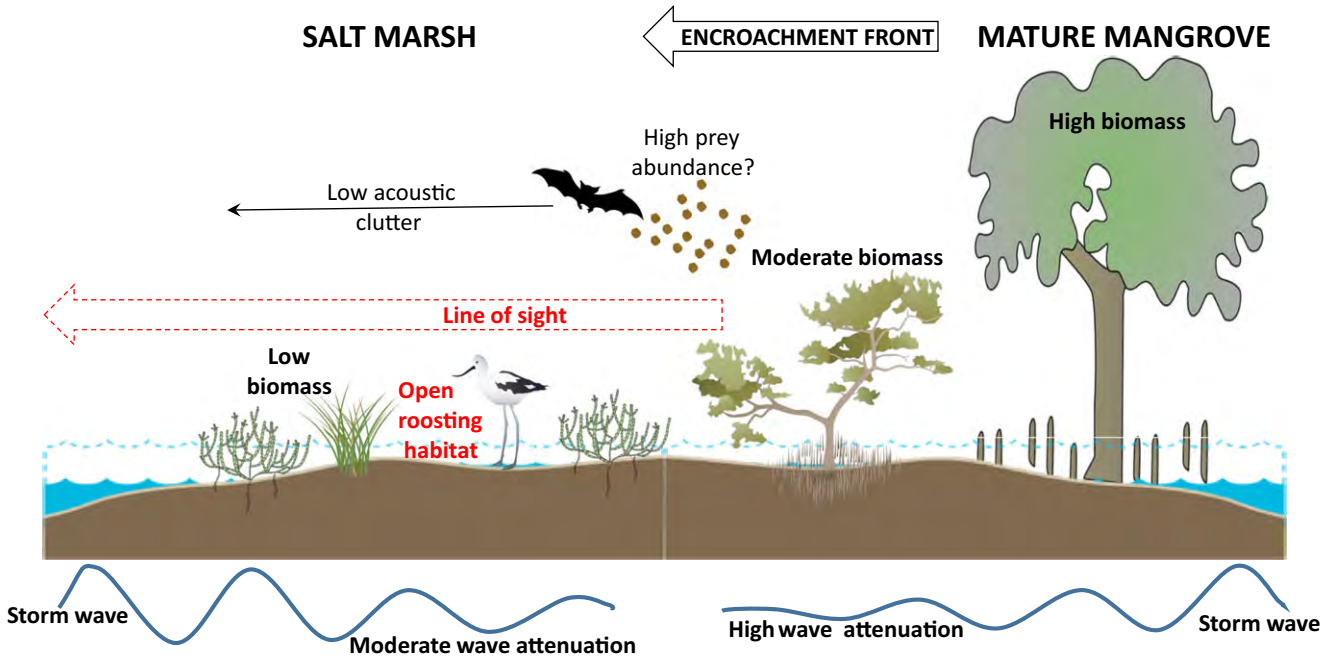


FIGURE 2 Conceptual diagram of the ways in which mangrove encroachment can alter ecosystem structure and ramifications for fauna habitat quality and wave attenuation capacity. The low vegetation structure of salt marsh provides birds that are roosting and/or feeding with a longer line of sight to any ambush predators. Insectivorous bats prefer to feed over open salt marsh or at the marsh–forest edge, avoiding the acoustic clutter of closed forest. The higher biomass and structural rigidity of mangrove may also increase storm wave attenuation [Colour figure can be viewed at wileyonlinelibrary.com]

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

allochthonous sediments and deposit organic matter, among other processes (Figure 3). Changes to these processes can alter coastal wetland function, with implications for human livelihoods and well-being, thereby presenting new challenges and opportunities for coastal managers. For the most part, however, there has been little quantification of the consequences of mangrove expansion for coastal wetland function and service provision. In this article, we review the current literature and propose likely changes in four broad categories of ecosystem services most relevant to mangrove and salt marshes. We conclude by proposing a research agenda to address key knowledge gaps and inform coastal management during a time of environmental change.

2 | WHAT ARE THE EXPECTED CHANGES IN ECOSYSTEM SERVICES?

2.1 | Coastal protection services

2.1.1 | Elevation maintenance during sea-level rise

Mangroves and salt marshes share a niche that lies approximately between mean sea level and highest astronomical tide (McKee et al., 2012). Consequently, these ecosystems—and the fate of the various ecosystem services they provide—are particularly susceptible to the influence of sea-level rise (SLR). If these ecosystems can maintain their optimal position within the tidal frame during SLR, they may also maintain their service provision and act as a buffer against flooding and storm damage for upslope settlements, infrastructure, and natural systems.

Maintenance of their position within a shifting tidal frame is achieved through the accumulation of mineral and/or organic materials. Mineral accumulation is generally dependent upon allochthonous material delivered on tidal waters, with the drag force of the sediment surface and the complex array of aerial roots (for mangroves) and stems and leaves (mangrove and salt marsh), critical in facilitating sedimentation of suspended particles (Mazda, Magi, Ikeda, Kurokawa, & Asano, 2006; Mazda et al., 1997; Morris, Sundareshwar, Nietch, Kjerfve, & Cahoon, 2002). Vegetation may also contribute in the form of the root materials that accumulate within sediments or organic litter at or below wetland surfaces. In addition to these processes contributing to elevation gain, belowground decomposition of organic matter, consolidation of mineral and organic matter, and dewatering of sediments may cause significant autocompaction or subsidence of sediments. The outcome of this subsidence is that the degree of vertical sediment accretion on the wetland surface may not produce an equivalent amount of elevation gain. Similarly, additions of organic material by roots to the sediment profile or saturation of the soil profile with water may increase surface elevations beyond that attributable to surface processes of vertical accretion alone (Cahoon et al., 2006).

Empirical studies have emphasized the efficiencies of the aerial components of mangroves in trapping sediments in tropical and

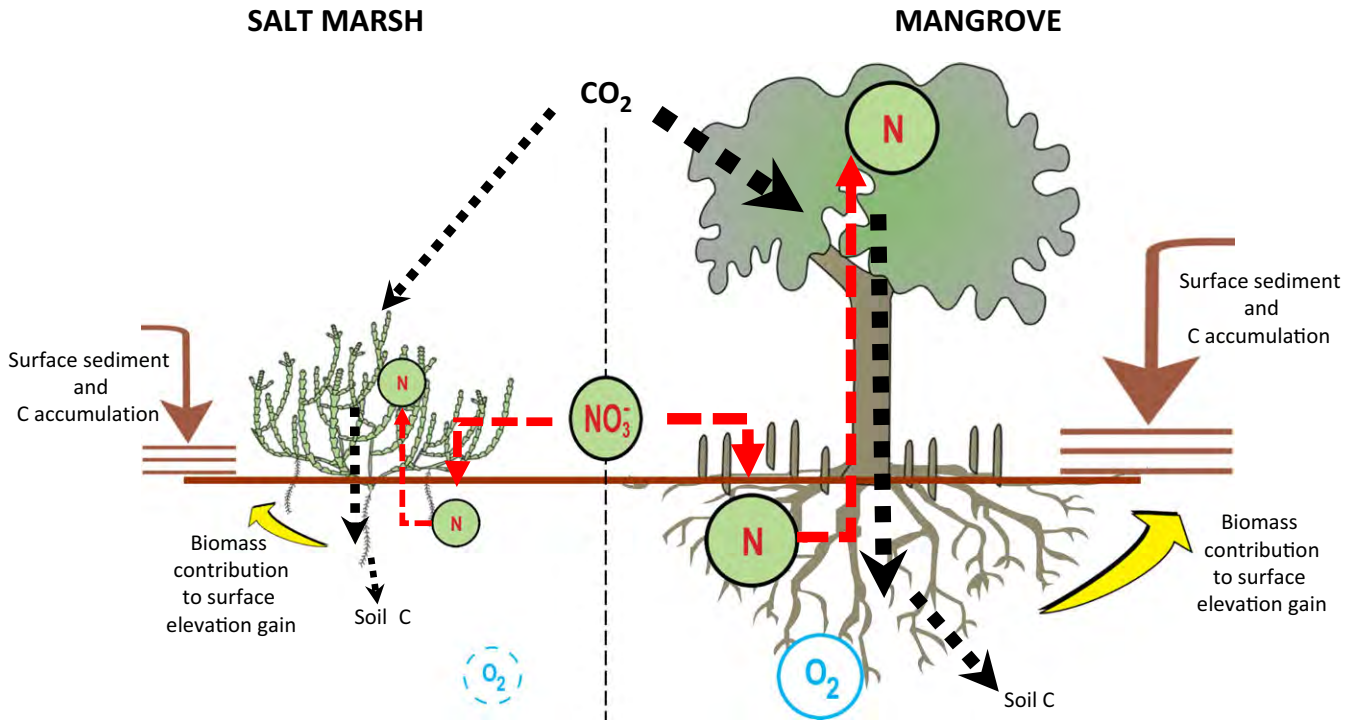


FIGURE 3 Conceptual diagram of the ways in which mangrove and salt marsh may differ in biogeochemical function. Mangrove encroachment will increase woody biomass, which may act as a larger and longer-term sink of carbon (CO_2) and nutrients including nitrogen (NO_3^-; N) relative to herbaceous biomass. Belowground biomass may be a long-term sink and contribute to surface elevation gain; however, deeper penetration of mangrove roots may alter belowground redox potential (O_2). Mangroves are particularly effective at accreting mineral sediments, detritus, and allochthonous carbon, although this capacity will vary among settings [Colour figure can be viewed at wileyonlinelibrary.com]

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

subtropical settings (Adame, Neil, Wright, & Lovelock, 2010; Furukawa, Wolanski, & Mueller, 1997; Spenceley, 1977). However, studies of sedimentation, accretion, and elevation dynamics within adjoining mangroves and salt marshes are few, and for the most part, spatially restricted. In the Fourchon region of Louisiana, Perry and Mendelssohn (2009) demonstrated similarity in short-term (sediment traps), medium-term (feldspar marker horizons), and decadal-scale (^{137}Cs dating) accretion rates from nearby *Avicennia* mangrove and *Spartina* salt marsh after ~15 years of mangrove expansion. In a similar scenario at Port Aransas, Texas (though with ~30 years of expansion), ^{210}Pb- and ^{137}Cs-derived accumulation rates indicated mineral trapping rates up to 4.1 times higher in mangrove relative to adjacent marsh (Bianchi et al., 2013; Comeaux, Allison, & Bianchi, 2012). In each of these locations, mangrove was recorded at elevations up to 5 cm higher than the adjacent marsh, although it is not known what impact this has had upon accretion dynamics. Interestingly, experimental removal of mangrove cover at an encroachment site in Port Aransas showed an opposite trend to the above, whereby accretion above feldspar marker horizons decreased with increasing mangrove cover (Guo et al., 2017). Following restoration of freshwater sheet flow across wetlands at Ten Thousand Islands National Wildlife Refuge, surface elevation change was found to decrease in mangrove and transition marshes, but remained stable in landward brackish marshes over the same period, despite relatively consistent rates of vertical accretion between each of the vegetation types (Howard et al., 2016).

A broader network of surface elevation tables and marker horizons (SET-MH) in southeastern (SE) Australia has enabled the detection of regional patterns of vertical accretion and surface elevation dynamics over a period exceeding 15 years (Lovelock et al., 2015; Rogers, Battley, et al., 2006, Rogers, Wilton, & Saintilan, 2006). Unlike the situation throughout the Gulf of Mexico, mangrove is almost always positioned lower in the tidal frame than salt marsh throughout Australia. In accordance with the tidal positions of mangrove and salt marsh, this network has consistently shown that vertical accretion is higher in mangroves than in adjoining salt marsh, and while compaction is also typically higher within the mangroves, it has not translated to lower-elevation gain (Figure 4). As a consequence, mangroves are generally regarded to have improved capacity to adjust to SLR. Analyses of sediment characteristics have demonstrated that differences relate not only to the improved capacity of mangroves to accrete mineral and organic sediments due to their lower tidal position relative to salt marsh in SE Australia (although this is generally not the case in North America) and complex vegetation structure (Rogers, Battley, et al., 2006, Rogers, Wilton, & Saintilan, 2006), but also to the contribution of mangrove roots to the soil profile (Rogers, Saintilan, & Cahoon, 2005; Figure 3). This pattern of greater sedimentation within lower intertidal mangroves relative to upper intertidal salt marshes has been replicated in analyses of sedimentation over longer timescales using sediment chronologies derived from analyses of ^{210}Pb radioactivity and other sedimentation proxies (Kelleway et al., 2016; Rogers & Saintilan, 2016).

2.1.2 | Protection from storms and flooding

Coastal wetlands have the capacity to provide protection against damage from storms, flooding, and erosion largely due to their ability to attenuate waves (Barbier et al., 2008; Gedan, Silliman, & Bertness,

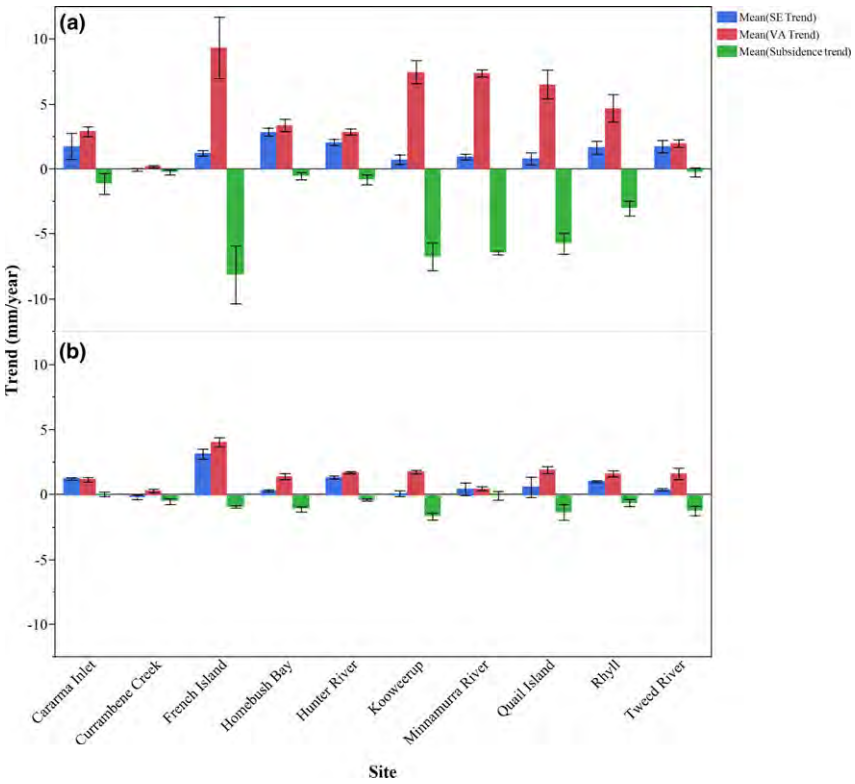


FIGURE 4 Mangrove (a) and salt marsh (b) vertical accretion, surface elevation, and compaction trends for adjacent mangrove and salt marsh in southeastern Australia. Unpublished data provided by Rogers K and Saintilan N (2016) from the SET-MH monitoring network in SE Australia. These data represent the linear trend in surface elevation gain over the SET study period of more than 15 years, the linear trend in vertical accretion over a shorter period corresponding to the detection period of marker horizons, and the difference between the two values. Error bars represent one standard error each side of the mean [Colour figure can be viewed at wileyonlinelibrary.com]

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2009; Koch et al., 2009). The provisioning of protection by coastal wetlands, however, is nonlinear and varies a great deal in space and time due to changes in the characteristics of vegetation, coastal geomorphology, and wave disturbance. Important vegetation characteristics include the width, density, and structure of the coastal wetland stands, with stems, leaves, and aerial roots all acting to dissipate wave energy (Coops, Verheij, & Boeters, 1996; Massel, Furukawa, & Brinkman, 1999). Total wave attenuation generally increases nonlinearly with the width and density of vegetation (Koch et al., 2009; Massel et al., 1999). For example, a modeling study by McIvor, Möller, Spencer, and Spalding (2012) found that a 100-m-wide stand of mangroves reduced short period wave heights by between 13% and 66%, while a study found that a ~1-km-wide English salt marsh reduced the total energy of short period waves by an average of 82% (Möller, Spencer, French, Leggett, & Dixon, 1999). Another study that modeled wave dissipation by mangroves in Vietnam found higher wave attenuation in species with higher densities of aboveground stilt roots (Cuc, Suzuki, de Ruyter van Steveninck, & Hai, 2015). There is also evidence of a positive relationship between standing biomass and wave attenuation among salt marsh species (Ysebaert et al., 2011).

There is uncertainty regarding the influence of coastal wetlands on extreme events such as large storm surges and tsunamis. There is evidence that mangroves can slow storm surges and reduce storm surge height (Krauss et al., 2009 and references therein; Zhang et al., 2012), but mangrove stands must be wide in order to have a significant effect on extreme tidal events (Alongi 2008, Spalding et al., 2014). Furthermore, there is uncertainty as to the magnitude of surge height reduction. One empirical study in the Gulf coast of Florida measured water-level reductions of up to 9.4 cm/km (Krauss et al., 2009), while hydrodynamic simulations in the same region estimated decay rates of up to 50 cm/km (Zhang et al., 2012). Coastal vegetation such as mangroves can reduce debris movement during extreme tidal events (Wolanski 2006, Alongi 2008); however, vegetation (e.g., mangroves) ripped loose by water motion can itself become a lethal hazard (Kathiresan & Rajendran, 2005). A number of studies on the effects of the 2004 Indian Ocean Tsunami found evidence that mangrove stands protected some areas from damage (Danielsen et al., 2005; Kar & Kar, 2005; Kathiresan & Rajendran, 2005). However, these results were later questioned by studies that found that other factors such as bathymetry, topography, and distance from shore explained the majority of variability in tsunami damage (Bhalla, 2007; Kerr & Baird, 2007; Kerr, Baird, & Campbell, 2005). There have been similar debates over the protection provided by coastal salt marshes during Hurricane Katrina in 2005, which destroyed vast areas of marsh in the northern Gulf of Mexico (Day et al., 2007; Feagin et al., 2010; Stokstad, 2005).

The degree to which mangrove encroachment will impact the provisioning of coastal protection is presently unclear, with no comparative studies completed to our knowledge in an area that has experienced encroachment of mangroves into salt marsh (or vice versa). While a meta-analysis of five mangrove sites and 10 salt marsh sites across multiple continents found no significant difference in wave attenuation between mangrove and salt marsh (Gedan et al., 2009), there are theoretical reasons to suspect change in protection capacity under mangrove encroachment. On the basis of plant structural differences (Figure 1; Figure 2) and results from disparate studies of salt marshes, mangroves, and related ecosystems, we suggest the following changes are possible outcomes of mangrove encroachment:

- Using aboveground biomass as a proxy for vegetation density and structural complexity (Koch et al., 2009), we expect mangroves to have higher potential for wave attenuation, relative to salt marsh;
- On the basis of stem stiffness (Bouma et al., 2005) plus the presence of pneumatophores (Mazda et al., 2006) increasing wave attenuation, we suggest that woody mangroves should be able to attenuate more energy than herbaceous salt marsh in the same hydrodynamic setting;
- We expect increasing protection from storm-driven winds under mangrove encroachment, due to the structure of forested wetlands acting as a wind break (Shaffer et al., 2009); and
- Short-statured vegetation—herbaceous salt marsh and/or low-statured mangroves—may become submerged by storm surge prior to the arrival of major storm waves, therefore reducing the effect of vegetation on wave suppression (Feller et al., 2015). Taller mangroves are likely to have greater biomass exposed above storm surge inundation depths.

However, much more work is needed to understand the role of vegetation structure in attenuating different wave types (i.e., wind waves, tsunamis, storm surge). In particular, there is a need for more empirical data for model parameterization and for the development of three-dimensional models of wave and surge attenuation (e.g., Lapetina & Sheng, 2014; Lara et al., 2016). It is also important to consider the role of vegetation structure upon coastal protection in the context of mangrove structure in encroachment areas, where mangroves expanding near their range limits are generally shrub-like, short in stature, sparsely distributed, and have relatively moderate levels of aboveground and belowground biomass (Figure 2). Consequently, any increases in coastal protection from mangrove expansion may be limited at first, and extrapolation from studies of wave attenuation or erosion resistance in fully developed forests may be misleading. There is a need for studies to specifically examine the effect of mangrove expansion on coastal protection, while wave attenuation models should be parameterized with accurate representations of the type of mangroves that are expanding into salt marshes.

2.2 | Provisional and habitat services

The ways in which humans make direct use of salt marshes vs. mangroves are related to (i) the types of plants and animals inhabiting each ecosystem and (ii) the level of economic development of the locations in which they each occur. Due to their low topographic

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

relief, lack of woody vegetation, and proximity to water, salt marshes have been subject to centuries of human use and modification (Adam, 2002; Gedan et al., 2009). Provisional services have included grazing and haymaking (Vestergaard, 1998), turf cutting (Gray, 1972), small-scale salt production, and harvesting of some succulent species for direct human consumption (Beeftink, Nieuwenhuize, Stoeppler, & Mohl, 1982). For the most part, however, these traditional practices underwent declines throughout the 20th century (Adam, 2002), concurrent with the modernization of agriculture in most temperate and subtropical regions.

The extractive uses of mangroves are more varied and continue to today, including supporting aquaculture (wood for canoes, fish traps, and for processing of prawn and fish catches), domestic (fencing, housing, fuel, charcoal, dyes), food (mangrove crab, fish, shellfish, reptiles, and honey), and medicinal uses (Dahdouh-Guebas, Mathenge, Kairo, & Koedam, 2000; Nurkin, 1994; Rasolofo, 1997; Walters et al., 2008). The use of wood, either from subsistence or from commercial forestry, is probably the most significant provisional service provided by tropical mangroves (Kovacs, 1999; Walters et al., 2008) that is not derived from salt marsh vegetation. While mangrove forestry may be highly valuable in those regions where mangroves are already dominant (Gilbert & Janssen, 1998), it is unclear what implications, if any, range expansion will have for wood use, seeing as mangroves at encroachment fronts may be shrubs or trees with stunted growth (Figure 2). Nipa palm (*Nypa fruticans*) harvested from mangrove forests has traditionally been harvested for roof thatching and many other uses, but may also support commercial enterprises such as ethanol production (Hamilton & Murphy, 1988; Tamunaidu, Matsui, Okimori, & Saka, 2013). In many developing countries, these uses often represent important contributions to livelihoods and regional economic activity (Beymer-Farris & Bassett, 2012; Jusoff, 2009; Mojiol, Lintangah, Ismenyah, Alamjuri, & Jaafar, 2016; Walters et al., 2008). Recent research has become increasingly analytical and multidisciplinary, investigating humans as agents of change and the impacts of mangrove forest shifts on livelihoods (Walters et al., 2008; Warner et al., 2016). Future human needs and pressures need to be mapped against predicted increases and decreases in mangroves forests to inform sustainable use. Some communities may indeed benefit socioeconomically from mangrove expansion, and some may experience cumulative loss effects.

2.2.1 | Fisheries habitat and production

Comparisons of the relative importance of mangrove and salt marsh to fisheries productivity in regions where the ecosystems co-occur have proceeded at two spatial scales. At the broader scale, fisheries landing data have been used to explore the influence of the aerial extent of mangrove and salt marsh on fish production across regions. Aburto-Oropeza et al. (2008) analyzed fish landing data from the Gulf of California in relation to climate, and the area of mangrove, seagrass, and open water lagoon habitat (salt marsh was not included). They found that mangrove alone predicted fish landings and that 31.7% of the small-scale fisheries landings comprised species dependent upon mangrove. Comparing fish landings across 55 estuaries in New South Wales (NSW), Saintilan (2004) found estuarine entrance conditions (whether fully or partially open) to be the dominant influence on estuarine fish landings, followed by the relative extent of estuarine habitat, with strong differentiation between subtidal seagrass and intertidal mangrove–salt marsh habitat. However, subtle differences were found between mangrove and salt marsh as predictors of fish landings. These included the importance of mangrove for long-finned eel *Anguilla reinhardtii* and the sand mullet *Myxus elongates*, both important predators in mangrove creeks. Landings of the commercially important mud crab *Scylla serrata* were more accurately predicted by a combination of mangrove and salt marsh rather than mangrove area alone. Meynecke, Lee, and Duke (2008) emphasized the importance of heterogeneity and connectivity between vegetated habitats in their study of predictors of commercial fish landings in tropical North Queensland.

At the scale of the intertidal flat, fish assemblages in salt marsh are strongly influenced by hydroperiod. Microtidal marshes in the USA support resident populations of killifish, while the mesotidal marshes of eastern Australia support itinerant populations dominated by ambassids, moving between salt marsh and low-tide seagrass and mudflat habitat (Meynecke, Lee, Duke, & Warnken, 2007; Saintilan, Hossain, & Mazumder, 2007). Where adjacent mangrove and salt marsh have been sampled in eastern Australia, higher fish numbers per unit area were found in mangrove (Mazumder, Saintilan, & Williams, 2005; Moussalli & Connolly, 1998), although numbers were comparable on the basis of water volume (Mazumder et al., 2005). Intersite variability in numbers and assemblage is considerable (Mazumder, Saintilan, & Williams, 2006) and confounds the characterization of a mangrove as opposed to salt marsh fish community. Only one study, Moussalli and Connolly (1998), compares mangrove and salt marsh at similar flooding depth, finding that mangrove species richness is higher. Comparative studies in the Gulf of Mexico (Lunt, Mcglaun, & Robinson, 2013; Smee, Sanchez, Diskin, & Trettin, 2017) suggest lower abundance of infauna in mangrove compared to *Spartina* marsh, contrasting with findings in China (Fu, Cai, Cao, & Chen, 2017) where *Spartina* is invading mangrove. Smee et al. (2017) sampled *Spartina* salt marshes with and without mangrove encroachment at lower elevations, controlling for salinity and inundation depth. They found higher abundance of blue crabs, grass, and brown shrimp and infaunal communities at sites dominated by *Spartina* compared to mangrove encroachment areas, although note that a previous study in Louisiana (Caudill, 2005) found more abundant shrimp in mangrove areas.

Finally, the infrequently inundated, upper intertidal salt marsh represents a distinct biogeomorphic unit, where the highest concentrations of invertebrate larvae may be found within estuaries. Burrowing crabs synchronize their spawning with the spring tide cycle, across the few monthly tides that reach the salt marsh (Mazumder, Saintilan, & Williams, 2009). This represents a uniquely efficient feeding opportunity for zooplanktivorous fishes, and surveys have noted high numbers of ambassids exiting the salt marsh with distended stomach on the ebb tide. While larvae are also produced by

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

crabs in the mangrove, the high larval concentrations are not reached (Mazumder et al., 2009), most probably due to the greater volume of water, although differences in crab assemblages may also contribute (Mazumder & Saintilan, 2010).

On the basis of these observations, we draw two conclusions concerning the implications of encroachment for fisheries. First, if barriers to landward migration of salt marsh remove upper intertidal habitat, a highly efficient feeding opportunity for zooplanktivores (in SE Australia, at least) is also likely to be lost. Second, if the intertidal profile is maintained, and the change is a floristic shift from salt marsh to mangrove, we currently do not have evidence to suggest a deleterious effect on fisheries, as both habitats support the bases of ecological function, contributing to autotrophic input and complex structural habitat.

2.2.2 | Habitat for threatened species

Mangrove encroachment is one of many factors contributing to global declines in the extent of salt marsh (Adam, 2002), adding to large areas lost to coastal reclamation. In recognition of the significance of these threats, Subtropical and Temperate Coastal Saltmarsh was listed in 2013 as an "Endangered Ecological Community" in Australia under the *Environmental Protection and Biodiversity Conservation (EPBC) Act*, following the listing as "Vulnerable" under the NSW *Threatened Species Conservation Act* in 2004. Globally, a number of important salt marsh sites are gazetted under international agreements such as the *Convention on Wetlands of International Importance (Ramsar Convention)*. The plants that comprise salt marsh flora may also be threatened species themselves, as is the case for two species of the genus *Wilsonia* in NSW. Where mangrove encroachment causes a decline in the extent or range of salt marsh, then this has obvious implications at both the ecological community level and for the threatened plant species therein. The implications for threatened fauna that utilize mangroves and salt marshes may be less clear and will likely depend upon the way in which they utilize habitat (e.g., for feeding, roosting, and/or breeding) and the specificity of their habitat needs. When migratory or itinerant species are impacted by encroachment, there may also be flow-on consequences to population dynamics and ecosystem function elsewhere, sometimes thousands of kilometers away and well outside of mangrove range.

One of the most globally significant faunal groups at risk to the effects of mangrove encroachment is the Arctic-breeding migratory shorebirds (Charadriiformes: suborder Charadrii), which have been subject to steep population declines in recent decades (Baker et al., 2004), largely due to pressures placed on nonbreeding habitat (Burton, Rehfisch, & Clark, 2002). Several of these species, including three listed as threatened by the International Union for Conservation of Nature (IUCN), utilize salt marsh habitats in South Africa (Velasquez & Hockey, 1992), North America (Erwin, Hatfield, Howe, & Klugman, 1994), Europe (Rosa, Palmeirim, & Moreira, 2003), and Australia (Spencer, Monamy, & Breitfuss, 2009). While some species, notably Whimbrels (*Numenius phaeopus*) and Gray-tailed Tattlers (*Tringa brevipes*), roost in mangrove, salt marsh is a preferred roosting habitat for species of Charadrii, particularly at night, for several reasons. First, the open salt marsh plain removes the structural complexity (Figure 2) preferred by ambush predators, such as predatory birds. The success of such attacks is lowered with distance from cover (Dekker & Ydenberg, 2004). While not specifying bird taxa, Guo et al. (2017) recorded nonlinear decreases in bird habitation of an encroachment site with increasing mangrove cover. Second, the presence of wide, shallow pools in the upper intertidal salt marsh provides additional protection from ground-based predators, a thermal benefit by the dissipation of endogenous heat (Rogers, Battley, et al., 2006, Rogers, Wilton, & Saintilan, 2006), and a secondary feeding habitat (Spencer et al., 2009). The encroachment of mangroves on open salt marsh plains therefore has the detrimental impact of reducing the utility of roosting habitat for migratory shorebirds. Birds in the Hunter estuary (NSW, Australia) have been observed to abandon historically important roosts when the line of sight to the estuary was interrupted by mangrove, and returned following their clearance (Spencer et al., 2009). Similar reasoning has supported the removal of mangrove for the protection of shorebird habitat in Hawaii (Chimner, Fry, Kaneshiro, & Cormier, 2006; Rauzon & Drigot, 2002). The clearance of mangrove in the upper intertidal zone of the Danshui River estuary in Taiwan resulted in a marked increase in their utilization by several species of shorebird, which congregated at the cleared sites, despite little change in sediment or infaunal characteristics (Huang, Shih, Ho, Chen, & Hsieh, 2012).

For some species, salt marshes are also important feeding habitat. The orange parrot *Neophema chrysogaster* ("Critically Endangered" under the EPBC Act) feeds largely upon seeds of chenopod shrubs of salt marsh (Spencer 2010) and may roost exclusively within the same shrubs (Loyn, Lane, Chandler, & Carr, 1986). During winter, when food resources may be most scarce, this species migrates to a region where mangrove encroachment is an important driver of salt marsh loss (Saintilan & Williams, 1999). In southern USA, salt marsh is the primary wintering roosting and feeding habitat of the whooping crane *Grus americana* ("Endangered" under the IUCN Red List), with natural populations restricted to the central Texas coast where colonization of *Avicennia germinans* has expanded into the whooping crane range (Chavez-Ramirez & Wehtje, 2012; Stehn & Prieto, 2010). Mangrove forests are unlikely to be utilized by whooping cranes (Chavez-Raminez 1996), and landward retreat of salt marsh is constrained along the Texas coastline by seawalls, industrial developments, and transport infrastructure (Chavez-Ramirez & Wehtje, 2012). Expansion of mangroves in the Ten Thousand Island National Wildlife Refuge in Florida may have implications for the federally listed endangered wood stork (*Mycteria americana*), compounding habitat losses to expanding *Melaleuca* and cattail vegetation in nearby freshwater habitats (Bancroft, Hoffman, Sawicki, & Ogden, 1992; Krauss, From, Doyle, Doyle, & Barry, 2011). The reliance of these species upon at-risk salt marsh for feeding and roosting habitat makes them particularly susceptible to the impacts of mangrove encroachment.

Among mammals, insectivorous bats may be particularly vulnerable to mangrove encroachment. Availability of the salt marsh

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

mosquito *Aedes vigilax* has been linked to greater abundance and feeding activity of bats of the genus *Vespadelus* over salt marsh plains in eastern Australia (Gonsalves, Law, Webb, & Monamy, 2013). This study found that feeding activity was disproportionately higher in salt marsh relative to adjacent forests (including mangrove), despite similar patterns of prey abundance, which they attribute to the absence of vegetative "clutter" and associated acoustic complexity. Although bats have been observed foraging in mangrove (McKenzie & Rolfe, 1986), feeding efficiency is maximized within the salt marsh at the mangrove or terrestrial forest edge (Figure 2), where prey may be concentrated (Gonsalves, Law, Webb, & Monamy, 2012). For this reason, Gonsalves et al. (2012) caution against the entire removal of mangrove, suggesting that the mangrove–salt marsh edge may be significant for the foraging of several species, including the threatened *Mormopterus morfolkensis*.

2.3 | Cultural services and values

Despite increasing awareness of the importance of mangroves and salt marshes to coastal livelihoods, there remains a major lack of assessment of the aesthetic, inspirational, and spiritual experiences of these ecosystems (Costanza et al., 2014; De Groot et al., 2012). Surveys from coastal regions of Mexico showed about 40% of local community value the recreational, aesthetic, and cultural opportunities (e.g., taking guests sightseeing, picnics, celebrating mass) services offered by mangroves (Kaplowitz, 2001). Furthermore, Mastaller (1997) described some spiritual values of mangroves roots that were carved into totemic objects in Indonesia, and this practice continues today (Walters et al., 2008). Use of mangrove woods for totemic carvings has also been reported in northern Australia, some of which now provide income through sales to tourists (Bird, 1986).

In areas such as the Gulf coast of Louisiana, outdoor recreation associated with tidal wetlands (including fishing, shrimping, crabbing, and waterfowl hunting) may represent a significant sector of the regional economy. The gross economic value of these activities is estimated to be more than $270 million annually (Bergstrom, Stoll, Titre, & Wright, 1990; value corrected for inflation). As already discussed, a salt marsh-to-mangrove transition may have varied positive or negative implications for fauna, including species that underpin outdoor recreation, commercial, and subsistence activities. While it is difficult to predict impacts on overall fish stocks, we have suggested that salt marsh loss may have implications for crustacean larvae production and consequently zooplanktivorous species. This in turn could alter stocks available for recreational shrimping, crabbing, and fishing of some fish species, although no such quantification of this impact has been undertaken to date. The habitat implications of mangrove encroachment on waterfowl appear more straightforward. That is, replacement of salt marsh by mangrove shrubs and trees represents a decline of preferred roosting habitat for many waterfowl, including migratory species (Lawler, 1996; Rogers, Battley, et al., 2006, Rogers, Wilton, & Saintilan, 2006; Spencer et al., 2009). Where this includes bird species important to recreation (e.g., bird-watching and/or hunting), declines in the quality of recreation activity may occur with the possibility of hunting restrictions in some cases. Where rare and/or migratory species are lost from an area, there may be important consequences for regional tourism and related industries, particularly in locations where bird diversity and the sighting of rare species are a recreation attraction.

Mangrove encroachment has the potential to impact upon Indigenous cultural, heritage, and education values. This may occur through change to or loss of culturally significant places, plant species, and fauna reliant upon the encroached habitat. For example, in Arnhem Land, northern Australia, encroachment of mangroves into (previously) freshwater *Melaleuca* wetlands has led to the death of sacred tree groves as well as the loss of gathering opportunities for Aboriginal communities (E. Ens *personal observation*). In O'ahu (Hawaiian Islands), Indigenous People are restoring ancient coastal fish traps for cultural, education, and tourism purposes. Mangrove encroachment and removal is one of their primary management challenges (Paepae o He'eia, 2016; http://paepaeoheeia.org/thefishpond/).

The expansion of mangroves may also impact upon aesthetic values, access to waterways, and consequently, the real estate value of coastal properties. On the north island of New Zealand, there have been multiple instances of coastal property owners removing mangroves (either with permission or illegally) in areas where they are spreading, in order to protect access to the coast and maintain open waterways (Morrisey et al., 2010; Stokes & Harris, 2015).

2.4 | Biogeochemistry services

The rate and magnitude of organic matter decomposition and nutrient cycling is thought to vary between mangrove and salt marsh (Currin, Newell, & Paerl, 1995; Nagelkerken et al., 2008) due to differences in structural complexity, litter fall, and other ecophysiological traits (Bianchi et al., 2013; Comeaux et al., 2012; Henry & Twilley, 2013; Krauss, McKee, & Hester, 2014; Lewis, Brown, & Jimenez, 2014; Osland et al., 2012; Patterson & Mendelssohn, 1991; Perry & Mendelssohn, 2009). For example, many herbaceous salt marsh species recycle almost all of their aboveground biomass annually as litter fall (Currin et al., 1995), while mangroves allocate more biomass to long-term storage structures (e.g., wood) (Figure 3). As a result, encroachment of mangroves into salt marsh is likely to have significant impacts on ecosystem processes such as nutrient and carbon storage, soil diagenesis, food web dynamics, and detrital subsidies to nearby ecosystems.

2.4.1 | Nutrient cycling

Multiple studies from subtropical and temperate regions have demonstrated both nitrogen (N) and phosphorus (P) limitation among mangrove species and locations (Feller, 1995; Feller, Whigham, O'Neill, & McKee, 1999; Feller, Whigham, McKee, & Lovelock, 2003; Feller, Chamberlain, Piou, Chapman, & Lovelock, 2013; Lovelock & Feller, 2003; Lovelock et al., 2007; Lovelock, Sorrell, Hancock, Hua, & Swales, 2010; Martin et al., 2010). This difference in nutrient

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

limitation between both young and old forests (Lovelock et al., 2010), combined with findings that N and P fertilization can increase growth, photosynthesis, and N resorption, suggests that mangroves may provide sustained sinks for nutrients. Thus, a transition from salt marsh to mangrove may also lead to a fundamental shift in the ecological stoichiometry of coastal ecosystems. Empirical work and allometric theory have demonstrated that whole plant N and P contents generally increase allometrically with plant size, with a common exponent of ¾ (Kerkhoff & Enquist, 2006). Furthermore, the total nutrient content of plant communities scales with total production and biomass (Kerkhoff & Enquist, 2006). As a result, increases in structural complexity and total biomass resulting from the expansion of woody mangroves into salt marsh would be expected to increase the uptake of excess nutrients and the size of the total community nutrient sink. For example, Kerkhoff, Fagan, Elser, and Enquist (2006) found that herbaceous plants consistently have higher N and P contents and lower N:P ratios than trees and shrubs. In coastal wetlands where plant tissue quality is directly linked to carbon and nutrient dynamics, fundamental differences in C:N:P stoichiometry of the foundation species may exert strong feedback on soil fertility, habitat quality, and community structure (Hobbie, 2015).

For mangroves, fertilization experiments have shown that leaf traits and C:N:P stoichiometry as well as growth and reproduction are influenced by soil nutrient availability (Feller, 1995; Feller et al., 1999; Feller et al., 2010, 2013). A number of studies have demonstrated large amounts of variability in nutrient resorption efficiency among vegetation types (Feller et al., 1999; Güsewell, Bolllens, Ryser, & Klötzli, 2003; Lovelock et al., 2007; Rejmánková, 2005), which could lead to changes in stoichiometry of leaf litter, which has a direct feedback on ecosystem stoichiometry and soil fertility when herbaceous salt marshes are converted to woody mangroves.

Eutrophication and atmospheric N deposition may also act to promote further mangrove expansion. Although field studies have found that growth rates of both herbaceous salt marsh and woody mangroves increase with nutrient fertilization, over time mangroves have been shown to displace salt marsh due to light competition (Ribeiro, Tiberio, & de Oliveira, 2015). Mangrove seedlings appear to show large plasticity in growth and nutrient acquisition, which may enable them to respond quickly to changes in nutrient concentrations and enhance their competitive advantage over salt marsh (Reef, Feller, & Lovelock, 2010; Simpson, Feller, & Chapman, 2013). However, another study on mangrove–salt marsh interactions found that competition from *Spartina alterniflora* suppressed the growth of *Avicennia germinans* seedlings under N-enriched conditions in mesocosm and field experiments (McKee & Rooth, 2008). Thus, other environmental changes (e.g., climate, disturbance) may be needed to allow mangroves to establish to a point where they can take advantage of increased nutrients and outcompete salt marsh.

Experimental studies suggest that there may be fundamental differences in the impact of nutrient enrichment on mangroves vs. salt marshes. In mangrove ecosystems, nutrient enrichment has been shown to increase both aboveground and belowground biomass, leading to increases in their capacity to store C and in their abilities to trap sediment and to build biogenic soil (McKee et al., 2012). An increased supply of nutrients results in higher productivity, which has been linked to a greater delivery and diversity of the ecosystem goods and services provided by mangroves (Ewel, Twilley, & Ong, 1998). In contrast, nutrient enrichment has been shown to be a major driver of ecosystem loss in salt marsh ecosystems (Deegan et al., 2012), where belowground biomass, C accumulation (Turner et al., 2009), and soil strength (Turner, 2011) are reduced with nutrient enrichment.

Based on these observations, we predict that replacement of salt marsh species by mangroves will alter the nutrient uptake and storage by coastal wetlands. Also, increases in nutrient deposition in coastal wetlands (e.g., coastal eutrophication) near these transition zones may increase mangrove growth, thereby enhancing their ability to outcompete salt marsh and promoting further mangrove expansion. As a result, this expansion may serve as a negative feedback that controls nutrient concentrations in some coastal wetlands. However, while nutrient uptake and storage are generally expected to increase with mangrove expansion, these processes may also become more variable. Nutrient enrichment has been shown to make mangroves more sensitive to environmental stressors and disturbances such as hurricanes (Feller et al., 2015) and droughts (Lovelock, Ball, Martin, & Feller, 2009). Climate change is expected to lead to increases in the intensity of tropical cyclones and droughts in certain parts of the subtropics (Meehl et al., 2007). Increases in mangrove mortality from these events may lead to the release of long-term reservoirs of carbon and nutrients (Donato et al., 2011), especially if vegetation cover (either new mangrove or salt marsh) is not re-established.

2.4.2 | Carbon sequestration

Salt marshes and mangroves (along with seagrasses) have been termed "blue carbon" habitats due to their exceptional capacity to accumulate and store carbon (C) for centuries or millennia (McLeod et al., 2011). There are three quantifiable terms that are used to define the C sequestration potential of coastal wetlands: (i) C stocks, or the amount of C stored within biomass and/or soil C pools; (ii) C accumulation rates, which measure the rate at which C is added to the ecosystem; and (iii) C flux, which refers to the quantity of emissions leaving the ecosystem.

In general, there is greater potential for C storage in the aboveground biomass of woody mangrove vegetation, compared to herbaceous salt marsh (McKee & Rooth, 2008; Murray, Pendleton, Jenkins, & Sifleet, 2011; Figure 3). However, aboveground C has a short residence time relative to C buried in the soil, which can be preserved over centuries or millennia (Souza Filho et al., 2004). Past global reviews have reported higher mean and maximum C stocks within the surface meter of mangrove soils (mean = 255 Mg C ha^{-1}; maximum = 683 Mg C ha^{-1}) than those of salt marsh soils (mean = 162 Mg C ha^{-1}; maximum = 259 Mg C ha^{-1}) (Duarte, Losada, Hendriks, Mazarrasa, & Marbà, 2013). For C accumulation rates, however, Chmura, Anisfeld, Cahoon, and Lynch (2003)

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

reported massive variability in both mangrove and salt marsh soils and no significant difference in the mean rates of each ecosystem. These global findings have prompted a number of local studies within coastlines experiencing encroachment, which have aimed to investigate the implications of encroachment on C sequestration at smaller spatial scales.

The *Spartina alterniflora* salt marshes of the southern United States (e.g., Figure 1c, g) have been the focal point of most of the encroachment C studies undertaken to date. Osland et al. (2012) observed increases in surface soil C stocks as mangroves replaced *S. alterniflora* in created tidal wetlands of the Tampa Bay region, Florida. On the Atlantic coast of Florida, Doughty et al. (2016) documented large increases in C storage over just seven years of encroachment, driven by rapid increases in aboveground biomass. Attempts to demonstrate changes in belowground C stocks in the southern United States, however, have been more equivocal (Comeaux et al., 2012; Doughty et al., 2016; Henry & Twilley, 2013; Perry & Mendelssohn, 2009; Yando et al., 2016), possibly due to the short time frame (i.e., <30 years) of encroachment in this region. Importantly, faster accumulation rates of bulk sediment, C, and lignin under mangrove encroachment relative to salt marsh have been demonstrated here (Bianchi et al., 2013).

Research undertaken in SE Australia over a 70-year chronosequence shows that C storage increases can in fact take place with encroachment over this longer time frame (Kelleway et al., 2016). Significant increases in overall belowground C (i.e., inclusive of root and non-root C) were observed following encroachment in two disparate geomorphic settings, but were not apparent until after > 30 years. Increases in belowground C also outweighed those of aboveground C pools, with annual increases in belowground C storage of up to 2.30 Mg C ha^{-1} $year^{-1}$, compared to increases in aboveground C storage equating to 0.58 Mg C ha^{-1} $year^{-1}$ (Kelleway et al., 2016). Results across a mangrove–marsh ecotone in the Nahoon Estuary in South Africa are consistent with this, with soil organic matter significantly higher in mangrove and transition areas, relative to salt marsh (Geldenhuys, Cotiyane, & Rajkaran, 2016). These findings, along with mangrove afforestation studies elsewhere (e.g., Lunstrum & Chen, 2014), show that given enough time for mangrove establishment to functional equivalence (achieved through the absence of dieback events caused by extreme cold temperatures) significant increases in belowground C stocks can become apparent under mangrove encroachment. Further support of this can be seen in the Osland et al.'s (2012) study of created wetlands outside the "encroachment front", where soil carbon reached functional equivalence within 20 years of wetland creation, once sites had converted from salt marsh to mangrove forest.

Quantification of stocks and accumulation rates is needed over a broader array of settings, as research to date has indicated spatial variability in encroachment C dynamics, potentially due to difference in plant assemblage, rainfall, nutrient, salinity, and/or geomorphic settings (Kelleway et al., 2016; Yando et al., 2016). There is also insufficient information on whether mangrove encroachment alters atmospheric flux. For example, while mangrove encroachment has been shown to increase redox potential down-profile by introducing oxygen to previously anoxic depths via deeper root growth (Comeaux et al., 2012; Figure 3), growth of mangrove roots may also increase the overall storage of compounds such as lignin (Bianchi et al., 2013), which are considered more resistant to remineralization than most other plant compounds. Clearly, more research is required to understand the long-term fate of C in these ecosystems. This should include quantification of any shifts in the relative fluxes of CO_2, CH_4, or N_2O resulting from mangrove encroachment, as this has important implications for the net greenhouse gas outcome of these changes.

3 | RESEARCH NEEDS FOR INFORMING MANGROVE–SALT MARSH MANAGEMENT

3.1 | Expanding the knowledge base through rigorous experimental design

Our review of the ecological, cultural, and biogeochemical implications of mangrove encroachment has identified potential impacts to habitat utilization and quality, nutrient and C accumulation, wetland resilience to climate change and storms, and social and cultural amenity. However, the evidence base is limited by the nature of studies conducted, many of which were envisaged for a somewhat different purpose or lack the rigor of experimental design necessary to provide unequivocal demonstration of impact. We can categorize these studies into four tiers of evidence at which impact was inferred, namely:

- Before-after-control-impact, as described by Stewart-Oaten, Murdoch, and Parker (1986), in which measures were commenced prior to and included mangrove encroachment in situ, with appropriate control. These were rare, although a subsample of the SET measures of Rogers, Wilton, & Saintilan (2006) includes quadrats invaded by mangrove over the measurement period (Section 2.2.1; Figure 4);
- Space for time substitution, in which sites were selected to represent a chronosequence of encroachment impact. Using this approach, both Osland et al. (2012) and Kelleway et al. (2016) have demonstrated mangrove contribution to belowground C accumulation in Florida, USA, and SE Australia, respectively (Section 2.4.2);
- Controlled spatial comparison, in which the ecological values are compared between mangrove and salt marsh habitat controlling for environmental variables as far as possible. For example, the in situ experimental manipulation of mangrove cover employed by Guo et al. (2017) in Port Aransas, Texas;
- Uncontrolled spatial comparison, in which the two habitats are compared with limited capacity to control for environmental variables likely to be influencing the provision of ecosystem service.

Many studies fell into the final category, with the effect that differences identified between mangrove and salt marsh could not be confidently attributed to the vegetation *per se*. This was true of most

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

studies of the contribution of mangrove and salt marsh to fish habitat, and the comparison of mangrove and salt marsh in nutrient cycling, wave attenuation, and vertical marsh accretion (Figure 4). Extrapolation on this basis is problematic, given the potential significance of environmental covariables (e.g., elevation, salinity, temperature) in influencing the structure and function of mangroves in the (former) salt marsh environment.

3.2 | Spatially explicit management planning

Managers are faced with three broad choices in responding to the encroachment of mangrove. First, a decision might be made to remove mangrove to protect an ecological or cultural service provided in the absence of mangrove. For example, in a priority migratory bird site in the Ramsar-listed Hunter Wetlands National Park, permission was granted for the removal of mangrove to protect migratory bird roosting habitat at the Stockton Sand Spit. The modest extent of clearance (~100 m of shorefront vegetation) was justified on the basis of long-term bird counts confirming abandonment, and the likely utilization if removal was effected (Spencer et al., 2009). Extensions to this approach could include water and salinity management which favors marsh over mangrove (Krauss et al., 2011; Troxler, Childers, & Madden, 2013) and the restoration or construction of new salt marsh habitat to the exclusion of mangrove.

Second, managers may choose to allow the transition from one ecosystem state to another. The view may be taken that the preservation of a prior state is unsustainable and even inappropriate in the face of fundamental changes to system drivers. In transitioning to a new stable state dominated by mangrove, a wetland may be responding to climatic and other environmental variables such that long-term survival is facilitated. For example, elevation gain may be enhanced, allowing greater resilience in the face of accelerated sea-level rise. Further, mangrove encroachment, if increasing the rate of C sequestration, may provide a negative feedback to radiative forcing that would be disrupted by widespread mangrove removal, as has occurred in the tropics. Extending this position further, managers may opt for a third approach, to facilitate and enhance the colonization of mangrove, speeding the transition to an alternative state.

The extent to which mangrove or salt marsh provides an ecosystem service will vary considerably between locations by virtue of landscape context and the species involved. For example, mangroves may degrade bird habitat in one location, but not another. There may even be locations where the encroachment scenario is reversed (i.e., salt marsh colonizing mangrove) (Mbense, Rajkaran, Bolosha, & Adams, 2016). Identification of the regional and local drivers of encroachment and ecosystem service provision will therefore be required when extrapolating research from other settings, modeling impacts, and ultimately making decisions about what management option(s) to take. Previous work has demonstrated the need to consider both hydrological and geomorphic (Rogers & Saintilan, 2008; Rogers, Saintilan, & Woodroffe, 2014) as well as macroclimatic drivers of mangrove expansion when assessing coastal vulnerability (Osland et al., 2016), and the same applies for assessments of future ecosystem service delivery. Historic literature and paleo sediment records may also provide locally relevant evidence of historic habitat change, record of some services, and provide an indication of future change.

The regional representation of habitat, whether mangrove and/or salt marsh, is also an important consideration when defining conservation priorities to meet a comprehensive, adequate, and representative array of protected sites in modified landscapes. In a world increasingly affected by climate change and other anthropogenic modifications, it is contingent on managers to set conservation priorities at the appropriate spatial scale, giving consideration to the range of ecological goods and services required of coastal wetland systems, without being overly encumbered by notions of or predevelopment reference states (Hobbs, Higgs, & Harris, 2009).

4 | CONCLUSIONS

Notwithstanding the limitations imposed by spatial scale and experimental design, our review suggests that conversion of salt marsh to mangrove will impact ecosystem service provisioning in the following ways. Mangroves have a higher capacity to adjust to sea-level rise via sediment accretion and organic matter accumulation, based upon some before-after-control-impact-type evidence (Rogers, Wilton, & Saintilan, 2006, Rogers, Saintilan, & Woodroffe, 2014). However, these studies have been largely limited to SE Australia, and so research in other regions that are experiencing mangrove encroachment is needed. The fact that mangroves generally have higher amounts of aboveground biomass than salt marsh suggests a higher potential for wave attenuation. However, this conclusion is still largely speculative as direct comparisons of wave attenuation by mangrove and salt marsh are limited and generally have not controlled for other environmental variables. While mangrove replacement of salt marsh may influence fish community structure, we did not find evidence that these impacts would either generally increase or decrease fisheries production. Impacts to fish landings are likely to be site specific and dependent on the particular species being targeted. Loss of salt marsh habitat is likely to have a negative impact on certain threatened species, especially for a number of migratory birds, but again these impacts will be site specific. We found some evidence that mangrove expansion may increase the potential for long-term C accumulation and storage; however, these studies were limited to two geographic regions: the southern USA and SE Australia. Also, it may take years to decades for the impacts of mangrove expansion on sediment properties to be realized (Kelleway et al., 2016; Osland et al., 2012). As with C storage, some studies have suggested that nutrient uptake and storage may increase with mangrove expansion, but these studies suffer from a limited capacity to control for other environmental variables (i.e., they are all Tier 4 evidence using the schema in Section 3.1). It is challenging to draw conclusions regarding the implications of mangrove replacement of salt marsh for cultural services as these services are both highly varied and relatively understudied. Importantly, accelerating rates of sea-level rise are likely to force the landward migration of both

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

mangroves and salt marsh. If coastal development prevents this migration ("coastal squeeze"), then all of the services described above are likely to be negatively impacted.

In suggesting a focus for further research, we stress (i) the importance of appropriate experimental design in demonstrating impact (acknowledging the challenge of replication at the spatial and temporal scales at which this phenomenon is occurring) and (ii) a consideration of local and regional drivers of variability relevant to the modeling of impact. Managers should be aware of the multiple and interrelated ecosystem and human services provided by both mangrove and salt marsh, taking a holistic approach to their management when planning conservation and restoration projects. Some services will be easier to quantify than others, and the availability of financial incentives for preserving or restoring certain services (e.g., C markets) is likely to be highly variable. We need a better understanding of services whose value is difficult to quantify (e.g., cultural and spiritual values), especially because many of these services cannot be replaced or restored once change has occurred.

ACKNOWLEDGEMENTS

Funding for this work was provided by grants from the National Aeronautics and Space Administration (NASA) Climate and Biological Response Program (NNX11AO94G) and New Investigator Program (NNX16AN04G).

REFERENCES

Aburto-Oropeza, O., Ezcurra, E., Danemann, G., Valdez, V., Murray, J., & Sala, E. (2008). Mangroves in the Gulf of California increase fishery yields. *Proceedings of the National Academy of Sciences*, *105*, 10456–10459.

Adam, P. (1993). *Saltmarsh ecology*. Cambridge, UK: Cambridge University Press.

Adam, P. (2002). Saltmarshes in a time of change. *Environmental Conservation*, *29*, 39–61.

Adame, M. F., Neil, D., Wright, S. F., & Lovelock, C. E. (2010). Sedimentation within and among mangrove forests along a gradient of geomorphological settings. *Estuarine, Coastal and Shelf Science*, *86*, 21–30.

Adams, J., Colloty, B., & Bate, G. (2004). The distribution and state of mangroves along the coast of Transkei, Eastern Cape Province, South Africa. *Wetlands Ecology and Management*, *12*, 531–541.

Alongi, D. M. (2008). Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science*, *76*, 1–13.

Baker, A. J., Gonzalez, P. M., Piersma, T., Niles, L. J., de Lima Serrano do Nascimento, I., Atkinson, P. W., … Aarts, G. (2004). Rapid population decline in red knots: Fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *271*, 875–882.

Bancroft, G. T., Hoffman, W., Sawicki, R. J., & Ogden, J. C. (1992). The importance of the Water Conservation Areas in the Everglades to the endangered wood stork (*Mycteria americana*). *Conservation Biology*, *6*, 392–398.

Barbier, E. B., Koch, E. W., Silliman, B. R., Hacker, S. D., Wolanski, E., Primavera, J., … Cramer, A. (2008). Coastal ecosystem-based management with nonlinear ecological functions and values. *Science*, *319*, 321–323.

Beeftink, W., Nieuwenhuize, J., Stoeppler, M., & Mohl, C. (1982). Heavy-metal accumulation in salt marshes from the Western and Eastern Scheldt. *Science of the Total Environment*, *25*, 199–223.

Bergstrom, J. C., Stoll, J. R., Titre, J. P., & Wright, V. L. (1990). Economic value of wetlands-based recreation. *Ecological Economics*, *2*, 129–147.

Beymer-Farris, B. A., & Bassett, T. J. (2012). The REDD menace: Resurgent protectionism in Tanzania's mangrove forests. *Global Environmental Change*, *22*, 332–341.

Bhalla, R. S. (2007). Do bio-shields affect tsunami inundation? *Current Science*, *93*, 831–833.

Bianchi, T. S., Allison, M. A., Zhao, J., Li, X., Comeaux, R. S., Feagin, R. A., & Kulawardhana, R. W. (2013). Historical reconstruction of mangrove expansion in the Gulf of Mexico: Linking climate change with carbon sequestration in coastal wetlands. *Estuarine, Coastal and Shelf Science*, *119*, 7–16.

Bird, E. C. (1986). 6. Human interactions with Australian mangrove ecosystems. Man in the Mangroves: The Socio-economic Situation of Human Settlements in Mangrove Forests, 68–78.

Bouma, T. J., De Vries, M. B., Low, E., Peralta, G., Tánczos, I. V., van de Koppel, J., & Herman, P. J. (2005). Trade-offs related to ecosystem engineering: A case study on stiffness of emerging macrophytes. *Ecology*, *86*, 2187–2199.

Burton, N. H., Rehfisch, M. M., & Clark, N. A. (2002). Impacts of disturbance from construction work on the densities and feeding behavior of waterbirds using the intertidal mudflats of Cardiff Bay, UK. *Environmental Management*, *30*, 0865–0871.

Cahoon, D. R., Hensel, P. F., Spencer, T., Reed, D. J., McKee, K. L., & Saintilan, N. (2006). Coastal Wetland Vulnerability to Relative Sea-Level Rise: Wetland Elevation Trends and Process Controls. In J. T. A. Verhoeven, B. Beltman, R. Bobbink & D. F. Whigham (Eds.), *Wetlands and Natural Resource Management* (pp. 271–292). Berlin: Springer.

Caudill, M. C. (2005). Nekton Utilization of Black Mangrove (*Avicennia germinans*) and Smooth Cordgrass (*Spartina alterniflora*) Sites in Southwest Louisiana. MS Thesis. Louisiana State University.

Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., & Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 723–727.

Chavez-Ramirez, F. (1996). *Food availability, foraging ecology, and energetics of Whooping Cranes wintering in Texas*. College Station, TX: Texas A&M University.

Chavez-Ramirez, F., & Wehtje, W. (2012). Potential impact of climate change scenarios on whooping crane life history. *Wetlands*, *32*, 11–20.

Chimner, R. A., Fry, B., Kaneshiro, M. Y., & Cormier, N. (2006). Current extent and historical expansion of introduced mangroves on O'ahu, Hawai'i 1. *Pacific Science*, *60*, 377–383.

Chmura, G. L., Anisfeld, S. C., Cahoon, D. R., & Lynch, J. C. (2003). Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles*, *17*, 22:21-22:12.

Comeaux, R. S., Allison, M. A., & Bianchi, T. S. (2012). Mangrove expansion in the Gulf of Mexico with climate change: Implications for wetland health and resistance to rising sea levels. *Estuarine, Coastal and Shelf Science*, *96*, 81–95.

Coops, H., Verheij, H. J., & Boeters, R. (1996). Interactions between waves, bank erosion and emergent vegetation : An experimental study in a wave tank. *Aquatic Botany*, *53*, 187–198.

Costanza, R., De Groot, R., Sutton, P., Van Der Ploeg, S., Anderson, S. J., Kubiszewski, I., … Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, *26*, 152–158.

Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., … Machmuller, M. (2009). Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Frontiers in Ecology and the Environment*, *7*, 73–78.

Cuc, N. T. K., Suzuki, T., de Ruyter van Steveninck, T. E. D., & Hai, H. (2015). Modelling the impacts of mangrove vegetation structure on wave dissipation in Ben Tre Province, Vietnam, under different climate change scenarios. *Journal of Coastal Research*, *31*, 340–347.

Currin, C. A., Newell, S. Y., & Paerl, H. W. (1995). The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs:

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series*, *121*, 99–116.

Dahdouh-Guebas, F., Mathenge, C., Kairo, J., & Koedam, N. (2000). Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. *Economic Botany*, *54*, 513–527.

Danielsen, F., Sørensen, M. K., Olwig, M. F., Selvam, V., Parish, F., Burgess, N. D., … Hansen, L. B. (2005). The Asian tsunami: A protective role for coastal vegetation. *Science (Washington)*, *310*(5748), 643.

Day, J. W., Boesch, D. F., Clairain, E. J., Kemp, G. P., Laska, S. B., Mitsch, W. J., … Shabman, L. (2007). Restoration of the Mississippi Delta: Lessons from Hurricanes Katrina and Rita. *Science*, *315*, 1679–1685.

De Groot, R., Brander, L., Van Der Ploeg, S., Costanza, R., Bernard, F., Braat, L., … Van Beukering, P. (2012). Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services*, *1*, 50–61.

Deegan, L. A., Johnson, D. A., Warren, R. S., Peterson, B. J., Fleeger, J. W., Fagherazzi, S., & Wollheim, W. M. (2012). Coastal eutrophication as a driver of salt marsh loss. *Nature*, *490*, 388–392.

Dekker, D., & Ydenberg, R. (2004). Raptor predation on wintering dunlins in relation to the tidal cycle. *The Condor*, *106*, 415–419.

Donato, D. C., Kauffman, J. B., Murdiyarso, D., Kurnianto, S., Stidham, M., & Kanninen, M. (2011). Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, *4*, 293–297.

Doughty, C. L., Langley, J. A., Walker, W. S., Feller, I. C., Schaub, R., & Chapman, S. K. (2016). Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuaries and Coasts*, *39*, 385–396.

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, *3*, 961–968.

Duke, N., Ball, M., & Ellison, J. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, *7*, 27–47.

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., … Lovett, G. M. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, *3*, 479–486.

Erwin, R. M., Hatfield, J. S., Howe, M. A., & Klugman, S. S. (1994). Waterbird use of saltmarsh ponds created for open marsh water management. *The Journal of Wildlife Management*, *58*, 516–524.

Eslami-Andargoli, L., Dale, P., Sipe, N., & Chaseling, J. (2009). Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science*, *85*, 292–298.

Ewel, K. C., Twilley, R. R., & Ong, J. E. (1998). Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography*, *7*, 83–94.

Feagin, R. A., Mukherjee, N., Shanker, K., Baird, A. H., Cinner, J., Kerr, A. M., … Jayatissa, L. P. (2010). Shelter from the storm? Use and misuse of coastal vegetation bioshields for managing natural disasters. *Conservation Letters*, *3*, 1–11.

Feller, I. C. (1995). Effects of nutrient enrichment on growth and herbivory in dwarf red mangrove (*Rhizophora mangle*). *Ecological Monographs*, *65*, 477–505.

Feller, I. C., Chamberlain, A. H., Piou, C., Chapman, S. K., & Lovelock, C. E. (2013). Latitudinal patterns of herbivory in mangrove forests: Consequences of nutrient over-enrichment. *Ecosystems*, *16*, 1203–1215.

Feller, I. C., Dangremond, E. M., Devlin, D. J., Lovelock, C. E., Proffitt, C. E., & Rodriguez, W. (2015). Nutrient enrichment intensifies hurricane damage and prolongs recovery in mangrove ecosystems in the Indian River Lagoon. *Ecology*, *96*, 2960–2972.

Feller, I. C., Lovelock, C. E., Berger, U., McKee, K. L., Joye, S. B., & Ball, M. C. (2010). The biocomplexity of mangrove ecosystems. *Annual Review of Marine Science*, *2*, 395–416.

Feller, I. C., Whigham, D. F., McKee, K. L., & Lovelock, C. E. (2003). Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia*, *134*, 405–414.

Feller, I. C., Whigham, D. F., O'Neill, J. P., & McKee, K. L. (1999). Effects of nutrient enrichment on within-stand nutrient cycling in mangrove ecosystems in Belize. *Ecology*, *80*, 2193–2205.

Friess, D. A. (2016). Ecosystem services and disservices of mangrove forests: Insights from historical colonial observations. *Forests*, *7*, 183.

Friess, D. A., Krauss, K. W., Horstman, E. M., Balke, T., Bouma, T. J., Galli, D., & Webb, E. L. (2012). Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biological Reviews of the Cambridge Philosophical Society*, *87*, 346–366.

Fu, S., Cai, L., Cao, J., & Chen, X. (2017). Nematode responses to the invasion of exotic *Spartina* in mangrove wetlands in southern China. *Estuaries and Coasts*, 1–13. https://doi.org/10.1007/s12237-017-0208-3

Furukawa, K., Wolanski, E., & Mueller, H. (1997). Currents and sediment transport in mangrove forests. *Estuarine, Coastal and Shelf Science*, *44*, 301–310.

Gedan, K. B., Silliman, B. R., & Bertness, M. D. (2009). Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science*, *1*, 117–141.

Geldenhuys, C., Cotiyane, P., & Rajkaran, A. (2016). Understanding the creek dynamics and environmental characteristics that determine the distribution of mangrove and salt marsh communities at Nahoon Estuary. *South African Journal of Botany*, *107*, 137–147.

Gilbert, A. J., & Janssen, R. (1998). Use of environmental functions to communicate the values of a mangrove ecosystem under different management regimes. *Ecological Economics*, *25*, 323–346.

Giri, C., & Long, J. (2016). Is the geographic range of mangrove forests in the conterminous United States really expanding? *Sensors*, *16*, 2010.

Godoy, M. D. P., & Lacerda, L. D. D. (2015). Mangroves response to climate change: A review of recent findings on mangrove extension and distribution. *Anais da Academia Brasileira de Ciências*, *87*, 651–667.

Gonsalves, L., Law, B., Webb, C., & Monamy, V. (2012). Are vegetation interfaces important to foraging insectivorous bats in endangered coastal saltmarsh on the Central Coast of New South Wales? *Pacific Conservation Biology*, *18*, 282–292.

Gonsalves, L., Law, B., Webb, C., & Monamy, V. (2013). Foraging ranges of insectivorous bats shift relative to changes in mosquito abundance. *PLoS ONE*, *8*, e64081.

Gray, A. (1972). The ecology of Morecambe Bay. v. The salt marshes of Morecambe Bay. *Journal of Applied Ecology*, *9*, 207–220.

Guo, H., Weaver, C., Charles, S., Whitt, A., Dastidar, S., D'Odorico, P., … Pennings, S. C. (2017). Coastal regime shifts: Rapid responses of coastal wetlands to changes in mangrove cover. *Ecology*, *98*, 762–772.

Guo, H., Zhang, Y., Lan, Z., & Pennings, S. C. (2013). Biotic interactions mediate the expansion of black mangrove (*Avicennia germinans*) into salt marshes under climate change. *Global Change Biology*, *19*, 2765–2774.

Güsewell, S., Bolllens, U., Ryser, R., & Klötzli, F. (2003). Contrasting effects of nitrogen, phosphorus and water regime on first- and second-year growth of 16 wetland plant species. *Functional Ecology*, *17*, 754–765.

Habary, A., Johansen, J. L., Nay, T. J., Steffensen, J. F., & Rummer, J. L. (2016). Adapt, move, or die–how will tropical coral reef fishes cope with ocean warming? *Global Change Biology*, *23*, 566–577.

Hamilton, L. S., & Murphy, D. H. (1988). Use and management of Nipa palm (*Nypa fruticans*, ARECACEAE): A review. *Economic Botany*, *42*, 206–213.

Henry, K. M., & Twilley, R. R. (2013). Soil development in a coastal Louisiana wetland during a climate-induced vegetation shift from salt marsh to mangrove. *Journal of Coastal Research*, *29*, 1273–1283.

Hobbie, S. E. (2015). Plant species effects on nutrient cycling: Revisiting litter feedbacks. *Trends in Ecology and Evolution*, *30*, 357–363.

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology and Evolution*, *24*, 599–605.

Howard, R. J., Day, R. H., Krauss, K. W., From, A. S., Allain, L., & Cormier, N. (2016). Hydrologic restoration in a dynamic subtropical mangrove-to-marsh ecotone. *Restoration Ecology*, 1–12. https://doi.org/10.1111/rec.12452

Howard, R. J., Krauss, K. W., Cormier, N., Day, R. H., Biagas, J., & Allain, L. (2015). Plant–plant interactions in a subtropical mangrove-to-marsh transition zone: Effects of environmental drivers. *Journal of Vegetation Science*, *26*, 1198–1211.

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Huang, S. C., Shih, S. S., Ho, Y. S., Chen, C. P., & Hsieh, H. L. (2012). Restoration of shorebird-roosting mudflats by partial removal of estuarine mangroves in northern Taiwan. *Restoration Ecology*, *20*, 76–84.

Jusoff, K. (2009). Managing sustainable mangrove forests in Peninsular Malaysia. *Journal of Sustainable Development*, *1*, 88.

Kaplowitz, M. D. (2001). Assessing mangrove products and services at the local level: The use of focus groups and individual interviews. *Landscape and Urban Planning*, *56*, 53–60.

Kar, R., & Kar, R. K. (2005). Mangroves can check the wrath of tsunami. *Current Science*, *88*, 675.

Kathiresan, K., & Rajendran, N. (2005). Coastal mangrove forests mitigated tsunami. *Estuarine, Coastal and Shelf Science*, *65*, 601–606.

Kelleway, J. J., Saintilan, N., Macreadie, P. I., Skilbeck, C. G., Zawadzki, A., & Ralph, P. J. (2016). Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Global Change Biology*, *22*, 1097–1109.

Kerkhoff, A. J., & Enquist, B. J. (2006). Ecosystem allometry: The scaling of nutrient stocks and primary productivity across communities. *Ecology Letters*, *9*, 419–427.

Kerkhoff, A. J., Fagan, W. F., Elser, J. T., & Enquist, B. J. (2006). Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *American Naturalist*, *168*, E103–E122.

Kerr, A. M., & Baird, A. H. (2007). Natural barriers to natural disasters. *BioScience*, *57*, 102–103.

Kerr, A., Baird, A. H., & Campbell, S. J. (2005). Comments on '"Coastal mangrove forests mitigated tsunami". *Estuarine, Coastal and Shelf Science*, *65*, 539–541.

Koch, E. W., Barbier, E. B., Silliman, B. R., Reed, D. J., Perillo, G. M. E., Hacker, S. D., … Wolanski, E. (2009). Non-linearity in ecosystem services: Temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment*, *7*, 29–37.

Kovacs, J. M. (1999). Assessing mangrove use at the local scale. *Landscape and Urban Planning*, *43*, 201–208.

Krauss, K. W., Doyle, T. W., Doyle, T. J., Swarzenski, C. M., From, A. S., Day, R. H., & Conner, W. H. (2009). Water level observations in mangrove swamps during two hurricanes in Florida. *Wetlands*, *29*, 142–149.

Krauss, K. W., From, A. S., Doyle, T. W., Doyle, T. J., & Barry, M. J. (2011). Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Islands region of Florida, USA. *Journal of Coastal Conservation*, *15*, 629–638.

Krauss, K. W., McKee, K. L., & Hester, M. W. (2014). Water use characteristics of black mangrove (*Avicennia germinans*) communities along an ecotone with marsh at a northern geographical limit. *Ecohydrology*, *7*, 354–365.

Lapetina, A., & Sheng, Y. P. (2014). Three-dimensional modeling of storm surge and inundation including the effects of coastal vegetation. *Estuaries and Coasts*, *37*, 1028–1040.

Lara, J. L., Maza, M., Ondiviela, B., Trinogga, J., Losada, I. J., Bouma, T. J., & Gordejuela, N. (2016). Large-scale 3-D experiments of wave and current interaction with real vegetation. Part 1: Guidelines for physical modeling. *Coastal Engineering*, *107*, 70–83.

Lawler, W. (1996). Guidelines for Management of Migratory Shorebird Habitat in Southern East Coast Estuaries, Australia. Department of Ecosystem Management, University of New England, Armidale, NSW.

Lee, S. Y., Primavera, J. H., Dahdouh-Guebas, F., Mckee, K., Bosire, J. O., Cannicci, S., … Record, S. (2014). Ecological role and services of tropical mangrove ecosystems: A reassessment. *Global Ecology and Biogeography*, *23*, 726–743.

Lewis, D. B., Brown, J. A., & Jimenez, K. L. (2014). Effects of flooding and warming on soil organic matter mineralization in *Avicennia germinans* mangrove forests and *Juncus roemerianus* salt marshes. *Estuarine, Coastal and Shelf Science*, *139*, 11–19.

López-Medellín, X., Ezcurra, E., González-Abraham, C., Hak, J., Santiago, L. S., & Sickman, J. O. (2011). Oceanographic anomalies and sea-level rise drive mangroves inland in the Pacific coast of Mexico. *Journal of Vegetation Science*, *22*, 143–151.

Lovelock, C. E., Ball, M. C., Martin, K., & Feller, I. C. (2009). Nutrient enrichment increases mortality of mangroves. *PLoS ONE*, *4*, e5600.

Lovelock, C. E., Cahoon, D. R., Friess, D. A., Guntenspergen, G. R., Krauss, K. W., Reef, R., … Triet, T. (2015). The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature*, *526*, 559–563.

Lovelock, C. E., & Feller, I. C. (2003). Photosynthetic performance and resource utilization of two mangrove species coexisting in hypersaline scrub forest. *Oecologia*, *134*, 455–462.

Lovelock, C. E., Feller, I. C., Ball, M. C., Ellis, J., Schwarz, A. M., & Sorrell, B. K. (2007). Growth rate hypothesis vs geochemical hypothesis for variation in plant nutrients over latitude: A test using mangroves. *Ecology Letters*, *10*, 1154–1163.

Lovelock, C. E., Feller, I. C., Ellis, J., Schwarz, A. M., Hancock, N., & Sorrell, B. (2007). Mangrove growth in New Zealand estuaries: The role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia*, *153*, 633–641.

Lovelock, C. E., Sorrell, B. K., Hancock, N., Hua, Q., & Swales, A. (2010). Mangrove forest and soil development on a rapidly accreting shore in New Zealand. *Ecosystems*, *13*, 437–451.

Loyn, R., Lane, B., Chandler, C., & Carr, G. (1986). Ecology of Orange-bellied Parrots *Neophema chrysogaster* at their main remnant wintering site. *EMU*, *86*, 195–206.

Lunstrum, A., & Chen, L. (2014). Soil carbon stocks and accumulation in young mangrove forests. *Soil Biology and Biochemistry*, *75*, 223–232.

Lunt, J., Mcglaun, K., & Robinson, E. M. (2013). Effects of black mangrove (*Avicennia germinans*) expansion on saltmarsh (*Spartina alterniflora*) benthic communities of the South Texas Coast. *Gulf and Caribbean Research*, *25*, 125–129.

Martin, K. C., Bruhn, D., Lovelock, C. E., Feller, I. C., Evans, J. R., & Ball, M. C. (2010). Nitrogen fertilization enhances water use efficiency in a saline environment. *Plant, Cell, and Environment*, *33*, 344–357.

Massel, S. R., Furukawa, K., & Brinkman, R. M. (1999). Surface wave propagation in mangrove forests. *Fluid Dynamics Research*, *24*, 219–249.

Mastaller, M. (1997). *Mangroves: The forgotten forest between land and sea*. Kuala Lumpur, Malaysia: Tropical Press.

Mazda, Y., Magi, M., Ikeda, Y., Kurokawa, T., & Asano, T. (2006). Wave reduction in a mangrove forest dominated by *Sonneratia* sp. *Wetlands Ecology and Management*, *14*, 365–378.

Mazda, Y., Wolanski, E., King, B., Sase, A., Ohtsuka, D., & Magi, M. (1997). Drag force due to vegetation in mangrove swamps. *Mangroves and Salt Marshes*, *1*, 193–199.

Mazumder, D., & Saintilan, N. (2010). Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. *Wetlands*, *30*, 375–380.

Mazumder, D., Saintilan, N., & Williams, R. J. (2005). Temporal variations in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. *Wetlands Ecology and Management*, *13*, 457–467.

Mazumder, D., Saintilan, N., & Williams, R. J. (2006). Fish assemblages in three tidal saltmarsh and mangrove flats in temperate NSW, Australia: A comparison based on species diversity and abundance. *Wetlands Ecology and Management*, *14*, 201–209.

Mazumder, D., Saintilan, N., & Williams, R. J. (2009). Zooplankton inputs and outputs in the saltmarsh at Towra Point, Australia. *Wetlands Ecology and Management*, *17*, 225–230.

Mbense, S., Rajkaran, A., Bolosha, U., & Adams, J. (2016). Rapid colonization of degraded mangrove habitat by succulent salt marsh. *South African Journal of Botany*, *107*, 129–136.

McIvor, A., Möller, I., Spencer, T., & Spalding, M. (2012). Reduction of wind and swell waves by mangroves. Natural Coastal Protection Series: Report 1, Cambridge Coastal Research Unit Working Paper 40. The Nature Conservancy and Wetlands International.

McKee, K., Rogers, K., & Saintilan, N. (2012). Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In B. A. Middleton (Ed.), *Global Change and the Function and Distribution of Wetlands*, (pp. 63–96). Dordrecht: Springer Netherlands.

McKee, K. L., & Rooth, J. E. (2008). Where temperate meets tropical: Multifactorial effects of elevated CO_2, nitrogen enrichment, and competition

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

on a mangrove-salt marsh community. *Global Change Biology*, *14*, 971–984.

McKenzie, N. L., & Rolfe, J. K. (1986). Structure of bat guilds in the Kimberley mangroves, Australia. *The Journal of Animal Ecology*, *55*, 401–420.

McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Bjork, M., Duarte, C. M., … Silliman, B. R. (2011). A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment*, *9*, 552–560.

Meehl, G. A., Stocker, T. F., Collins, W. D., Friedlingstein, P., Gaye, A. T., Gregory, J. M., … Zhao, Z.-C. (2007). Global climate projections. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller (Eds.), *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (pp. 747–845). Cambridge, UK and New York, NY, USA: Cambridge University Press.

Meynecke, J. O., Lee, S. Y., & Duke, N. C. (2008). Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. *Biological Conservation*, *141*, 981–996.

Meynecke, J.-O., Lee, S. Y., Duke, N. C., & Warnken, J. (2007). Relationships between estuarine habitats and coastal fisheries in Queensland, Australia. *Bulletin of Marine Science*, *80*, 773–793.

Mojiol, A. R., Lintangah, W., Ismenyah, M., Alamjuri, R. H., & Jaafar, C. S. Z. (2016). Mangroves forest produce (Mfp): Importance and contribution to the local communities at Banggi Island Malaysia using free listing. *International Journal of Agriculture, Forestry and Plantation*, *3*, 89–94.

Morris, J. T., Sundareshwar, P., Nietch, C. T., Kjerfve, B., & Cahoon, D. (2002). Responses of coastal wetlands to rising sea level. *Ecology*, *83*, 2869–2877.

Möller, I., Spencer, T., French, J. R., Leggett, D., & Dixon, M. (1999). Wave transformation over salt marshes: A field and numerical modelling study from North Norfolk, England. *Estuarine, Coastal and Shelf Science*, *49*, 411–426.

Morrisey, D. J., Swales, A., Dittmann, S., Morrison, M. A., Lovelock, C. E., Beard, C. M., & Gibson, R. (2010). *The ecology and management of temperate mangroves*. Boca Raton (USA): CRC Press.

Moussalli, A., & Connolly, R. M. (1998). Fish use of the inundated waters of a subtropical saltmarsh-mangrove complex in Southeast Queensland, Australia. Short communication. In I. R. Tibbetts, N. J. Hall, & W. D. Dennison (Eds.), *Moreton Bay and catchment* (pp. 471–472). Brisbane: School of Marine Science, The University of Queensland.

Murray, B. C., Pendleton, L., Jenkins, W. A., & Sifleet, S. (2011). Green payments for blue carbon: Economic incentives for protecting threatened coastal habitats. Nicholas Institute for Environmental Policy Solutions, Report NI, 11.

Nagelkerken, I., Blaber, S., Bouillon, S., Green, P., Haywood, M., Kirton, L., … Sasekumar, A. (2008). The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany*, *89*, 155–185.

Nurkin, B. (1994). Degradation of mangrove forests in South Sulawesi, Indonesia. *Hydrobiologia*, *285*, 271–276.

Osland, M. J., Day, R. H., From, A. S., Mccoy, M. L., Mcleod, J. L., & Kelleway, J. J. (2015). Life stage influences the resistance and resilience of black mangrove forests to winter climate extremes. *Ecosphere*, *6*, art160.

Osland, M. J., Enwright, N., Day, R. H., & Doyle, T. W. (2013). Winter climate change and coastal wetland foundation species: Salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology*, *19*, 1482–1494.

Osland, M. J., Enwright, N. M., Day, R. H., Gabler, C. A., Stagg, C. L., & Grace, J. B. (2016). Beyond just sea-level rise: Considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. *Global Change Biology*, *22*, 1–11.

Osland, M. J., Spivak, A. C., Nestlerode, J. A., Lessmann, J. M., Almario, A. E., Heitmuller, P. T., … Dantin, D. D. (2012). Ecosystem development after mangrove wetland creation: Plant–soil change across a 20-year chronosequence. *Ecosystems*, *15*, 848–866.

Paepae o He'eia. (2016). "The Fishpond | Paepae O He'Eia". Retrieved from http://paepaeoheeia.org/thefishpond/ Web. 20 Dec. 2016.

Patterson, C. S., & Mendelssohn, I. A. (1991). A comparison of physicochemical variables across plant zones in a mangal/salt marsh community in Louisiana. *Wetlands*, *11*, 139–161.

Perry, C. L., & Mendelssohn, I. A. (2009). Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. *Wetlands*, *29*, 396–406.

Peterson, J. M., & Bell, S. S. (2015). Saltmarsh boundary modulates dispersal of mangrove propagules: Implications for mangrove migration with sea-level rise. *PLoS ONE*, *10*, e0119128.

Raabe, E. A., Roy, L. C., & McIvor, C. C. (2012). Tampa bay coastal wetlands: Nineteenth to twentieth century tidal marsh-to-mangrove conversion. *Estuaries and Coasts*, *35*, 1145–1162.

Rasolofo, M. V. (1997). Use of mangroves by traditional fishermen in Madagascar. *Mangroves and Salt Marshes*, *1*, 243–253.

Rauzon, M. J., & Drigot, D. C. (2002). Red mangrove eradication and pickleweed control in a Hawaiian wetland, waterbird responses, and lessons learned. In C. R. Veitch (Ed.), *Eradication of island invasive: Practical actions and results achieved* (pp. 94–102). Auckland, New Zealand: International Union for the Conservation of Nature.

Reef, R., Feller, I. C., & Lovelock, C. E. (2010). Nutrition of mangroves. *Tree Physiology*, *30*, 1148–1160.

Rejmánková, E. (2005). Nutrient resorption in wetland macrophytes: Comparison across several regions of different nutrient status. *New Phytologist*, *167*, 471–482.

Ribeiro, J. P. N., Tiberio, F. C. S., & de Oliveira, A. A. (2015). The role of soil nutrients in boundaries between mangrove and herbaceous assemblages in a tropical estuary. *Biotropica*, *47*, 517–520.

Rogers, K. & Saintilan, N. (2016). *Surface elevation table and marker horizon network of southeast Australian mangrove and saltmarsh*, Unpublished data.

Rogers, D. I., Battley, P. F., Piersma, T., Van Gils, J. A., & Rogers, K. G. (2006). High-tide habitat choice: Insights from modelling roost selection by shorebirds around a tropical bay. *Animal Behaviour*, *72*, 563–575.

Rogers, K., & Saintilan, N. (2008). Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *Journal of Coastal Research*, *24*, 63–69.

Rogers, K., Saintilan, N., & Cahoon, D. (2005). Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetlands Ecology and Management*, *13*, 587–598.

Rogers, K., Saintilan, N., & Woodroffe, C. D. (2014). Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: Implications for coastal wetland response to climate change. *Estuarine, Coastal and Shelf Science*, *149*, 46–56.

Rogers, K., Wilton, K. M., & Saintilan, N. (2006). Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science*, *66*, 559–569.

Rosa, S., Palmeirim, J. M., & Moreira, F. (2003). Factors affecting waterbird abundance and species richness in an increasingly urbanized area of the Tagus estuary in Portugal. *Waterbirds*, *26*, 226–232.

Saintilan, N. (2004). Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine, Coastal and Shelf Science*, *61*, 591–601.

Saintilan, N., Hossain, K., & Mazumder, D. (2007). Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. *Wetlands Ecology and Management*, *15*, 277–286.

Saintilan, N., Rogers, K., & McKee, K. (2009). Salt marsh-mangrove interactions in Australasia and the Americas.

Saintilan, N., & Williams, R. J. (1999). Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography*, *8*, 117–124.

Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., & Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*, *20*, 147–157.

Shaffer, G. P., Day Jr, J. W., Mack, S., Kemp, G. P., Van Heerden, I., Poirrier, M. A., … Morris, C. A. (2009). The MRGO navigation project: A massive human-induced environmental, economic, and storm disaster the MRGO navigation project: A massive human-induced

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

environmental, economic, and storm disaster. *Journal of Coastal Research*, *54*, 206–224.

Simpson, L. T., Feller, I. C., & Chapman, S. K. (2013). Effects of competition and nutrient enrichment on *Avicennia germinans* in the salt marsh-mangrove ecotone. *Aquatic Botany*, *104*, 55–59.

Smee, D. L., Sanchez, J. A., Diskin, M., & Trettin, C. (2017). Mangrove expansion into salt marshes alters associated faunal communities. *Estuarine, Coastal and Shelf Science*, *187*, 306–313.

Souza Filho, P. W. M., Cohenf, M. C. L., Laraj, R. J., Lessaoo, G. C., Koch, B., & Behling, H. (2004). Holocene coastal evolution and facies model of the Bragança Macrotidal Flat on the Amazon Mangrove Coast, Northern Brazil. *Journal of Coastal Research SI*, *39*, 306–310.

Spalding, M. (2010). *World atlas of mangroves*. London, UK: Routledge.

Spalding, M. D., Ruffo, S., Lacambra, C., Meliane, I., Zeitlin, L., Shepard, C. C., & Beck, M. W. (2014). The role of ecosystems in coastal protection: Adapting to climate change and coastal hazards. *Ocean and Coastal Management*, *90*, 50–57.

Spenceley, A. P. (1977). The role of pneumatophores in sedimentary processes. *Marine Geology*, *24*, M31–M37.

Spencer, J. (2010). *Migratory shorebird ecology in the Hunter estuary, south-eastern Australia*. PhD Thesis, Australian Catholic University, Sydney, NSW.

Spencer, J., Monamy, V., & Breitfuss, M. (2009). Saltmarsh as habitat for birds and other vertebrates. In N. Saintilan (Ed.), *Australian saltmarsh ecology* (pp. 149–165). Collingwood: CSIRO Publishing.

Stehn, T. V., & Prieto, F. (2010). Changes in winter whooping crane territories and range 1950–2006 North American Crane Workshop Proceedings. Paper 145. Retrieved from http://digitalcommons.unl.edu/nacwgproc/145

Stevens, P. W., Fox, S. L., & Montague, C. L. (2006). The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management*, *14*, 435–444.

Stewart-Oaten, A., Murdoch, W. W., & Parker, K. R. (1986). Environmental impact assessment: "Pseudoreplication" in time? *Ecology*, *67*, 929–940.

Stokes, D. J., & Harris, R. J. (2015). Sediment properties and surface erodibility following a large-scale mangrove (*Avicennia marina*) removal. *Continental Shelf Research*, *107*, 1–10.

Stokstad, E. (2005). Louisiana's wetlands struggle for survival. *Science*, *310*, 1264–1266.

Swales, A., Bentley, S. J., & Lovelock, C. E. (2015). Mangrove-forest evolution in a sediment-rich estuarine system: Opportunists or agents of geomorphic change? *Earth Surface Processes and Landforms*, *40*, 1672–1687.

Tamunaidu, P., Matsui, N., Okimori, Y., & Saka, S. (2013). Nipa (*Nypa fruticans*) sap as a potential feedstock for ethanol production. *Biomass and Bioenergy*, *52*, 96–102.

Troxler, T. G., Childers, D. L., & Madden, C. J. (2013). Drivers of decadal-scale change in southern everglades wetland macrophyte communities of the coastal ecotone. *Wetlands*, *34*, 81–90.

Turner, R. E. (2011). Beneath the salt marsh canopy: Loss of soil strength with increasing nutrient loads. *Estuaries and Coasts*, *34*, 1084–1093.

Turner, R. E., Howes, B. L., Teal, J. M., Milan, C. S., Swenson, E. M., & Goehringer-Toner, D. D. (2009). Salt marshes and eutrophication: An unsustainable outcome. *Limnology and Oceanography*, *54*, 1634–1642.

Valiela, I., Bowen, J. L., & York, J. K. (2001). Mangrove forests: One of the world's threatened major tropical environments. *BioScience*, *51*, 807–815.

Velasquez, C. R., & Hockey, P. A. R. (1992). The importance of supratidal foraging habitats for waders at a south temperate estuary. *Ardea*, *80*, 243–253.

Vestergaard, P. (1998). Vegetation ecology of coastal meadows in Southeastern Denmark, [Council for Nordic Publications in Botany].

Walters, B. B., Rönnbäck, P., Kovacs, J. M., Crona, B., Hussain, S. A., Badola, R., … Dahdouh-Guebas, F. (2008). Ethnobiology, socio-economics and management of mangrove forests: A review. *Aquatic Botany*, *89*, 220–236.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., … Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.

Warner, R., Kaidonis, M., Dun, O., Rogers, K., Shi, Y., Nguyen, T. T. X., & Woodroffe, C. D. (2016). Opportunities and challenges for mangrove carbon sequestration in the Mekong River Delta in Vietnam. *Sustainability Science*, *11*, 661–677.

Wolanski, E. (2006). Thematic paper: Synthesis of the protective functions of coastal forests and trees against natural hazards. In S. Braatz, S. Fortuna, J. Broadhead, & R. Leslie (Eds.), *Coastal protection in the aftermath of the Indian Ocean tsunami: What role for forests and trees* (pp. 157–179). Khao Lak, Thailand: Food and Agriculture Organization of the United Nations Regional Office for Asia and The Pacific.

Yando, E. S., Osland, M. J., Willis, J. M., Day, R. H., Krauss, K. W., & Hester, M. W. (2016). Salt marsh-mangrove ecotones: Using structural gradients to investigate the effects of woody plant encroachment on plant-soil interactions and ecosystem carbon pools. *Journal of Ecology*, *104*, 1020–1031.

Ysebaert, T., Yang, S. L., Zhang, L., He, Q., Bouma, T. J., & Herman, P. M. (2011). Wave attenuation by two contrasting ecosystem engineering salt marsh macrophytes in the intertidal pioneer zone. *Wetlands*, *31*, 1043–1054.

Zhang, K. H., Liu, Y., Li, H., Xu, J., Shen, J., & Rhome Smith, T. J. (2012). The role of mangroves in attenuating storm surges. *Estuarine, Coastal and Shelf Science*, *103*, 11–23.

How to cite this article: Kelleway JJ, Cavanaugh K, Rogers K, et al. Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Glob Change Biol*. 2017;23:3967–3983. https://doi.org/10.1111/gcb.13727

13652486, 2017, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13727 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Chapter 3: Response of Mangroves and Saltmarshes to Sea Level Rise

3.1 **Saintilan, N**., Khan, N. S., Ashe, E., Kelleway, J.J., Rogers, K., Woodroffe, C. D., & Horton, B. P. (2020). Thresholds of mangrove survival under rapid sea level rise. *Science*, *368*(6495), 1118-1121.

3.2 Woodroffe, C.D., Rogers, K., McKee, K.L., Lovelock, C.E., Mendelssohn, I.A. & **Saintilan, N.** 2016, 'Mangrove Sedimentation and Response to Relative Sea-Level Rise', Annual Review of Marine Science, vol. 8, pp. 243-266

3.3 Rogers, K., & **Saintilan, N.** (2008). Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *Journal of Coastal Research*, (24), 63-69.

3.4 Rogers K., **Saintilan N.** and Wilton K. 2006. Vegetation change and surface elevation dynamics of the estuarine wetlands of southeast Australia. *Estuarine Coastal and Shelf Science*. 66. 559-569

3.5 Rogers K., **Saintilan N.** and Heijnis H. 2005.Mangrove encroachment of saltmarsh in Westernport Bay; the role of sedimentation, subsidence and sea-level rise. *Estuaries*. 28(4)-551-559

3.6 Rogers, K., **Saintilan, N.** & Woodroffe, C.D. 2014, 'Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: Implications for coastal wetland response to climate change', Estuarine, Coastal and Shelf Science, vol. 149, pp. 46-56

3.7 Rogers, K., Zawadzki, A., Mogensen, L. A., & **Saintilan, N.** (2022). Coastal wetland surface elevation change is dynamically related to accommodation space and influenced by sedimentation and sea-level rise over decadal timescales. *Frontiers in Marine Science*.

3.8 **Saintilan, N.,** Sun, Y., Lovelock, C. E., Rogers, K., Goddard, M., Hutley, L. B., ... & Jones, A. (2023). Vertical Accretion Trends in Australian Tidal Wetlands. *Estuaries and Coasts*, 1-14.

3.9 Lovelock, C.E., Cahoon, D.R., Friess, D.A., Guntenspergen, G.R., Krauss, K.W., Reef, R., Rogers, K., Saunders, M.L., Sidik, F., Swales, A., **Saintilan, N**., Thuyen, L.X. & Triet, T. 2015, 'The vulnerability of Indo-Pacific mangrove forests to sea-level rise', *Nature*, vol. 526, no. 7574, pp. 559-563*

3.10 Rogers, K., & **Saintilan, N.** (2021). Processes Influencing Autocompaction Modulate Coastal Wetland Surface Elevation Adjustment with Sea-Level Rise. *Frontiers in Marine Science*, 879.

3.11 Sun, Y., Rogers, K., Lal, K. K., & **Saintilan, N.** (2024). Living root contributions dominate vertical accretion, but not carbon burial, in two SE Australian tidal wetlands. *Estuarine, Coastal and Shelf Science*, 108776

3.12 **Saintilan N**. Kovalenko K. Guntenspergen G. Rogers K, et al (2022). Constraints on the response of tidal marshes to accelerating sea-level rise. *Science* 377.6605 523-527

PALEOECOLOGY

Thresholds of mangrove survival under rapid sea level rise

N. Saintilan[1]*, N. S. Khan[2,3], E. Ashe[4], J. J. Kelleway[5,6], K. Rogers[5,6], C. D. Woodroffe[5,6], B. P. Horton[7,8]

The response of mangroves to high rates of relative sea level rise (RSLR) is poorly understood. We explore the limits of mangrove vertical accretion to sustained periods of RSLR in the final stages of deglaciation. The timing of initiation and rate of mangrove vertical accretion were compared with independently modeled rates of RSLR for 78 locations. Mangrove forests expanded between 9800 and 7500 years ago, vertically accreting thick sequences of organic sediments at a rate principally driven by the rate of RSLR, representing an important carbon sink. We found it very likely (>90% probability) that mangroves were unable to initiate sustained accretion when RSLR rates exceeded 6.1 millimeters per year. This threshold is likely to be surpassed on tropical coastlines within 30 years under high-emissions scenarios.

The rate of relative sea level rise (RSLR) in tropical and subtropical locations is projected to accelerate from current trends of ~3.4 mm year^{-1} to a mean estimate of ~5 mm year^{-1} under low-emissions scenarios and ~10 mm year^{-1} under high-emissions scenarios by 2100 (*1*, *2*). Modeling of feedbacks between RSLR, vertical accretion, root mass formation, and tidal marsh and mangrove vulnerability under sustained high rates of RSLR is vital for the survival of these ecologically and economically important coastal environments (*2*). Some tidal marshes have been projected to survive RSLR of more than 10 mm year^{-1} where supported by high available suspended sediment concentrations (*3*), on the basis of accretion data that span annual to decadal time scales. Reconstructions using paleoenvironmental proxies, however, have suggested that UK marshes were vulnerable to retreat at RSLR of 7 mm year^{-1} (*4*).

Mangroves grow in sheltered intertidal environments that are exposed to the effects of RSLR (*5*). They support among the highest rates of carbon burial of all ecosystems (*6*), and a growing body of evidence suggests that this efficiency is enhanced by RSLR (*7*). However, empirical data on mangrove response to high rates of RSLR are lacking, given the limited observation period (1 to 16 years) of real-time measurements (*5*).

Here, we assess the mangrove response to RSLR from the paleorecord of mangrove vertical accretion preserved in the sedimentary archives of continental shelves and coastal lowlands. Mangrove forests have established and drowned in association with variability in the rate of RSLR after the onset of deglaciation ~26,000 to 20,000 years ago (*8*). Before the Holocene, long-term RSLR rates of >12 mm year^{-1} (*8*) exceeded the capacity of mangroves to maintain position in situ through vertical accretion, and mangroves were displaced landward (*9*), with few exceptions (*10*, *11*). During the early to mid-Holocene, RSLR slowed in association with the final phase of deglaciation of the Laurentide ice sheet (*12*). The rate of RSLR varied across the globe owing to glacio-isostatic adjustment, the response of the solid Earth and gravity field to ice mass redistribution during a glacial cycle (*13*). Far-field sites, those distal from regions of former ice sheet extent and incorporating most of the tropics, exhibit a decline in the rate of RSLR (*14*) from 10,000 to 7000 years ago (phase 1 in Fig. 1A) to a mid-Holocene highstand, followed by stable or falling sea level to near the current position from ~6000 years ago to the present (phase 2 in Fig. 1A). By contrast, at intermediate-field sites closer to centers of glaciation (for example, the Gulf of Mexico and the Caribbean), sea level rose continuously throughout the Holocene owing to isostatic response to melting of the Laurentide ice sheet. These coastlines have experienced a decelerating rate of RSLR from 10,000 years ago to the present (Fig. 1B and figs. S5 and S6).

The spatially variable deceleration of RSLR from 10,000 to 8000 years ago across tropical and subtropical latitudes coincided with the initiation of vertically continuous, organic-rich mangrove sediments several meters thick, as rising seas flooded shallow continental shelves (phase 1 in Fig. 1, A and B) (*15*). This deceleration provides an opportunity to explore whether (i) the rate of mangrove vertical accretion responds to changes in RSLR; (ii) ice sheet proximity (intermediate versus far field), geomorphic setting, or tidal range constrains the capacity of mangroves to accrete in relation to RSLR; (iii) upper thresholds of mangrove vertical accretion can be detected; and (iv) mangrove development and vertical accretion correspond in timing to changes in the global atmospheric carbon budget.

We present empirical data from 122 reconstructions of the timing and rate of mangrove vertical accretion associated with Holocene RSLR in cores collected from 78 tropical and subtropical locations [Fig. 2; (*14*)]. We independently estimate rates of RSLR for each of the 78 locations before and for the duration of mangrove vertical accretion from a glacio-isostatic adjustment model using an ensemble of different Earth parameters (*16*) (Fig. 3 and figs. S5 and S6).

Slowing RSLR during the early to mid-Holocene coincided with the initiation of extensive mangrove forests (Figs. 1A, phase 1, and 3, A and B). Our analysis suggests that sustained mangrove vertical accretion began across far-field regions (Africa, Asia, Australasia, and South America) at ~10,000 to 8000 years ago and intermediate-field regions (Caribbean and Gulf of Mexico) at ~8000 to 6000 years ago (Fig. 3 and figs. S1 and S2). Data were discriminated on the basis of ice sheet proximity and geomorphic setting and differentiated by tidal regime to explore differences in the timing of initiation and rates of vertical accretion (*14*). The intermediate- and far-field classifications, defined as a function of a location's proximity to areas of major ice sheet retreat during the last deglaciation, act as a surrogate variable for the temporal pattern of RSLR rates through the Holocene, which in turn influences the availability of accommodation space within which mangroves can accrete vertically. In a generalized linear model of several variables, only the proximity to former ice sheets proved to have a significant relationship with accretion rates (*14*).

We found a strong relationship ($p < 0.001$, generalized linear model) between rates of mangrove vertical accretion and RSLR rate across all sites (51% of the variation in the accretion rate can be explained by the RSLR variation; Fig. 3). Mangrove vertical accretion first initiated ~9800 years ago in the Ganges-Brahmaputra River Delta, as RSLR decreased from ~9 to ~6 mm year^{-1}, and continued for ~650 years at high rates until replaced by subtidal deposits as RSLR increased again to >7 mm year^{-1} (*14*, *17*). Elsewhere in far-field locations, mangrove vertical accretion initiated as RSLR decreased below ~7 mm year^{-1} starting 8800 years ago (Fig. 3). Rates of vertical accretion of >6 mm year^{-1} were sustained for more than 1000 years in mangrove forests in Australia, Africa, South America, Central America, and Asia (Fig. 2 and data S1), irrespective of geomorphic setting (fig. S1).

Mangrove vertical accretion initiated in intermediate-field regions later than in far-field locations, first in Belize ~7800 years ago as

[1]Department of Earth and Environmental Sciences, Macquarie University, Macquarie Park, NSW, Australia. [2]Department of Earth Sciences, University of Hong Kong, Hong Kong, China. [3]Swire Institute of Marine Science, University of Hong Kong, Hong Kong, China. [4]Department of Earth and Planetary Sciences, Rutgers University, Piscataway NJ, USA. [5]School of Earth, Atmospheric, and Life Sciences, University of Wollongong, Wollongong, NSW, Australia. [6]Geoquest Research Centre, University of Wollongong, Wollongong, NSW, Australia. [7]Asian School of Environment, Nanyang Technological University, Singapore. [8]Earth Observatory of Singapore, Nanyang Technological University, Singapore.
*Corresponding author. Email: neil.saintilan@mq.edu.au

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

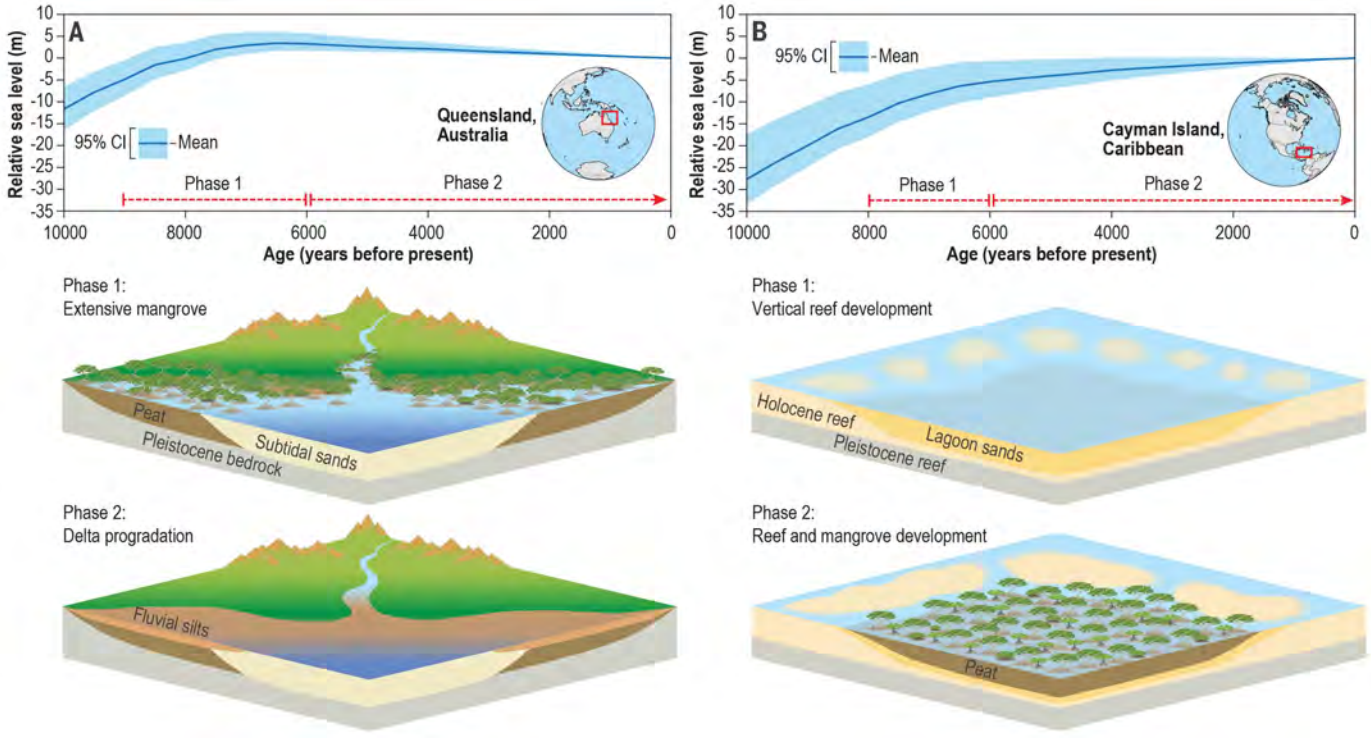
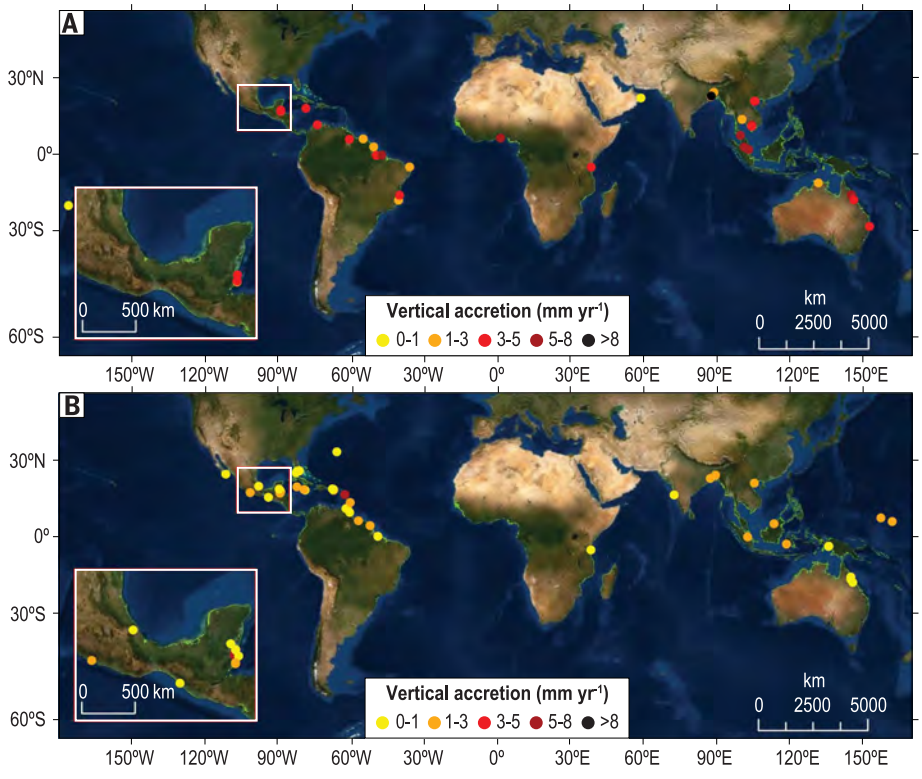


Fig. 1. Holocene RSLR and associated mangrove development in far-field estuarine and intermediate-field calcareous settings. (**A**) Far-field estuarine settings. (**B**) Intermediate-field calcareous settings. As the rate of RSLR decelerated, development of organic-rich mangrove sediments was initiated, which facilitated maintenance of vertical position with respect to sea level, forming extensive mangrove forests. When RSLR stabilizes, ongoing sedimentation infills estuaries, building deltas and replacing mangrove with freshwater wetlands, terrestrial forest, or saltpan, depending on climatic setting. CI, credible interval.

Fig. 2. Sampling locations and corresponding rates of mangrove vertical accretion. (**A** and **B**) Mangrove sedimentary units initiating between 10,000 and 6500 years ago (A) and mangrove sedimentary units initiating after 6500 years ago (B). Contemporary mangrove shorelines are indicated in bright green, representing mangrove distribution in 2012 (*30*).



Downloaded from https://www.science.org at Macquarie University on June 23, 2024

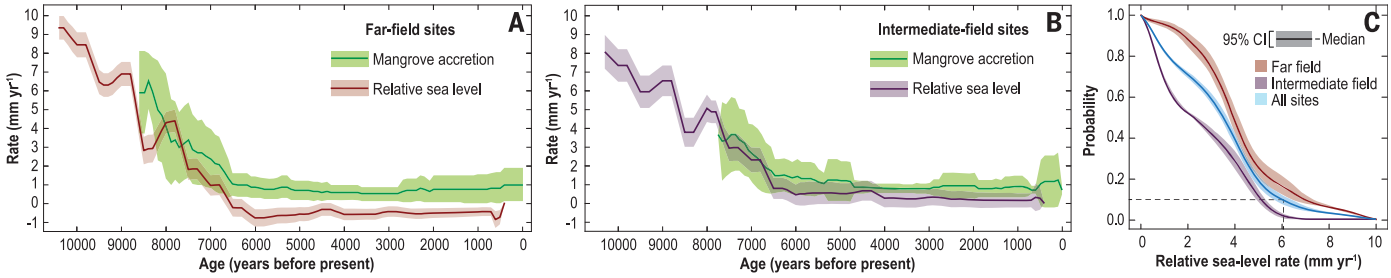


Fig. 3. Rates of mangrove vertical accretion and RSLR. (**A** and **B**) Accretion rates are derived from the depth of mangrove organic sediment between calibrated ^{14}C dates in individual cores, and rates of RSLR (median and 95% CI) were derived from the glacio-isostatic adjustment (GIA) model ensemble for the same sites for far-field (A) and intermediate-field (B) locations. (**C**) The probability of initiation of sustained mangrove accretion at or above associated rates of RSLR across all sites. The dotted line shows the RSLR rate at which there is a 10% probability that mangroves can initiate accretion and/or, conversely, that there is a 90% probability that they are unable to initiate accretion.

Table 1. Probability that mangroves are unable to initiate sustained vertical accretion at rates of RSLR. See (*14*). RSLR rates at all sites (global) and intermediate- and far-field sites at which it is very likely (>90% probability) and extremely likely (>95% probability) that mangroves are unable to initiate sustained accretion and the associated 95% uncertainty interval (UI). For example, at all sites, there is a 94.3 to 95.4% probability (95% UI) that mangroves are unable to initiate at rates that exceed 7.6 mm year^{-1}.

Sites	RSLR rates above which accretion did not initiate (very likely: 90% median probability)		RSLR rates above which accretion did not initiate (extremely likely: 95% median probability)	
	RSLR rate (mm year^{-1})	Uncertainty interval (%)	RSLR rate (mm year^{-1})	Uncertainty interval (%)
Global	6.1	(88.1–92.8)	7.6	(94.3–95.4)
Intermediate-field (Gulf of Mexico, Caribbean)	5.2	(88.1–92.8)	5.7	(93.7–96.9)
Far-field	7.1	(87.3–91.6)	8.8	(94.4–95.8)

RSLR fell below ~5 mm year^{-1} and in other Caribbean and Gulf of Mexico sites between 7500 and 6000 years ago (Figs. 2 and 3 and table S1). This later initiation, in comparison to far-field regions, may be related to the limited allochthonous sediment supply available in the carbonate (reef) settings, although in Belize, rates of accretion of more than 6 mm year^{-1} were observed at two sites (data S1), driven by strong authochthonous inputs.

We used a Bayesian framework to estimate the probability of initiation of mangrove accretion conditional on rates of RSLR within the Holocene dataset (*14*). The empirical Holocene data (data S1), which span a wide range of geomorphic settings and tidal regimes (fig. S2), suggest that when RSLR rates exceed 6.1 and 7.6 mm year^{-1}, respectively, mangroves are very likely (>90% probability) and extremely likely (>95% probability) to be unable to initiate sustained accretion. We found lower RSLR thresholds for intermediate-field sites and higher thresholds for far-field sites (Table 1).

Our database also reveals spatial variability in the duration of mangrove accretion (figs. S1 and S2). In only 3 of 50 far-field locations was there indication of drowning of mangroves during a marine transgression (i.e., mangrove sediments overlain by tidal or subtidal deposits; data S1). In most far-field locations (30 of 50), accretion and progradation of the fluvial delta led to the replacement of mangrove by saltmarsh (characteristic of upper intertidal elevations), freshwater wetland, or terrestrial forest, often by the mid-Holocene when relative sea level stabilized (phase 2 in Fig. 1A and data S1). For this reason, contemporary mangrove extent is highly contracted compared with the early- and mid-Holocene mangrove development in many major river deltas such as the Ord River, Australia; the Red River, Vietnam; and the Mekong River, Vietnam and Cambodia (*15*, *18*–*20*). Mangrove accretion persisted significantly longer at intermediate-field locations (fig. S2) because accommodation space was enhanced by glacio-isostatic adjustment.

The extensive development of mangrove environments under RSLR has exerted an influence on global carbon cycles over geologic time scales (*21*), including, we suggest, during the early to mid-Holocene (Fig. 4). Carbon balance modeling based on stable carbon isotope signatures suggests that the 5 parts per million by volume reduction in atmospheric CO_2 in the early Holocene was driven by increases in the uptake of carbon by the land biosphere on the order of 290 Pg C (*22*, *23*) before 7000 years ago. The timing and volume of this uptake have been attributed to the northward expansion of boreal vegetation after ice sheet retreat [~110 Pg C (*24*)] and organic soil development [180 Pg C (*23*)], of which circum-Arctic peatlands may have sequestered 20 to 60 Pg C based on the depth of peat formation at the time (*24*). We conservatively estimate a somewhat larger contribution (~85 Pg C) from mangrove carbon sequestration and burial over the period 8600 to 6000 years ago (*14*). The extensive development of mangrove forests over this period largely replaced methanogenic environments {freshwater wetlands and floodplains [data S1; (*25*)]} and corresponds to declining rates of methane emission, particularly in the Southern Hemisphere (*26*). The $\delta^{13}CH_4$ signals in the Southern Hemisphere for this period show a 1.5 per mil depletion consistent with a replacement of vegetation using the C_4 photosynthetic pathway (tropical grasslands and saltmarsh adapted to low atmospheric CO_2), with mangroves using the C_3 pathway (*26*, *27*).

As RSLR increases in the 21st century, an increase in the rate of mangrove vertical accretion, coupled with landward expansion as sea level rises, can be expected to drive increases in the rate of carbon sequestration and preservation in mangrove environments, providing a negative feedback on radiative forcing, as suggested more broadly for coastal wetlands (*7*). Although

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

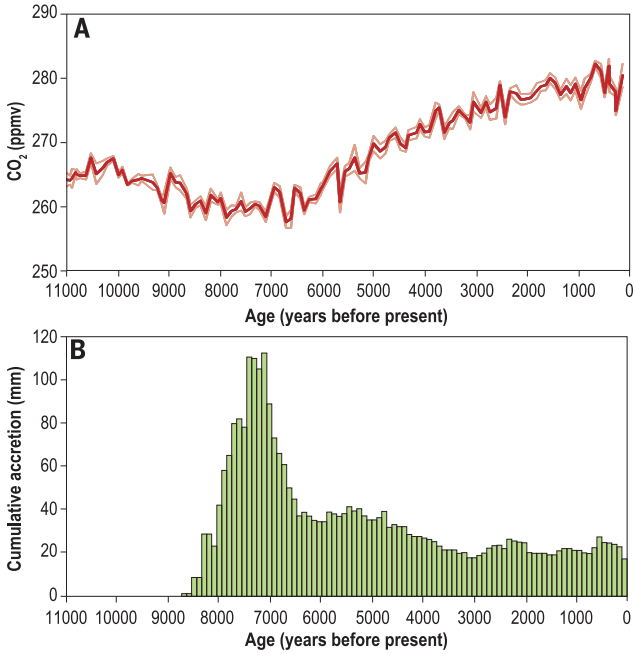


Fig. 4. Timing of mangrove vertical accretion in relation to greenhouse gas concentrations. (**A** and **B**) Atmospheric CO_2 concentrations [from Antarctic ice cores (*23*)] (A) and mangrove organic soil formation (B) [the sum of all observations spanning each century weighted by the vertical accretion rate of each observation (*14*)]. Light colored curves in (A) represent ± 1 standard error for CO_2 (B), as presented in the original datasets. ppmv, parts per million by volume.

our results demonstrate that accretion in mangroves increases in response to RSLR, we found that it was very likely (>90% probability) that mangroves were unable to initiate sustained accretion when RSLR rates exceeded 6.1 mm $year^{-1}$ in any but the most sediment-laden settings. RSLR is projected to remain below 5 mm $year^{-1}$ under low-emissions scenarios [Representative Concentration Pathway (RCP) 2.6] throughout the 21st century (*1*). However, RSLR is expected to exceed 5 mm $year^{-1}$ by 2030 and 7 mm $year^{-1}$ by 2050 under high-emissions scenario RCP8.5 in low-latitude mangrove settings where rates of RSLR are expected to be higher than the global average (*1*, *2*).

Where a deficit commences between vertical accretion and RSLR, time to submergence will be a function of the position of the mangrove within the tidal frame. In settings of low tidal range, mangroves are more likely to be situated at elevations close to the threshold of submergence from the outset. In settings of high tidal range, mangroves are more likely to be situated at elevations well above this threshold and tolerate a deficit between the rates of accretion and RSLR for decades to centuries (*5*). Geomorphic setting will also influence vulnerability to submergence, because allochthonous sediment contributions in tide- and river-dominated estuaries may provide an elevation subsidy not available in environments receiving low sediment supply, such as coral reefs. In this context, sediment retention in catchments affected by water resource development (i.e., trapped behind dams) and local sediment controls may decrease mangrove resilience to RSLR in river estuaries (*5*). The natural response of mangrove encroachment across flooded coastal lowlands is therefore the main determinant of future extent (*28*), although this is already greatly impeded by coastal developments along many coastlines (*29*). Our findings therefore emphasize the importance of (i) mitigating the magnitude of rapid RSLR and (ii) ensuring that coastal adaptation measures allow for the expansion of mangrove across coastal lowlands.

REFERENCES AND NOTES

1. J. A. Church *et al.*, in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T. F. Stocker *et al.*, Eds. (Cambridge Univ. Press, 2013), chap. 13.
2. R. E. Kopp *et al.*, *Earths Futur.* **2**, 383–406 (2014).
3. M. L. Kirwan, S. Temmerman, E. E. Skeehan, G. R. Guntenspergen, S. Fagherazzi, *Nat. Clim. Chang.* **6**, 253–260 (2016).
4. B. P. Horton *et al.*, *Nat. Commun.* **9**, 2687 (2018).
5. C. E. Lovelock *et al.*, *Nature* **526**, 559–563 (2015).
6. D. C. Donato *et al.*, *Nat. Geosci.* **4**, 293–297 (2011).
7. K. Rogers *et al.*, *Nature* **567**, 91–95 (2019).
8. K. Lambeck, H. Rouby, A. Purcell, Y. Sun, M. Sambridge, *Proc. Natl. Acad. Sci. U.S.A.* **111**, 15296–15303 (2014).
9. C. D. Woodroffe, *Mar. Freshw. Res.* **69**, 917–932 (2018).
10. T. J. Hanebuth, H. K. Voris, Y. Yokoyama, Y. Saito, J. I. Okuno, *Earth Sci. Rev.* **104**, 92–110 (2011).
11. W. A. Nicholas *et al.*, *Cont. Shelf Res.* **83**, 129–142 (2014).
12. N. S. Khan *et al.*, *Curr. Clim. Change Rep.* **1**, 247–262 (2015).
13. W. E. Farrell, J. A. Clark, *Geophys. J. Int.* **46**, 647–667 (1976).
14. Materials and methods are available as supplementary materials.
15. C. D. Woodroffe, B. G. Thom, J. Chappell, *Nature* **317**, 711–713 (1985).
16. S. Dendy, J. Austermann, J. R. Creveling, J. X. Mitrovica, *Quat. Sci. Rev.* **171**, 234–244 (2017).
17. T. E. Törnqvist, N. P. Hijma, *Nat. Geosci.* **5**, 601–606 (2012).
18. B. G. Thom, L. D. Wright, J. M. Coleman, *J. Ecol.* **63**, 203–232 (1975).
19. S. A. Woodroffe, B. P. Horton, *J. Asian Earth Sci.* **25**, 29–43 (2005).
20. S. Tanabe, K. Hori, Y. Saito, S. Haruyama, A. Kitamura, *Quat. Sci. Rev.* **22**, 2345–2361 (2003).
21. D. S. Collins *et al.*, *Nat. Commun.* **8**, 15698 (2017).
22. A. Indermühle *et al.*, *Nature* **398**, 121–126 (1999).
23. J. Elsig *et al.*, *Nature* **461**, 507–510 (2009).
24. G. M. Macdonald *et al.*, *Science* **314**, 285–288 (2006).
25. H. J. Poffenbarger, B. A. Needelman, J. P. Megonigal, *Wetlands* **31**, 831–842 (2011).
26. J. Beck *et al.*, *Biogeosciences* **15**, 7155–7175 (2018).
27. T. Sowers, *Quat. Sci. Rev.* **29**, 213–221 (2010).
28. M. Schuerch *et al.*, *Nature* **561**, 231–234 (2018).
29. L. K. Phan, J. S. van Thiel de Vries, M. J. Stive. *J. Coast. Res.* **31**, 233–243 (2014).

ACKNOWLEDGMENTS

We thank J. Mitrovica of Harvard University for providing the GIA model. T. A. Shaw of Nanyang Technology University assisted with the preparation of the figures. Figure 1 used the image library of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/). **Funding:** N.S. was supported by an Outside Studies Program grant from Macquarie University and AINSE. B.P.H. is supported by the Singapore Ministry of Education Academic Research Fund MOE2018-T2-1-030, the National Research Foundation Singapore, and the Singapore Ministry of Education, under the Research Centers of Excellence initiative. This article is a contribution to PALSEA2 (Palaeo-Constraints on Sea-Level Rise), a working group of the International Union for Quaternary Sciences (INQUA), and International Geoscience Program (IGCP) Project 639, "Sea-Level Changes from Minutes to Millennia." This work is Earth Observatory of Singapore contribution 294. K.R. received funding from the Australian Research Council (FT130100532). **Author contributions:** N.S. conceived the study. N.S., N.S.K., and B.P.H. assembled the contributing mangrove sediment data. E.A. extracted RSLR estimates from GIA models. N.S., E.A., and J.J.K. conducted data analyses. N.S., N.S.K., E.A., and K.R. prepared the figures. All authors contributed to the writing of the manuscript. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data are available in the main text or the supplementary materials.

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/368/6495/1118/suppl/DC1
Materials and Methods
Figs. S1 to S6
Tables S1 to S2
References (*30*–*124*)
MDAR Reproducibility Checklist
Data S1

18 November 2019; accepted 16 April 2020
10.1126/science.aba2656

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

ANNUAL REVIEWS Further
Click here to view this article's online features:
- Download figures as PPT slides
- Navigate linked references
- Download citations
- Explore related articles
- Search keywords

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Mangrove Sedimentation and Response to Relative Sea-Level Rise

C.D. Woodroffe,[1] K. Rogers,[1] K.L. McKee,[2] C.E. Lovelock,[3] I.A. Mendelssohn,[4] and N. Saintilan[5]

[1]School of Earth and Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia; email: colin@uow.edu.au, kerrylee@uow.edu.au

[2]National Wetlands Research Center, US Geological Survey, Lafayette, Louisiana 70506; email: mckeek@usgs.gov

[3]Centre for Marine Studies and School of Biological Sciences, University of Queensland, St. Lucia, Queensland 4072, Australia; email: c.lovelock@uq.edu.au

[4]Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana 70803; email: imendel@lsu.edu

[5]Department of Environmental Sciences, Macquarie University, North Ryde, New South Wales 2109, Australia; email: neil.saintilan@mq.edu.au

Annu. Rev. Mar. Sci. 2016. 8:243–66

First published online as a Review in Advance on September 25, 2015

The *Annual Review of Marine Science* is online at marine.annualreviews.org

This article's doi: 10.1146/annurev-marine-122414-034025

Copyright © 2016 by Annual Reviews. All rights reserved

*A visual abstract of this article is also available online at **http://prezi.com/dtfasu6khdti** and as **Supplemental Material.**

Keywords

mangrove ecosystems, sea-level rise, sediment accumulation, hydrodynamics, carbon sequestration

Abstract

Mangroves occur on upper intertidal shorelines in the tropics and subtropics. Complex hydrodynamic and salinity conditions, related primarily to elevation and hydroperiod, influence mangrove distributions; this review considers how these distributions change over time. Accumulation rates of allochthonous and autochthonous sediment, both inorganic and organic, vary between and within different settings. Abundant terrigenous sediment can form dynamic mudbanks, and tides redistribute sediment, contrasting with mangrove peat in sediment-starved carbonate settings. Sediments underlying mangroves sequester carbon but also contain paleoenvironmental records of adjustments to past sea-level changes. Radiometric dating indicates long-term sedimentation, whereas measurements made using surface elevation tables and marker horizons provide shorter perspectives, indicating shallow subsurface processes of root growth and substrate autocompaction. Many tropical deltas also experience deep subsidence, which augments relative sea-level rise. The persistence of mangroves implies an ability to cope with moderately high rates of relative sea-level rise. However, many human pressures threaten mangroves, resulting in a continuing decline in their extent throughout the tropics.*

Supplemental Material

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

INTRODUCTION

Halophyte: a plant that is able to tolerate salinity; all mangrove species are halophytes

Tidal frame: the vertical range over which the tide varies at a site, generally between the lowest and highest astronomical tide

Accommodation space: the space within which mangrove sediments may accumulate (see **Figure 2**, below)

Accretion: short-term vertical aggradation of sediment; where surface elevation table–marker horizon instruments are deployed, accretion is measured relative to the marker horizon

Subsidence: the net movement of a land surface; deep subsidence includes tectonic, hydro-isostatic, and flexural geological processes, often exacerbated by groundwater extraction, and shallow subsidence includes subsurface autocompaction (see also Subsidence and Relative Sea-Level Rise sidebar, below)

Coastal squeeze: a loss of intertidal habitat arising when biota encounter solid structures as they attempt to extend landward following an increase in sea level

Mangroves comprise trees and shrubs that colonize upper intertidal shorelines along tropical and subtropical coasts. These halophytes have morphological, physiological, and reproductive adaptations in common that enable growth in saline and anoxic conditions. Worldwide, mangroves occupy $\sim 1.5 \times 10^5$ km^2, with several species extending into temperate latitudes (Spalding et al. 2010, Giri et al. 2011). Some mangroves grow along open coasts subject to moderate wave processes; however, most occur in more sheltered, muddy locations that are either frequently or occasionally inundated by tides.

Many mangrove forests fringe coastal plains, comprising estuarine, deltaic, and other depositional landforms. Mangroves are generally limited to a narrow elevation range within the tidal frame (McKee et al. 2012). The extent of such suitable intertidal habitats, referred to as accommodation space, is a function of the stage, or maturity and geomorphological complexity, of these larger depositional systems. The distribution of mangroves on a shoreline changes with time, involving subtle balances between accretion and subsidence, erosion and vegetative stabilization, productivity and decomposition, and tidal flushing and drainage efficiency (FitzGerald et al. 2008).

Dense mangrove forests contain substantial aboveground biomass, and belowground stores of organic matter are often even more substantial (Twilley et al. 1992, Donato et al. 2011, McLeod et al. 2011, Lovelock et al. 2014). Carbon that is sequestered by mangroves, known as blue carbon, has become a focus of attention because of its potential for climate-change mitigation (Breithaupt et al. 2012, Pendleton et al. 2012, Siikamaki et al. 2012, Duarte et al. 2013, Alongi 2014). Donato et al. (2011) measured above- and belowground carbon stores in tropical mangroves across the Indo-Pacific region and found that belowground carbon accounted on average for 1,074 (±171) Mg C ha^{-1} of carbon storage in estuarine settings and 990 (±96) Mg C ha^{-1} in oceanic-island settings.

Observed and anticipated future rates of sea-level rise (SLR) are likely to have far-reaching impacts on mangrove forests, raising concerns that such wetlands are vulnerable to drowning and coastal squeeze (Phan et al. 2015). However, measured sediment accumulation rates beneath subtropical mangrove forests have shown rapid accretion, in many cases more rapid than the rate of SLR (Krauss et al. 2014). It has become apparent, particularly through use of surface elevation-change methodologies developed in herbaceous wetlands, that subsurface processes play a much more important role than was hitherto realized. This role includes subsurface movements (e.g., subsidence caused by autocompaction, or expansion caused by root growth) that combine with sediment accretion on the surface to drive elevation change. At broader regional scales, many low-lying delta environments are subsiding through geological processes, exacerbated by anthropogenic activities such as groundwater extraction (Syvitski et al. 2009, Erban et al. 2014), which augment the relative rate of SLR. Land movement in combination with the increase in ocean height, termed relative SLR (Cahoon 2014), creates accommodation space for future deposition of sediment and organic matter beneath mangroves.

This review focuses on sediment accumulation rates beneath mangrove forests and the hydrodynamic conditions that affect them. It concludes that there is insufficient understanding of nonlinear feedbacks to realistically forecast or model the future behavior of most mangrove shorelines.

ENVIRONMENTAL SETTINGS

Investigations of mangrove habitat and ecosystem functioning need to discriminate among the different environmental settings in which mangrove stands can occur. For instance, on relatively sheltered open coasts, some locations may have a narrow mangrove fringe, often comprising several species of mangroves growing in shore-parallel zones. This pattern contrasts with locations

where mangrove forests form complex mosaics, such as sediment-rich deltas, along the flanks of estuarine channels within embayments, or behind spits and other sandy barriers (Thom 1982, Woodroffe 1992). A particular geomorphological setting may contain a range of hydrodynamic conditions, sediment fluxes, and organic and geochemical characteristics of the substrate, all of which influence the growth of mangroves. Sediments that have accumulated also record aspects of geomorphological history and longer-term dynamics.

An early attempt at ecological classification of mangroves, developed in the Caribbean, differentiated fringe, basin, overwash, scrub, and riverine mangroves (Lugo & Snedaker 1974). This hydrogeomorphic scheme, also called ecomorphodynamics, combines aspects of mangrove growth forms and hydrodynamics (Twilley & Rivera-Monroy 2005, 2009). It was developed to address functional differences between stands of *Rhizophora mangle* that are regularly and effectively flushed by tides and basin mangroves that are flooded seasonally or by only the highest tides, favoring accumulation of mangrove-derived organic carbon (Twilley 1985).

Figure 1 illustrates several geomorphological settings in which mangrove forests occur and summarizes schematically some gross stratigraphic relationships from which long-term sedimentation patterns can be reconstructed. The four examples—delta, estuary, lagoon, and carbonate reef environments—do not represent all settings within which mangroves are found, but serve to focus on several contrasting aspects.

Autocompaction: shallow subsidence of sediments under their own weight; this process includes consolidation, compression, and loss of organic matter

Progradation: lateral extension of the shoreline, characterized by mangrove establishment as a consequence of sediment accretion in the lower intertidal zone

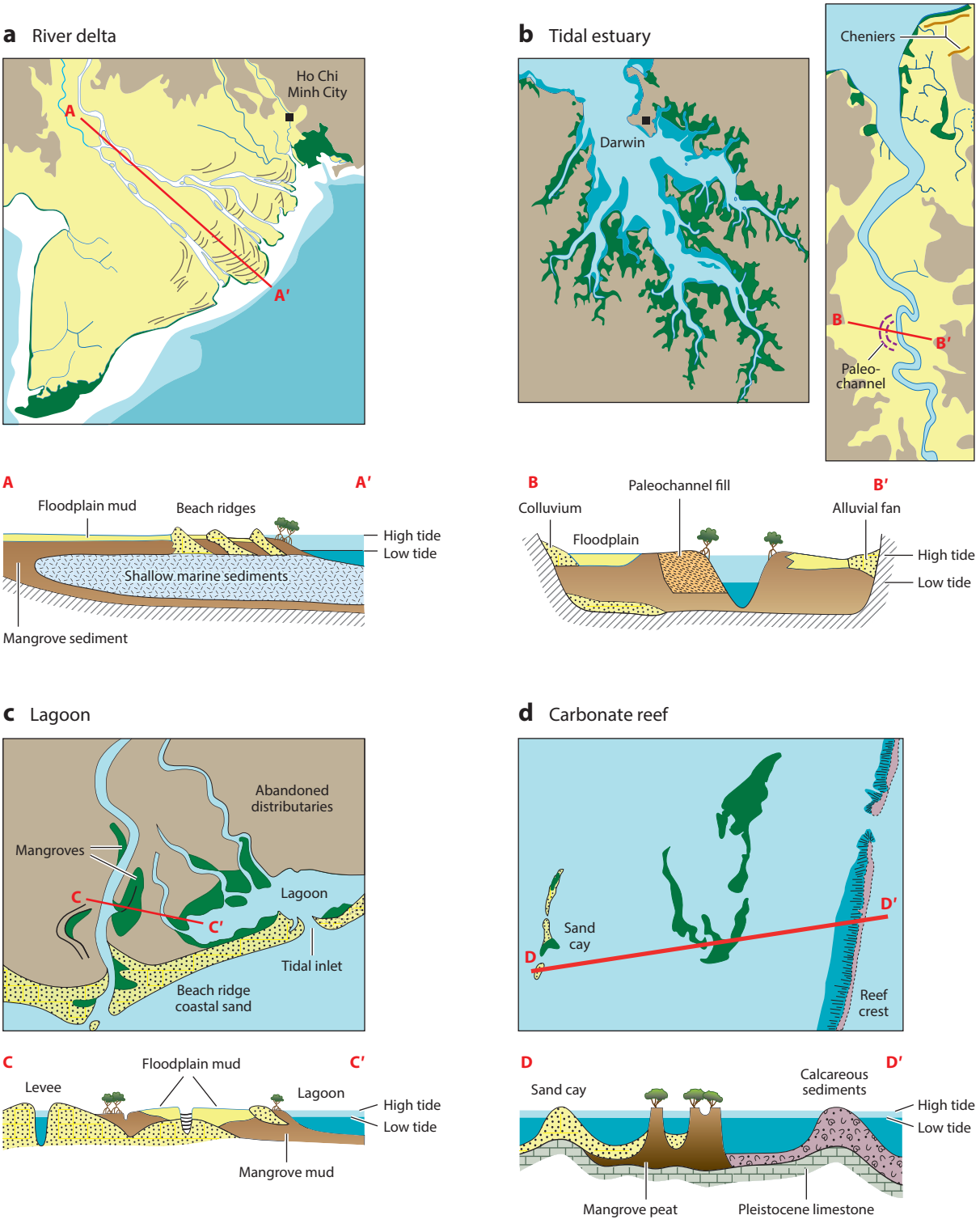
Deltas

Figure 1*a* shows a schematic representation of the Mekong River Delta, one of several Asian megadeltas fed by large rivers draining from the monsoonal Himalayan massif. The Mekong River, which has peak flows of ~50,000 $m^3\ s^{-1}$ and an estimated annual sediment load of 160 million tonnes, discharges sediment via many distributaries into the South China Sea. During periods of particularly rapid postglacial SLR, mangrove forests were drowned or displaced landward, as shown by peats recovered from cores on the Sunda Shelf (Hanebuth et al. 2011). The final stages are recorded in the Mekong River Delta by basal transgressive sediments overlying Pleistocene basement, culminating in a period of abrupt SLR approximately 8,200 years ago. At the apex of the modern delta, a vertical sequence of mangrove sediments in southern Cambodia indicates the persistence of mangrove forests during this period (Tamura et al. 2009, Li et al. 2012). Since then, the delta has gradually built more than 200 km southward to form the modern coast. Mangrove organic matter in cores extracted from across the deltaic plain indicates the persistence of mangrove ecosystems as the shoreline prograded (Ta et al. 2002, Proske et al. 2010).

The interaction of tidal, wave, and riverine hydrodynamic processes is apparent in the Mekong River Delta and is also typical of other large deltas. The effects on sedimentation and on the distribution of mangroves around the delta are also clear, although there has been severe degradation associated with human impacts such as reclamation and defoliation (Phan & Hoang 1993). Tides are semidiurnal along the southeastern margin of the delta, with a range of >3 m, reaching a maximum of 4 m near Ho Chi Minh City, where there are extensive tide-dominated mangrove forests. Mangroves on the adjacent open coast are exposed to wave energy (Bao 2011), which has periodically built sandy beach ridges. A sequence of stranded ridges across the southern delta indicates that this section of the delta has been wave dominated for at least the past 3,000 years (Tamura et al. 2012). Sediment from the river mouth is carried southwestward along the coast, with rapid progradation of the Ca Mau Peninsula and establishment of mangrove forests over the accreting mudbanks. Tides are diurnal in the Gulf of Thailand, with a range of 1–1.5 m, and this coast receives much less sediment.

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.



Estuaries

Northern Australia has a series of macrotidal estuaries along its northern and northwestern coasts (**Figure 1*b***). The stratigraphy of the underlying sediments is broadly similar to that beneath southeast Asian deltas, comprising transgressive, basal, organic-rich mangrove muds overlain by more marine muddy sands, which record the landward retreat of mangroves during the final stages of postglacial SLR. Extensive mangrove forest development took place after the sea level stabilized at its modern level approximately 7,000 years ago, a period described as the "big swamp" phase (Woodroffe et al. 1993). Sediment accretion led to the demise and gradual replacement of these mangrove forests by alluvial floodplains. Pollen analysis during this regressive phase indicates that *Sonneratia* was replaced by *Rhizophora* and then by *Avicennia*, culminating in grass and sedgeland, which characterizes modern plains flanking these estuaries. This vertical core sequence mirrors the horizontal plant zonation from midtide to the highest tidal level on the modern shore and in larger embayments such as Darwin Harbor.

Whereas this sequence is typical of the open coast, the largely infilled estuaries have a series of mangrove environments upstream, several of which are illustrated schematically in **Figure 2**. Backwater swamps lie below the elevation reached by high tides at the coast (Wolanski & Chappell 1996), and saline intrusion and tidal creek extension have been observed on many estuarine plains with landward extension of mangroves (Mulrennan & Woodroffe 1998, Winn et al. 2006, Cobb et al. 2007, Eliot & Eliot 2012).

Lagoonal Environments

Figure 1*c* represents a sandy barrier on a wave-exposed coast with mangroves established in a sheltered back-barrier lagoon. This example is based on the Grijalva River Delta in Tabasco, Mexico, where delta distributary channels have undergone periodic switching and have built levees. Sedimentation and subsidence determine suitable environments for mangrove growth. Mangrove forests flourish in several geomorphological environments; there are tidally flushed mangroves on accreting mudflats, which contrast with interdistributary basins that receive little inorganic sediment and have accumulated thicknesses of mangrove peat (Thom 1967). Mangroves occur in back-barrier settings like this on many other sandy, wave-dominated coasts (López-Medellin et al. 2011).

Sediment-Starved Reef Environments

In carbonate settings, mangroves have accumulated peat in the absence of a supply of terrestrial sediment. The example in **Figure 1*d*** schematically represents overwash mangrove islands, locally termed mangrove ranges, on the Belize Barrier Reef. Peat thicknesses of 10 m or more indicate that mangroves have persisted on these islands as sea level rose at a decelerating rate over the past 8,000 years (Toscano & Macintyre 2003, Macintyre et al. 2004, McKee et al. 2007). Mangrove peats are buried beneath calcareous sands in the lagoons on the Belize Barrier Reef, indicating that not all mangroves kept pace with the rising sea (Macintyre et al. 2004) and that the present

Figure 1

Examples of mangrove settings, showing the distribution of modern mangroves and schematic stratigraphy indicating past changes in mangrove distribution. (*a*) A river delta, based on the Mekong River Delta. (*b*) Two types of tidal estuary, based on Darwin Harbor and the Alligator Rivers region in northern Australia. (*c*) A lagoon, based on Grijalva River Delta in Tabasco, Mexico. (*d*) A carbonate reef, based on the Belize Barrier Reef.

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

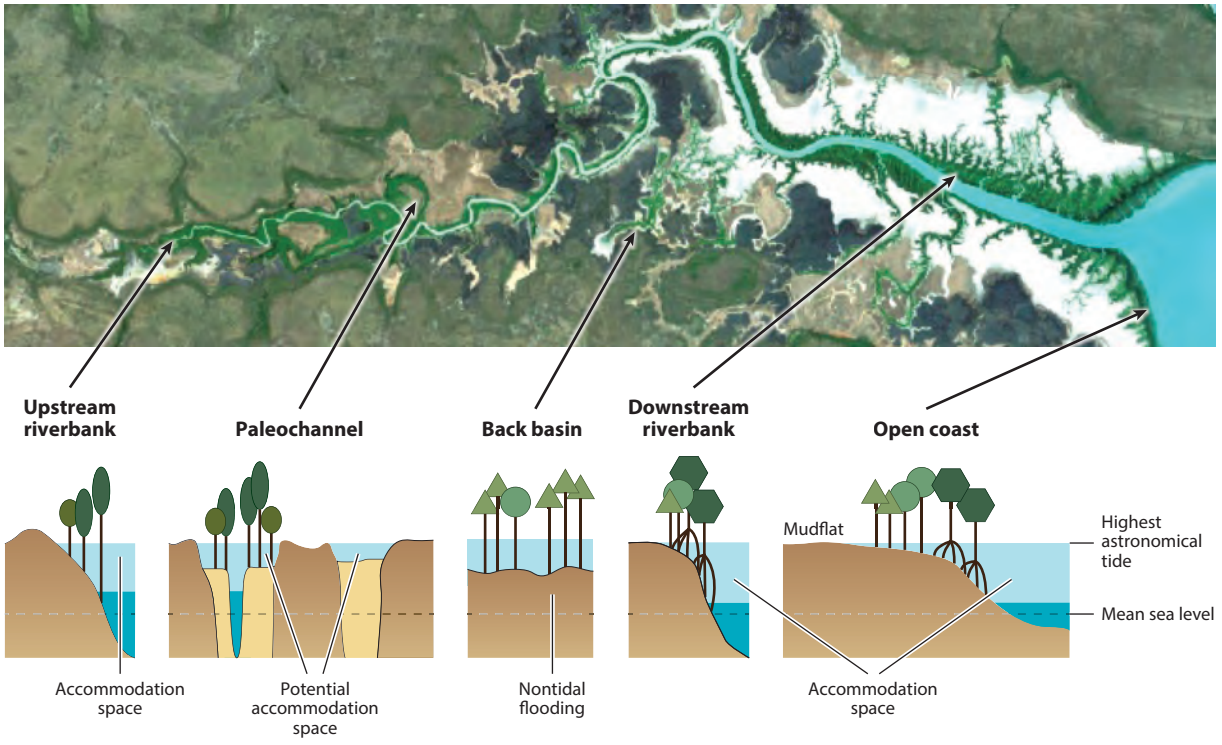


Figure 2

Hydrodynamics and accommodation space. On the open coast, mangrove forests often show a zonation of species, with a few pioneer species able to establish on sediments that have accreted to an elevation close to mean sea level, and species less tolerant of inundation occurring landward and higher in the tidal frame. More complex hydrodynamic settings occur farther upstream in deltaic-estuarine systems, illustrated schematically in this example from the Alligator Rivers in northern Australia. *Rhizophora* species (appearing as *dark green*) are flooded by most tides but are replaced by other species up to the highest astronomical tide level, beyond which are saline mudflats. Tidal flows become increasingly distorted upstream along the estuarine funnel, and other mangroves occupy a contracted accommodation space on the riverbanks near the tidal limit. Mangroves also occur away from the tidal river estuary itself within seasonally flooded basins. Low-lying areas within the extensive adjacent floodplains, particularly incompletely infilled paleochannels, lie below the highest elevation at which mangroves can grow and represent potential accommodation space. This area can be colonized by mangroves if a tidal connection is reestablished, as in the case of the abandoned paleochannel meander in this example. Landsat image © 2009 Commonwealth of Australia (Geoscience Australia).

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

islands are erosional remnants. Even within these relatively simple mangrove environments, there are geographical variations in mangrove composition and structure in island interiors. Variations also occur in rates of elevation change and surface accretion observed in different habitats (McKee 2011). Similar peats underlie wetlands in other microtidal reef settings and in southwestern Florida, where mangroves have gradually extended landward into the freshwater Everglades as the sea level has risen (Woodroffe et al. 2014).

MORPHODYNAMICS AND SCALE

Figure 3 provides a framework, across several scales, within which to consider mangrove ecosystems. At the broadest geomorphological macroscale, involving entire deltas or estuaries, climate and relative sea-level change influence the system. Climate determines the intertidal

floristic composition (mangrove, salt marsh, or algal mat), influences the delivery of sediment to the coast, and dictates the nature of adjacent terrestrial ecosystems, which are likely to replace mangrove vegetation over time. Intertidal wetlands are flanked by saline mudflats in arid and semiarid locations, seasonally flooded freshwater wetlands in monsoonal tropics, and peat-swamp forests underlain by domed woody peat in perennially wet equatorial regions of Southeast Asia. Periodic climate influences, such as hurricanes (referred to as tropical cyclones in Australia and typhoons in Asia) and El Niño–Southern Oscillation phenomena, can also be a significant influence on inundation and recruitment dynamics.

Hydroperiod: the flooding characteristics of an area, such as frequency, depth, and duration of inundation; for mangroves, this is driven primarily by tidal hydrodynamics

Also important is relative sea-level change, which is the combination of local changes in sea level and the net movement of the land surface. Where the land is lowered, by various physical and biological processes broadly termed subsidence, the coast experiences relative SLR (see sidebar, Subsidence and Relative Sea-Level Rise). These phenomena can influence vegetation productivity and the transition of one vegetation type into another and are examined in greater detail below.

At the mesoscale, there are likely to be distinctive mangrove habitats, often associated with different landforms or microtopography. **Figure 3** uses the functional classification introduced by Lugo & Snedaker (1974) as an illustration. Hydrodynamics, particularly the hydroperiod, influence how a particular stand of mangroves functions. The position within the tidal frame, which is partly mediated by the elevation of the ground surface beneath mangroves, is particularly important in determining frequency, duration, and interflood periodicity. The hydroperiod influences the

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

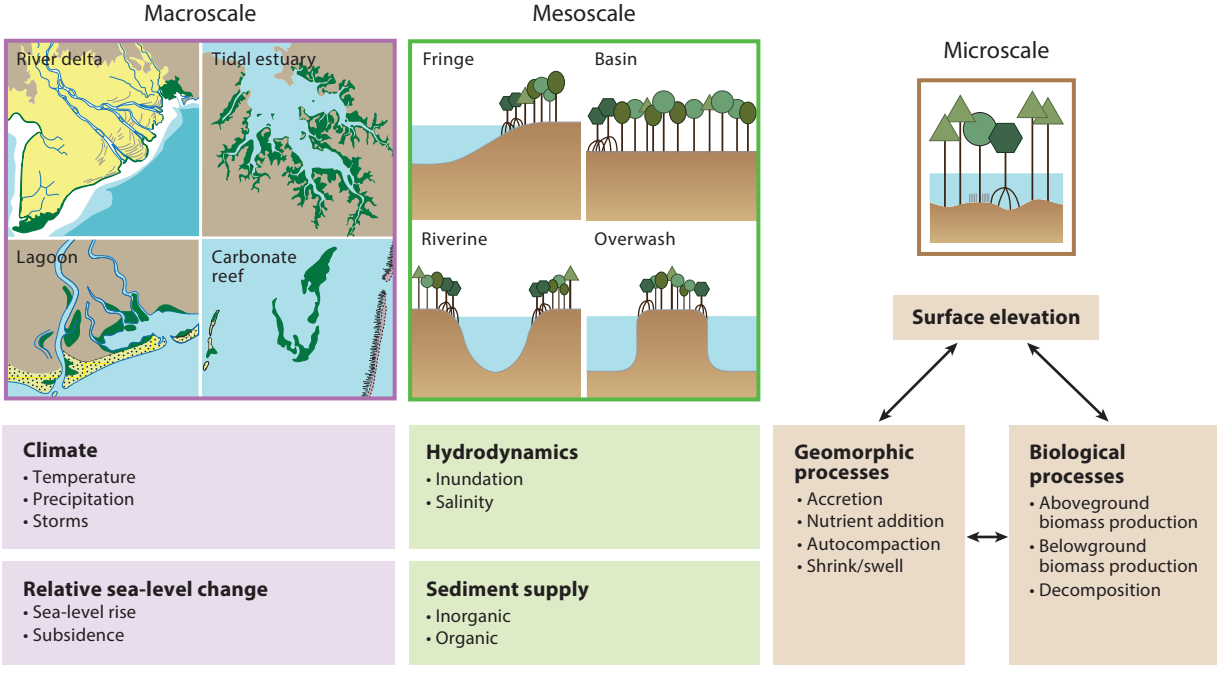


Figure 3

A scale-based framework within which to view mangrove systems, comprising macroscale regional boundary conditions (climate and relative sea-level change, which includes both subsidence and sea-level rise); mesoscale processes, in which hydrodynamics and sediment supply are important influences on mangrove systems; and microscale at-a-site interactions within a mangrove stand, including surface and subsurface processes.

SUBSIDENCE AND RELATIVE SEA-LEVEL RISE

Relative sea-level rise on a particular shoreline refers to the net change caused by adjustments of the sea surface and those of the land. The latter are captured by the term subsidence, but this incorporates a range of processes operating at different timescales, divided into deep and shallow subsidence. Many large deltas of the world are subsiding at rates up to an order of magnitude greater than the global rate of sea-level rise (Syvitski et al. 2009, Hanebuth et al. 2013, Auerbach et al. 2015). Geophysical processes of deep subsidence include tectonic movements, hydro-isostatic adjustments to the mass of water accumulated in ocean basins following postglacial ice melt, and flexure in response to sediment loading of the lithosphere. These natural processes can be further exacerbated by several anthropogenic factors, primarily groundwater or hydrocarbon extraction, with alarmingly rapid rates of subsidence beneath megacities, such as Bangkok (where the rate in the 1980s was up to 120 mm $year^{-1}$; Phien-wej et al. 2006).

The term shallow subsidence describes a suite of processes that are presently inadequately differentiated. Surface elevation table measurements in combination with marker horizons (SET-MH), which record accretion, allow calculation of shallow subsidence rates over short timescales. This approach measures changes in the thickness of sediments between the base of a benchmark pole or bedrock and the marker horizon (see **Figure 4*b***) but does not indicate the causes of these changes. Bulk density and organic content provide some indication of compressibility over several years, and correlations with rainfall or groundwater levels enable inferences about likely shorter-term variations in water content (Whelan et al. 2005, Rogers & Saintilan 2008, McIvor et al. 2013, Rogers et al. 2013a).

In large deltas, such as the Mississippi River Delta, the principal component is compaction of sediments (Törnqvist et al. 2008). Rates of inferred subsidence are alarmingly high, but paleoenvironmental evidence implies that they must be nonlinear, because if observed rates had been occurring over centuries, fossil mangrove material would not have been preserved at elevations similar to those of its modern counterpart.

environmental factors that determine which mangrove species are able to establish, persist, and be productive (Crase et al. 2013).

The functional forest types described by Lugo & Snedaker (1974) are less easily discriminated in the more structurally complex mangrove forests of the Indo-West Pacific. Mangroves are extensive along estuaries, and hydrodynamics become increasingly complex owing to frictional distortions along channels and to flows across low-gradient vegetated wetlands (**Figure 2**). Despite attempts at classifying settings, there is still no adequate conceptual morphodynamic framework within which to view the mutual coadjustment between the topography of landforms and the associated hydrodynamic processes that control sediment movement over time (Cowell & Thom 1994). Climate and sea level may be important long-term drivers of change in these systems, but mangrove systems are subject to significant shorter-term internal morphodynamic adjustments, mediated by sediment supply, that may be harder to explain or predict (Chappell & Thom 1986).

At the microscale, involving an individual site, a range of geomorphological and biological surface and subsurface processes operate (**Figure 3**). The hydroperiod influences the rate of sediment accretion and root production, with negative feedback decreasing the flooding depth and accretion rate as surface elevation builds (Adame et al. 2009). As sediment accretes, the hydroperiod changes and the accommodation space is reduced. Negative feedbacks promote recurring, self-regulating forms that imply equilibrium (Woodroffe 1995). Because processes operate in nonlinear ways, complex systems must be studied at appropriate timescales. Rates of surface elevation change measured over decades are extremely variable and often independent of the rate of SLR. However, because the upper limit to mangrove growth is constrained by the highest tides, accumulation rates measured over longer timescales appear to track SLR. At century to millennial scales,

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

the stratigraphy of coastal plains indicates that accumulation beneath mangroves has culminated in a threshold beyond which mangroves have been replaced by adjacent terrestrial ecosystems. Forest structure responds to elevation changes, although response times may be slow because once mangroves are established, mature trees cannot be replaced quickly. Although zonation has been interpreted as evidence of plant succession in the past (e.g., Davis 1946), there have been few observations of replacement of mangrove species over time (Lucas et al. 2007). Antecedent conditions can influence observed vegetation change (e.g., mangrove reoccupation of paleochannels; see **Figure 2**). Such factors will complicate forecasts and simulation modeling of future mangrove forest behavior in response to changing sea level.

Ecological accommodation: vertical and horizontal adjustments by mangrove forests as the sea level changes, involving accumulation of both organic and mineral sediments

ACCOMMODATION SPACE AND HYDRODYNAMICS

The distribution of mangrove species coincides with the intertidal accommodation space, which progressively fills through sediment accumulation. Emergent properties and biocomplexity are a function of hydroperiod and are related to salinity and flooding tolerance, the latter of which is related to root morphologies, physiology, and reproductive traits such as vivipary (Feller et al. 2010).

Accommodation Space

The term accommodation space has been adopted from sequence stratigraphy, where it was defined by Jervey (1988, p. 47) as "the space available for potential sediment accumulation." Sediment accretion progressively fills the space unless countered by erosion. Tide-borne sediment can be deposited up to the highest tide level, which can change as a result of SLR or land movements (such as subsidence). Effective, or available, accommodation space generally refers to the one vertical dimension, depicting the relationship between sediment surface and the upper limiting tidal level. Within a mangrove forest, the accommodation space is usually greatest at the seaward edge, where mangroves may be rooted at elevations close to mean sea level (MSL) (**Figure 4*a***). At the landward edge, where only the highest spring tides reach, the accommodation space is smallest. However, there may be more complex patterns; in basin forests, remote from tidal inundation, flooding may be sporadic or seasonal, and elsewhere, episodic increases in accommodation space occur during storms or flood events.

There may also be areas of potential accommodation space (see **Figure 2**), which could be inundated if they are tidally reconnected or the highest tide level increases slightly. Vegetation is not an intrinsic component of the sedimentological definition of accommodation space, and from a geological perspective, mangroves only fleetingly occupy part of the tidal frame. However, it is useful to consider ecological accommodation (broadly defined for organisms in carbonate stratigraphy by Pomar & Kendall 2008). For mangroves, this accommodation lies between the upper and lower bounds within which mangroves can establish, and these bounds are spatially variable. This concept is particularly important because mangroves and associated organisms (such as molluscs, foraminifera, and algae) produce and accumulate organic matter that contributes to filling accommodation space.

Tidal Hydrodynamics and Hydroperiod

Both mineral accretion and biological accretion are affected by the hydroperiod, which is related to elevation and reflects a combination of frequency, depth, and duration of tidal inundation (Krauss et al. 2006). Each of these factors will vary at individual sites as a function of distortion of the tidal

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

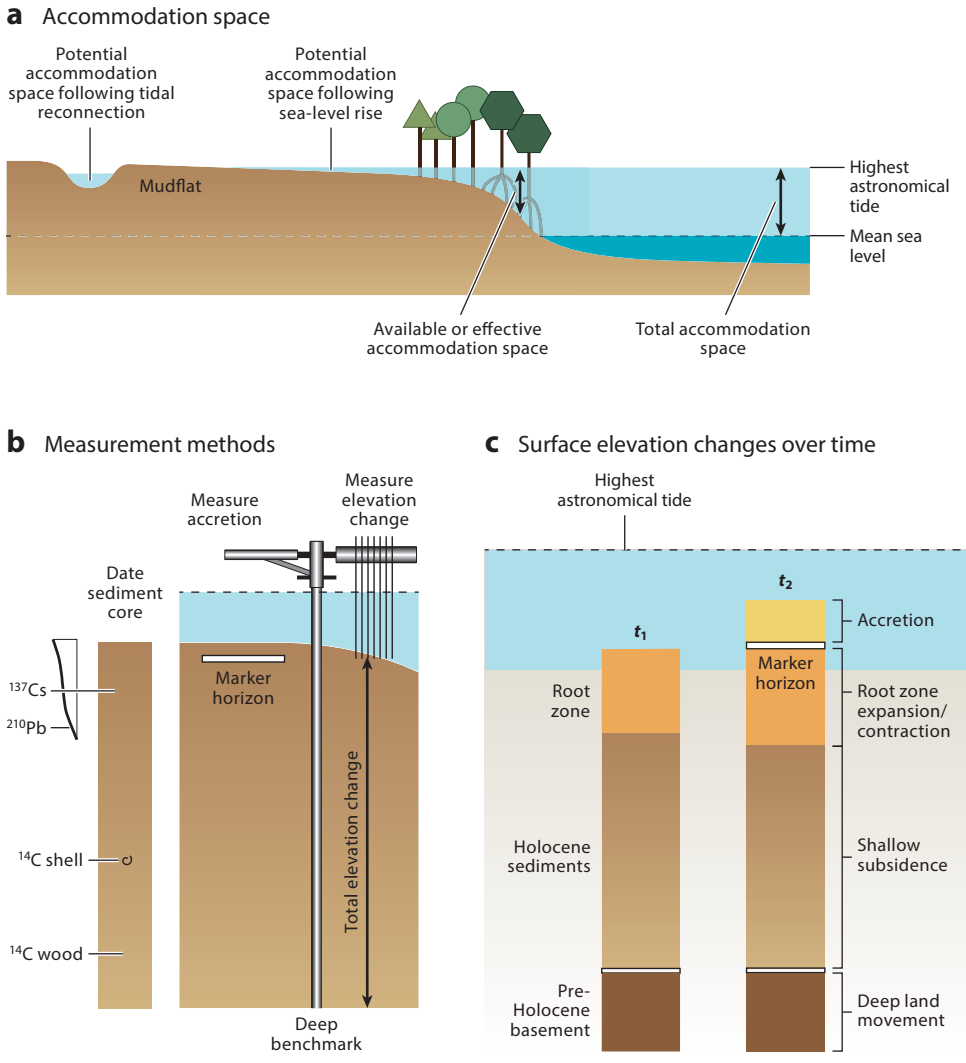


Figure 4

(*a*) Schematic cross section of substrate beneath mangroves, showing variations in accommodation space. (*b*) Measurement methods adopted to assess sedimentary processes beneath mangroves. (*c*) Surface elevation changes that occur over time.

curve as well as additional parameters, such as distance to a creek (Janssen-Stelder et al. 2002). On open coasts, the lower bound to mangrove ecological accommodation space is set by the lowest elevation at which seedlings can persist and grow to become trees (Balke et al. 2013). The upper bound is the highest level to which tides or storms rise, although bounding water levels differ in mangrove forests that are located well inland and infrequently flooded (see **Figure 2**).

Watson (1928) described the relationship of mangrove zones to tidal inundation, indicating that the lowermost mangroves are flooded on average by 45 tides a month, the middle section by 20–45 tides a month, and the uppermost by <20 tides a month. However, site-specific assessments of hydroperiod are needed. In Can Gio, east of the Mekong River Delta, elevation classes have

been independently determined: Medium-high tides reach up to 0.9 m above MSL, inundating *Avicennia* and *Sonneratia*; Rhizophoraceae dominate up to 1.5 m above MSL; and above that, *Lumnitzera*, along with *Bruguiera* and *Ceriops*, is flooded less frequently (van Loon et al. 2007). This pattern contrasts markedly with that of the Ca Mau Peninsula in the southwest of the delta, where tides are diurnal and the tidal range is approximately 1 m; here, mangroves are restricted to a much narrower accommodation space, reaching elevations of no more than 0.6 m above MSL. The actual area available for mangrove establishment is a function not only of this vertical accommodation space but also of the gradient of the substrate and the pattern of sedimentation. Mangroves are rapidly prograding across the actively building Ca Mau Peninsula, where there are particularly unusual tidal conditions as a consequence of the differing tidal regimes in the two seas (Phan & Hoang 1993). Despite the profuse supply of sediment, mangroves contribute a substantial organic component, even in this environment, with recent measurements indicating that mangroves in Ca Mau have sequestered more than 600 tonnes per hectare in belowground organic carbon (Tue et al. 2014).

In Darwin Harbor, where there is a larger tidal range, *Rhizophora* is replaced at an elevation of 2.0–2.5 m above MSL by *Ceriops*, and more landward mangroves, such as *Excoecaria*, are present at elevations up to 3.6 m above MSL (Woodroffe 1995). Mangrove species distribution appears to be related to hydroperiod (Crase et al. 2013), but broad characterizations of hydroperiod are only very approximate estimates and require assessment for individual sites (Clarke 2014). Mangrove distribution patterns change substantially in response to tidal distortions upstream in estuaries (Duke 2006) (see **Figure 2**). The tide becomes increasingly asymmetric upstream along tidal channels, with the flood tide of shorter duration but greater velocity than the ebb (Davies & Woodroffe 2010). Tidal range is amplified in systems that taper abruptly (e.g., Capo et al. 2006, Pethick & Orford 2013) but is attenuated in broader waterways (e.g., Knight et al. 2008). Lateral trapping of mud occurs because tidal waters flowing into mangroves can carry abundant sediment, but a large proportion is deposited as flow decelerates. The velocity in the main channel, typically >1 m s^{-1}, contrasts with the much slower flows, generally <0.08 m s^{-1}, within mangrove forests (Wolanski et al. 1992, Mazda et al. 1995, Quartel et al. 2007).

By contrast, where small tidal creeks flood extensive intertidal mangrove wetlands, inflowing tides tend to have a constant velocity as the tide rises; however, the velocity increases as water spills overbank into mangroves. After slack high water, the ebb tide is characterized by flows that accelerate to a peak velocity. Ebb dominance maintains channel depth by scouring the creeks (Wolanski et al. 1992), assisting outwelling of organic carbon from these wetlands (Hemminga et al. 1994, Lee 1995). The morphology of the mangrove system (i.e., both the forests and the associated channels) influences hydrodynamics and, consequently, sedimentation patterns through complex morphodynamic feedbacks.

SEDIMENTS AND SEDIMENT SUPPLY

The substrate beneath mangroves is composed of both inorganic mineral sediments and organic components derived from mangroves and other organisms. Where large rivers supply abundant terrigenous sediment, these allochthonous mineral sediments can accumulate rapidly in mudbanks, which provide habitats for opportunistic colonization by mangroves (Proisy et al. 2009, Lovelock et al. 2010, Swales et al. 2015). In more complex systems, sediments are redistributed by tides. In sediment-poor settings, mangroves themselves contribute to accumulation of autochthonous material; these often form peats composed predominantly of root matter incorporated into the substrate, but with some accumulation of leaf litter and other aboveground biomass, as well as algal mats (McKee & Faulkner 2000, Alongi et al. 2004, McKee 2011, Saintilan et al. 2013).

Allochthonous sediments: sediments produced from outside a site; these can include terrigenous sediment from rivers, tidally resuspended muds, or biogenic calcareous reef sediments

Autochthonous sediments: sediments produced in situ by living organisms such as mangroves or calcareous organisms

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Rates of mangrove leaf production and turnover may be high (Komiyama et al. 2008), but a large proportion of litterfall is labile and tidally exported or is processed by crabs (Lee 1995). This contrasts with the fate of more refractory root material (Krauss et al. 2014). Stable-isotope analysis of carbon in temperate mangrove substrates indicates that mangrove roots dominate belowground carbon accumulation (Saintilan et al. 2013), although allochthonous carbon from adjacent sources dominates some sections of coastal wetland (Yang et al. 2013, 2014).

Rivers supply large volumes of sediment to the oceans, much of which accumulates in deltas. Extensive mangrove forests are associated with the megadeltas of Asia; for example, the enormous delivery of sediment from the Ganges and Brahmaputra Rivers has enabled vertical accretion that has maintained the shoreline at close to its present position during rapid postglacial SLR (Wilson & Goodbred 2015). The morphology of individual deltas varies according to the relative balance of river, tide, and wave processes, and the locus of mud deposition also varies. Mud is retained in some estuarine channels, whereas in others it is dispersed to delta-front and deep-water fans or moved along the delta front by longshore transport (Walsh & Nittrouer 2009, Woodroffe & Saito 2011). For example, because of mud deposition at the mouth of the Amazon, mangroves have increased by >700 km^2 in 12 years (Nascimento et al. 2013). Highly mobile mudbanks extend for more than 1,500 km along the northeast coast of South America between the mouths of the Amazon and Orinoco Rivers. The mudbanks migrate alongshore, protected from wave attack by the dampening effect of mud, and are colonized by mangroves, which are subsequently overwhelmed by a further phase of mudbank instability (Fromard et al. 2004, Anthony et al. 2010). In some locations, the dynamics of the mangrove fringe appear to be related to the 18.6-year cycle of highest tides (Gratiot et al. 2008). Similarly rapid mudbank accretion and mangrove colonization occur in the sediment-rich Gulf of Papua, with vertical accumulation rates of several centimeters per year prior to mangrove establishment (Walsh & Nittrouer 2004, Shearman 2010). In these cases, mangrove ecological accommodation is controlled by dynamic topographic changes following mud redistribution.

Mud, comprising silt and clay particles, is deposited only when there is minimal velocity of flow; however, once deposited, it is cohesive and requires much more rapid flows for resuspension. Muds are also prone to flocculation; when suspended sediments reach saline waters, they form a turbidity maximum. Tidal pumping occurs when flood tides carry sediment upstream farther than ebb flows carry it downstream, and such mechanisms can trap sediments in the turbid estuary. In tidal rivers in northern Australia, such as the Daly River, import of sediment by tidal pumping occurs in the dry season, and sediment export occurs in the wet season (Wolanski 2006).

Mangroves growing in sediment-deficient locations represent the other extreme of this continuum. Substrate is built by the plants, and organic input into the substrate contributes to increases in surface elevation (McKee 2011). For example, within predominantly carbonate islands in Belize, peat accumulation has tracked sea level as it has risen at a decelerating rate over the past few millennia (McKee et al. 2007). Mangrove islands have persisted amid the biogenic calcareous sediment that dominates these reef environments, but they now appear to be threatened by a combination of human pressures, including accelerated SLR (McKee & Vervaeke 2009).

Accumulation of organic and inorganic material is not continuous in time, but can undergo perturbations as a result of disturbance (**Figure 4*b***). For example, storms can have profound effects on carbon retention and surface elevation within mangrove forests. Hurricanes can devastate mangroves, causing windthrow and defoliation, which interrupt forest growth. These hurricanes can also erode the substrate and deposit unusually thick layers of sediment that result in forest mortality (Ellison 1999, McCloskey & Liu 2013). Subsurface processes identified following a storm include accretion or erosion that causes elevation change, shrinkage, root decomposition, root growth, and other changes of volume (Cahoon 2006, Smith et al. 2009, Lovelock et al. 2011b,

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Smoak et al. 2012). Oxidation of the upper meter of substrate can cause rapid carbon loss to the atmosphere (Granek & Ruttenberg 2008, Auerbach et al. 2015); short-term CO_2 loss from cleared mangrove substrate has been measured at 29 Mg ha^{-1} year^{-1} (Lovelock et al. 2011c).

SEDIMENT ACCUMULATION AND RELATIVE SEA-LEVEL RISE

Measuring Sedimentation and Elevation Change

Figure 4*c* shows a schematic cross section of mangrove substrate down to the pre-Holocene basement. The sediments have accumulated over the past few thousand years, often beneath earlier generations of mangroves. The upper section is the root zone. The surface of the substrate can change over time, generally increasing in elevation, as a result of several surface and subsurface processes (Gilman et al. 2008, Soares 2009, McIvor et al. 2013, Krauss et al. 2014). The most obvious is sediment accretion on the surface, primarily of fine-grained mud but also potentially of some organic matter, such as leaf (and other plant) litter and perhaps algal-mat development (Cahoon et al. 2006, McKee 2011, Krauss et al. 2014). Organic subsurface processes are also very important, particularly root growth. Other subsurface processes include decomposition of root material (Middleton & McKee 2001) and bioturbation by burrowing animals (Kristensen et al. 2008). Autocompaction occurs gradually and includes several poorly differentiated processes, collectively termed shallow subsidence (Whelan et al. 2005). These processes include consolidation as sediment grains readjust; compression, particularly of organic material such as roots; and changes in water content.

Figure 4*b* shows a series of methods that have been used to determine sediment accumulation. Several radiometric dating techniques provide age control on the stratigraphy beneath mangrove forests. Sediment cores can be dated using radiocarbon analyses on either the organic remains of plants or fossil molluscs. The decay of ^{14}C enables an estimate of the time at which an organism died, but it is necessary to know how the dated material related to both the sediment surface and the tidal frame in order to determine the sea level at that time. Although most mangrove roots are concentrated in the top 10–20 cm, some can penetrate as much as 1 m into the substrate, meaning that the age of the root does not necessarily represent the former sediment surface. Fossil molluscs are easily moved and may not be found now in the location at which they lived. Radiocarbon ages require calibration, and carbonate samples require an environmental correction before they can be compared with ages of plant matter. As a consequence, radiocarbon chronologies have provided age control over past millennia but are not as effective in the past century or two; ^{14}C in the atmosphere increased considerably following atomic bomb testing in the 1950s (Nolte et al. 2013).

Whereas the "bomb spike" confounds radiocarbon dating since 1950, this period of atomic bomb testing has left other markers that can be used to provide estimates of sediment accumulation in the past 60–70 years. One widely used isotope is ^{137}Cs, which first appeared in the early 1950s and reached a peak around 1963. Cesium has a relatively short half-life (~30 years), and most of it has decayed; however, it may be possible to identify a bomb spike using plutonium, which has a substantially longer half-life. Also based on the decay chain of uranium is ^{210}Pb; excess ^{210}Pb is also supplied from the atmosphere and delivered by river and ocean waters, such that the profile of this unsupported lead provides a down-core indication of time (Van Santen et al. 2007, Sanders et al. 2008, Comeaux et al. 2012).

A still shorter-term technique for determining sediment dynamics is direct observation with surface elevation tables (SETs). This is a precise, nondestructive method for measuring relative changes in substrate elevation, adapted for mangroves from its use in salt marshes (Cahoon et al. 2000). It consists of a rod or pole driven to refusal on hard underlying basement. A portable

Surface elevation table (SET): an elevation-change apparatus comprising a rod driven to the basement with a portable horizontal arm from which pins are lowered to the ground surface

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

horizontal arm is positioned on top of the rod, and pins are lowered until they touch the ground surface. The length of the pins extending above the measuring arm is remeasured at successive points in time to record changes in the relative elevation of the surface. The most recent version of this approach, rod SET, has allowed placement of benchmarks at greater depths because the rods have less frictional resistance than the aluminum pipes used in the original SET technique (Cahoon et al. 2002).

Marker horizon (MH): a distinctive layer, generally of feldspar, that is placed on the substrate surface and resampled over time to measure sediment accretion

Vertical accretion of sediment is usually determined at the same time as SET measurements. Marker horizons (MHs) of feldspar or sand are established near the SET, and the thickness of the sediment deposited above these is measured in short cores. Marker layers have proved difficult to relocate in mangroves owing to the effects of tidal resuspension and bioturbation, particularly those lower in the tidal frame. If cumulative vertical accretion over a period of several years substantially exceeds net surface elevation change over that period, then shallow subsidence is inferred (Rogers et al. 2005, 2006). In some locations, however, elevation change may exceed accretion, which indicates subsurface expansion, typically caused by root matter accumulation (McKee et al. 2007).

SET-MH measurements of surface elevation change allow users to distinguish between surface processes of accretion and subsurface processes. Results have shown that subsurface processes beneath mangroves can lead to considerable variation in surface elevation, in both sites with highly organic sediments and those with mineral sediments (Webb et al. 2013). These subsurface processes include autocompaction and hydrologically driven processes of shrink and swell that are not necessarily unidirectional (Rogers et al. 2014). They also include organic processes, such as root growth and decomposition. Together, subsurface processes can make a substantial contribution to net change in mangrove substrate elevation. For example, vertical change caused by root volume inputs to the substrate varied across mangrove islands in Belize from 1.2 to 10.8 mm year^{-1} and accounted for 52% of variation in elevation change (McKee et al. 2007); by contrast, subsidence and accretion explained 36% and 2% of variation, respectively. In Micronesia, accretion rates were highly variable (2.9 to 20.8 mm year^{-1}), but 7 out of 13 mangrove sites showed decreases in elevation (−0.6 to −5.8 mm year^{-1}), implying significant shallow subsidence caused by autocompaction and related processes (Krauss et al. 2010). **Table 1** summarizes published observations using SET-MH methods and demonstrates the apparent disparity between measured rates of sediment accretion and surface elevation gain (Alongi 2012, Krauss et al. 2014).

Sedimentation in mangrove habitats can be beneficial and can promote plant growth in several ways. Sedimentation can directly increase wetland elevation and reduce inundation stress. Mangroves quickly generate roots that grow into newly accumulated sediment, promoting soil development and elevation change (Lovelock et al. 2011a). In addition, fine-grained sediments contain active redox metals, moderating redox intensity and root oxygen stress. They may

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Table 1 Published ranges of surface elevation change, vertical accretion, and subsurface adjustment for different mangrove hydrogeomorphic settings determined using surface elevation table–marker horizon (SET-MH) methods (for a full list of references, see Krauss et al. 2014)

Hydrogeomorphic setting	Surface elevation change (mm year^{-1})	Vertical accretion (mm year^{-1})	Subsurface change (mm year^{-1})
Fringe	−1.3 to +5.9	+1.6 to +8.6	−9.7 to +2.4
Riverine	+0.9 to +6.2	+6.5 to +13.0	−11.2 to −0.2
Basin/interior	−3.7 to +3.9	+0.7 to +20.8	−19.9 to +2.8
Scrub	−1.1	−2.0	−3.1
Overwash	−0.6 to −2.5	+4.4 to +6.3	−3.8

provide a nutrient subsidy that stimulates mangrove growth, particularly as soil conditions are often nitrogen or phosphorus limited. Sediments can also indirectly promote uptake of nutrients by limiting sulfide availability; soluble sulfide is a known phytotoxin that impairs salt-marsh vegetation (Mendelssohn & Morris 2000) and may affect mangroves similarly (McKee 1993). Too much sediment can be detrimental to mangrove growth, however, depending on the sediment texture, volume of sediment delivered, and period of accretion. Mangrove breathing roots (pneumatophores and prop roots) can be completely or partially smothered after burial by sediment, resulting in root anoxia that leads to mortality (Ellison 1999).

Elevation deficit: a condition in which the rate of elevation gain in accommodation space (accretion plus subsurface movement) is less than the local sea-level trend

Relative Sea-Level Rise

There is ample evidence that sea level has risen in the past, and paleoenvironmental studies provide important perspectives on how mangroves and associated wetlands have coped with these changes (Woodroffe 1990, McKee et al. 2007, Ellison 2008, Semeniuk 2013). A key question is whether surface elevation beneath mangroves is able to keep pace with rising sea level. Linear regression of sediment accretion rate against SLR rate indicates that many forests are presently accreting at rates exceeding SLR (Alongi 2015). It is important to link SET-MH measurements with nearby tide-gauge observations (Cahoon 2014); however, presently there are few SET-MH measurements or tide-gauge observations in the most extensive mangrove areas (Webb et al. 2013).

Progressive accretion, slowing through time because of negative feedback, will eventually lead to such infrequent tidal inundation at the rear of the mangrove forest that a threshold is crossed and the mangroves are replaced by terrestrial ecosystems, the nature of which depends on the regional climate. Contrary to concerns expressed about the ability of mangroves to keep up with SLR, accretion rates in many mangrove forests appear to exceed present rates of SLR (**Table 1**). SLR raises that threshold, enabling mangrove ecosystems to expand landward. However, accretion does not necessarily occur at the same rate as sea level rises: In several locations where both have been measured, the rate of elevation gain (accretion plus subsurface movement) is less than the local sea-level trend (measured by tide gauges)—i.e., an elevation deficit exists.

Thus, subsurface movements may play a major role in determining whether a mangrove forest adjusts to SLR. Subsurface movements include deep geophysical processes (such as tectonics, hydro-isostasy, and lithospheric flexure), as well as shallower autocompaction within Holocene sediments (comprising undifferentiated processes such as consolidation, compression, dewatering, and decomposition of organic matter). Until recently, the principal concern was about the capacity of mangroves to accrete sediment at sufficiently rapid rates to track the rate of eustatic SLR, but it is increasingly apparent that accommodation space is also augmented by subsurface processes, including both shallow and deeper subsidence. Filling the accommodation space requires ample sediment, leading to concerns that even large deltas, many of which receive less sediment because of dam construction in their catchments, will no longer receive sufficient sediment to accrete across their entire surface (Ibáñez et al. 2013, Giosan et al. 2014). By contrast, the peat-forming mangroves studied to date appear to be keeping pace with SLR through subsurface expansion driven by mangrove root ingrowth (McKee et al. 2007, McKee 2011).

If there is no change in sea level and no subsidence, then accommodation space (in the vertical plane) will diminish as sediments fill it over time (assuming a sediment supply). Such a succession is evident from the stratigraphy of coastal and deltaic plains, which reveals that considerable horizontal advance (progradation) has occurred (Grindrod 1985). Once the substrate reaches the height of the highest tide, it is no longer inundated, and because the intertidal accommodation space is filled, no further tide-borne sediment accretion occurs except in the event of a storm surge that temporarily raises water level. However, there may be other processes of accumulation, for

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

example, alluvial sediment deposition from river floods. Another source of accumulation is peat, as occurs in the peat-swamp forests in Southeast Asia, but these generally occur at much lower rates than intertidal sedimentation (Woodroffe 1993).

Marine transgression: a rise in sea level that causes the shoreline to move landward

In most settings, mangroves persist because there is a continual increase in accommodation space as ocean height increases and the land subsides. This enables vertical sediment accretion (organic and inorganic). Many studies conclude that mangrove sediment accretion will keep pace with sea level, but more realistic scenarios must incorporate surface and subsurface processes. However, if the rate of vertical land development (through accretion and subsurface root accumulation) is less than relative SLR, mangroves will become progressively drowned (Ellison & Stoddart 1991). In such a scenario, mangroves could potentially expand landward into the hinterland, where they are unimpeded, producing further accommodation, which also requires sediment. Such displacement of mangroves landward has been modeled (e.g., Traill et al. 2011, Di Nitto et al. 2014). This is not possible where rock abuts mangroves or where infrastructure such as embankments and roads limit landward extension, causing coastal squeeze (Phan et al. 2015). If sediment accumulation occurs more rapidly than relative SLR and raises surface elevation to the level of the highest tide, then conditions favoring invasion by hinterland vegetation develop.

Sediment accumulation rates are spatially variable, and therefore models that adopt rates that vary geographically should be more realistic than lumped parameter models. Such modeling, incorporating rates observed at SETs, has been attempted in southeastern Australia; however, the results are highly dependent on the rates used and the underlying model assumptions (Rogers et al. 2012, 2013b; Oliver et al. 2012). Using accretion rates alone to predict the sustainability of mangroves will often overestimate survival, especially in locations with high rates of shallow subsidence, or may underestimate survival in locations where roots make a significant contribution to elevation adjustment.

The stratigraphic record of postglacial SLR provides some indication of how mangroves might respond to renewed marine transgression. In one sense, it can be inferred that the mangrove wetlands have kept pace with sea level. In the Caribbean, continuous sequences of mangrove peat spanning thousands of years illustrate that mangroves persisted during the past 7,000–8,000 years of relative SLR (Macintyre et al. 2004, McKee et al. 2007). Clearly, there is a rate of SLR above which mangrove substrate cannot accumulate fast enough to keep pace with rising sea levels, but this rate remains difficult to determine from paleoenvironmental analyses, although high rates of adjustment have been identified. Peat sequences are interrupted by calcareous layers in other places, indicating periodic disruption by storms or seismic activity (McCloskey & Liu 2013). By contrast, the sea was at or above its present level for much of the past 7,000 years in the Indo-Pacific, and mangroves that occupied many of the coastal and deltaic plains that formed over this period have been replaced, with only a narrow fringe persisting along the modern shoreline. The future of mangroves is thus likely to vary between sites, depending on a range of surface and subsurface processes and on rates of relative SLR.

DISCUSSION AND CONCLUSIONS

Mangroves occur in locations where topography exposes them to suitable tidal or other flooding regimes. Sedimentation within the available accommodation space can be rapid where there is abundant supply of inorganic sediment (Lovelock et al. 2010). Organic matter, particularly root matter, accumulates beneath mangroves and is now recognized as a globally significant repository of blue carbon. In some conditions, organic sediments build substrate even in the absence of terrigenous sediment. Paleoenvironmental studies indicate that mangroves have persisted during SLR, building substrate rapidly enough to keep up with the rise or being displaced landward onto

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

previous hinterland. Fossil mangrove deposits provide important evidence for reconstruction of past sea level.

Sediment accretion and elevation-change rates are more rapid at lower elevations, decreasing as the substrate builds in the tidal frame, and in the short term they appear to be independent of the rate of SLR (Lovelock et al. 2015). Subsurface processes further decouple surface elevation gains from SLR, augmenting accommodation space because of the larger rate of relative SLR. The view that mangrove sedimentation tracks or keeps up with sea level is therefore misleading. The accommodation space for mangroves is directly constrained by the upper limit of tidal flooding. Mangrove forests that appear to track SLR, either in the past or based on measurements using SETs, have been filling the accommodation space to this limit. Mangroves have been replaced by terrestrial ecosystems once that upper threshold has been exceeded, as is clear from the stratigraphy of broad plains throughout much of the tropics. However, both shallow and deep land movements increase accommodation space, whereas sediment accretion reduces it. When sediment accumulation rates (both organic and inorganic) equal the combined rates of land and sea movements, mangroves maintain their elevation relative to MSL. When there is insufficient elevation change, mangrove forests may be drowned unless they can establish themselves in more landward locations as their existing locations are inundated (Ellison 2008).

Mangrove resilience at a site is largely dependent on the relationship between accretion (both allochthonous and autochthonous) and relative sea-level change. Assessment of resilience needs to incorporate nonlinear feedbacks among hydrodynamic conditions, sediment inputs, plant productivity, and elevation change. Rising sea levels, augmented by subsidence, can be expected to alter the size and characteristics of accommodation space and thus the composition of mangrove forests as inundation conditions come to favor particular species over their competitors. However, a focus on vertical adjustment within a particular mangrove stand risks missing the broader regional picture. Mangrove extent has changed substantially over time, including during the relatively stable sea level of the past few millennia and during the slowly rising sea level of the past century. Mangroves can extend seaward where subtidal accretion makes habitat available, and there may be considerable potential accommodation space on low-lying coastal plains that have not been occupied by people or impacted by land-use change but can be colonized by mangroves when tidally reconnected (Traill et al. 2011, Eliot & Eliot 2012, Rogers et al. 2013a). Such natural expansion of mangroves provides an important opportunity for carbon sequestration, facilitating both climate-change adaptation and mitigation (Rogers et al. 2013a). The topography of the land being inundated is the most significant control on changes in accommodation space resulting from higher water levels, and is therefore the most important factor to quantify when forecasting the future response of mangroves to relative SLR.

Unfortunately, human impacts have too often severely reduced the area occupied by mangrove forests (Giri et al. 2011) or monopolized areas into which they might have expanded. Land-use changes not only directly affect mangrove forests, but also reduce the opportunities for mangroves to extend farther landward as the sea rises, because embankments and infrastructure cause coastal squeeze. Human activities are imposing many additional pressures on mangrove forests, including accelerating rates of subsidence through groundwater extraction. Mangrove clear-cutting eliminates production of organic sediments and increases erosion of accumulated sediments (McKee & Vervaeke 2009).

Programs of restoration, rehabilitation, and planting can reverse declines in mangrove forest areas if appropriate hydrodynamic and sedimentary prerequisites are met, including returning tidal flooding to previously empoldered areas and enabling mangrove reestablishment. Mangroves of the Mekong River Delta have been especially impacted by human activities, including extensive destruction by defoliants during military conflict in the 1960s and 1970s, cutting for timber, and

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

reclamation for shrimp ponds (Ha et al. 2012). Nevertheless, the 10 million or more inhabitants of the delta have traditionally coped with vagaries of water management (including engineering structures such as dykes and sluice gates), broadening the range of adaptation and policy options available (Smajgl et al. 2015).

Although several simple models have been developed to simulate the response of salt marshes to SLR, it is questionable whether there is sufficient understanding of the ecological dynamics of mangroves, and of the morphodynamic behavior of sedimentary settings in which they grow, to extrapolate such models confidently to mangrove systems. As in the case of salt marshes, process studies of mangrove systems are often too short to understand the timescale at which these systems operate, and few address hydrodynamic processes or their variability in space. The few stratigraphic studies, which have focused on sparse auger or drill-hole evidence, provide a tunneled view through time with insufficient insight into variations in space. There remain sparse data on sediment accumulation and subsurface processes beneath most mangroves. Much more focused research is needed to disentangle interrelationships before modeling will be sufficiently useful for coastal managers to realistically forecast future mangrove extent.

SUMMARY POINTS

1. Mangroves are confined largely to the upper intertidal part of the tidal frame, referred to as the accommodation space, which is a function of hydrodynamics (or hydroperiod).
2. Mangroves can grow on a range of substrate types, from allochthonous terrigenous sediment to autochthonous mangrove-derived peat. Mangrove systems sequester significant volumes of carbon in sediments, termed blue carbon.
3. The paleoenvironmental record indicates that over millennial timescales, mangrove shorelines have been exposed to different sea-level trajectories, which suggests a broad capacity to adjust to sea-level changes.
4. Rates of surface elevation change beneath mangroves vary spatially and temporally and involve sediment accumulation as well as a range of subsurface processes, broadly termed subsidence. To persist, mangrove substrates must build vertically at a rate equal to the combined rates of eustatic sea-level rise and land subsidence.
5. Inorganic sediment supply and sequestration of organic matter endow mangrove forests with considerable natural resilience in response to sea-level rise. However, there are many other anthropogenic pressures that interfere with accretion processes and decrease mangroves' capacity to adjust to sea-level change.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We gratefully acknowledge the Global Challenges program of the University of Wollongong, which supported a workshop from which this review was developed. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

LITERATURE CITED

Adame MF, Neil D, Wright SF, Lovelock CE. 2009. Sedimentation within and among mangrove forests along a gradient of geomorphological settings. *Estuar. Coast. Shelf Sci.* 86:21–30

Alongi DM. 2012. Carbon sequestration in mangrove forests. *Carbon Manag.* 3:313–22

Alongi DM. 2014. Carbon cycling and storage in mangrove forests. *Annu. Rev. Mar. Sci.* 6:195–219

Alongi DM. 2015. The impact of climate change on mangrove forests. *Curr. Clim. Change Rep.* 1:30–39

Alongi DM, Sasekumar A, Chong VC, Pfitzner J, Trott LA, et al. 2004. Sediment accumulation and organic material flux in a managed mangrove ecosystem: estimates of land–ocean–atmosphere exchange in peninsular Malaysia. *Mar. Geol.* 208:383–402

Anthony EJ, Gardel A, Gratiot N, Proisy C, Allison MA, et al. 2010. The Amazon-influenced muddy coast of South America: a review of mud bank–shoreline interactions. *Earth Sci. Rev.* 103:99–121

Auerbach LW, Goodbred SL Jr, Mondal DR, Wilson CA, Ahmed KR, et al. 2015. Flood risk of natural and embanked landscapes on the Ganges–Brahmaputra tidal delta plain. *Nat. Clim. Change* 5:153–57

Balke T, Bouma TJ, Herman PMJ, Horstman EM, Sudtongkong C, Webb EL. 2013. Cross-shore gradients of physical disturbance in mangroves: implications for seedling establishment. *Biogeosciences* 10:5411–19

Bao TQ. 2011. Effect of mangrove forest structures on wave attenuation in coastal Vietnam. *Oceanologia* 53:807–18

Breithaupt JL, Smoak JM, Smith TJ III, Sanders CJ, Hoare A. 2012. Organic carbon burial rates in mangrove sediments: strengthening the global budget. *Glob. Biogeochem. Cycles* 26:GB3011

Cahoon DR. 2006. A review of major storm impacts on coastal wetland elevations. *Estuaries Coasts* 29:889–98

Cahoon DR. 2014. Estimating relative sea-level rise and submergence potential at a coastal wetland. *Estuaries Coasts* 38:1077–84

Cahoon DR, Hensel PF, Spencer T, Reed DJ, McKee KL, Saintilan N. 2006. Coastal wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In *Wetlands and Natural Resource Management*, ed. JTA Verhoeven, B Beltman, R Bobbink, DF Whigham, pp. 271–92. Heidelberg, Ger.: Springer

Cahoon DR, Lynch JC, Perez BC, Segura B, Holland RD, et al. 2002. High-precision measurements of wetland sediment elevation: II. The rod surface elevation table. *J. Sediment. Res.* 72:734–39

Cahoon DR, Marin PE, Black BK, Lynch JC. 2000. A method for measuring vertical accretion, elevation, and compaction of soft, shallow-water sediments. *J. Sediment. Res.* 70:1250–53

Capo S, Sottolichio A, Brenon I, Castaing P, Ferry L. 2006. Morphology, hydrography and sediment dynamics in a mangrove estuary: the Konkoure Estuary, Guinea. *Mar. Geol.* 230:199–215

Chappell J, Thom BG. 1986. Coastal morphodynamics in north Australia: review and prospect. *Aust. Geogr. Stud.* 24:110–27

Clarke PJ. 2014. Seeking global generality: a critique for mangrove modellers. *Mar. Freshw. Res.* 65:930–33

Cobb SM, Saynor MJ, Eliot M, Eliot I, Hall R. 2007. *Saltwater intrusion and mangrove encroachment of coastal wetlands in the Alligator Rivers Region, Northern Territory, Australia*. Supervis. Sci. Rep. 190, Aust. Dep. Environ. Resour., Darwin, Aust.

Comeaux RS, Allison MA, Bianchi TS. 2012. Mangrove expansion in the Gulf of Mexico with climate change: implications for wetland health and resistance to rising sea levels. *Estuar. Coast. Shelf Sci.* 96:81–95

Cowell PJ, Thom BG. 1994. Morphodynamics of coastal evolution. In *Coastal Evolution: Late Quaternary Shoreline Morphodynamics*, ed. RWG Carter, CD Woodroffe, pp. 33–86. Cambridge, UK: Cambridge Univ. Press

Crase B, Liedloff A, Vesk PA, Burgman MA, Wintle BA. 2013. Hydroperiod is the main driver of the spatial pattern of dominance in mangrove communities. *Glob. Ecol. Biogeogr.* 22:806–17

Davies G, Woodroffe CD. 2010. Tidal estuary width convergence: theory and form in North Australian estuaries. *Earth Surf. Process. Landf.* 35:737–49

Davis JH Jr. 1946. *The Peat Deposits of Florida: Their Occurrence, Development and Uses*. Fla. Geol. Surv. Bull. 30. Tallahassee: Fla. Geol. Surv.

Di Nitto D, Neukermans G, Koedam N, Defever H, Pattyn F, et al. 2014. Mangroves facing climate change: landward migration potential in response to projected scenarios of sea level rise. *Biogeosciences* 11:857–71

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Donato DC, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M. 2011. Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* 4:293–97

Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N. 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Change* 3:961–68

Duke NC. 2006. *Australia's Mangroves: The Authoritative Guide to Australia's Mangrove Plants*. Brisbane, Aust.: Univ. Queensland Press

Eliot M, Eliot I. 2012. Interpreting estuarine change in northern Australia: physical responses to changing conditions. *Hydrobiologia* 708:3–21

Ellison JC. 1999. Impact of sediment burial on mangroves. *Mar. Pollut. Bull.* 37:420–26

Ellison JC. 2008. Long-term retrospection on mangrove development using sediment cores and pollen analysis: a review. *Aquat. Bot.* 89:93–104

Ellison JC, Stoddart DR. 1991. Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *J. Coast. Res.* 7:151–65

Erban LE, Gorelick SM, Zebker HA. 2014. Groundwater extraction, land subsidence, and sea-level rise in the Mekong Delta, Vietnam. *Environ. Res. Lett.* 9:084010

Feller IC, Lovelock CE, Berger U, McKee KL, Joye SB, Ball MC. 2010. Biocomplexity in mangrove ecosystems. *Annu. Rev. Mar. Sci.* 2:395–417

FitzGerald DM, Fenster MS, Argow BA, Buynevich IV. 2008. Coastal impacts due to sea-level rise. *Annu. Rev. Earth Planet. Sci.* 36:601–47

Fromard F, Vega C, Proisy C. 2004. Half a century of dynamic coastal change affecting mangrove shorelines of French Guiana: a case study based on remote sensing data analyses and field surveys. *Mar. Geol.* 208:265–80

Gilman E, Ellison J, Duke NC, Field C. 2008. Threats to mangroves from climate change and adaptation options: a review. *Aquat. Bot.* 89:237–50

Giosan L, Syvitski JPM, Constantinescu S, Day J. 2014. Protect the world's deltas. *Nature* 516:31–33

Giri C, Ochieng E, Tieszen LL, Zhiu Z, Singh A, et al. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. *Glob. Ecol. Biogeogr.* 20:154–59

Granek E, Ruttenberg BI. 2008. Changes in biotic and abiotic processes following mangrove clearing. *Estuar. Coast. Shelf Sci.* 80:555–62

Gratiot N, Anthony EJ, Gardel A, Gaucherel C, Proisy C, Wells JT. 2008. Significant contribution of the 18.6 year tidal cycle to regional coastal changes. *Nat. Geosci.* 1:169–72

Grindrod J. 1985. The palynology of mangroves on a prograded shore, Princess Charlotte Bay, North Queensland, Australia. *J. Biogeogr.* 12:323–48

Ha TTT, van Dijk H, Bush SR. 2012. Mangrove conservation or shrimp farmer's livelihood? The devolution of forest management and benefit sharing in the Mekong Delta, Vietnam. *Ocean Coast. Manag.* 69:185–93

Hanebuth TJJ, Kudrass HR, Linstädter J, Islam B, Zander AM. 2013. Rapid coastal subsidence in the central Ganges-Brahmaputra Delta (Bangladesh) since the 17th century deduced from submerged salt-producing kilns. *Geology* 41:987–90

Hanebuth TJJ, Voris HK, Yokoyama Y, Saito Y, Okuno J. 2011. Formation and fate of sedimentary depocentres on Southeast Asia's Sunda Shelf over the past sea-level cycle and biogeographic implications. *Earth Sci. Rev.* 104:92–110

Hemminga MA, Slim FJ, Kazungu J, Ganssen GM, Nieuwenhuize J, Kruyt NM. 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Mar. Ecol. Prog. Ser.* 106:291–301

Ibáñez C, Day JW, Reyes E. 2013. The response of deltas to sea-level rise: natural mechanisms and management options to adapt to high-end scenarios. *Ecol. Eng.* 65:122–30

Janssen-Stelder BM, Augustinus PGEF, van Santen WAC. 2002. Sedimentation in a coastal mangrove system, Red River Delta, Vietnam. *Proc. Mar. Sci.* 5:455–67

Jervey MT. 1988. Quantitative geological modeling of siliciclastic rock sequences and their seismic expression. In *Sea-Level Changes: An Integrated Approach*, ed. CK Wilgus, BS Hastings, H Posamentier, J Van Wagoner, CA Ross, CGSC Kendall, pp. 47–69. SEPM Spec. Publ. 42. Tulsa, OK: Soc. Econ. Paleontol. Mineral.

Knight JM, Dale PER, Dunn RJK, Broadbent GJ, Lemckert CJ. 2008. Patterns of tidal flooding within a mangrove forest: Coombabah Lake, Southeast Queensland, Australia. *Estuar. Coast. Shelf Sci.* 76:580–93
Komiyama A, Ong JE, Poungparn S. 2008. Allometry, biomass and productivity of mangrove forests: a review. *Aquat. Bot.* 89:128–37
Krauss KW, Cahoon DR, Allen JA, Ewel KC, Lynch JC, Cormier N. 2010. Surface elevation change and susceptibility of different mangrove zones to sea-level rise on Pacific high islands of Micronesia. *Ecosystems* 13:129–43
Krauss KW, Doyle TW, Twilley RR, Rivera-Monroy VH, Sullivan JK. 2006. Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. *Hydrobiologia* 569:311–24
Krauss KW, McKee KL, Lovelock CE, Cahoon DR, Saintilan N, et al. 2014. How mangrove forests adjust to rising sea level. *New Phytol.* 202:19–34
Kristensen E, Bouillon S, Dittmar T, Marchand C. 2008. Organic carbon dynamics in mangrove ecosystems: a review. *Aquat. Bot.* 89:201–19
Lee SY. 1995. Mangrove outwelling: a review. *Hydrobiologia* 295:203–12
Li Z, Saito Y, Mao L, Tamura T, Li Z, et al. 2012. Mid-Holocene mangrove succession and its response to sea-level change in the upper Mekong River delta, Cambodia. *Quat. Res.* 78:386–99
López-Medellin X, Ezcurra E, González-Abraham C, Hak J, Santiago LS, Sickman JO. 2011. Oceanographic anomalies and sea-level rise drive mangroves inland in the Pacific coast of Mexico. *J. Veg. Sci.* 22:143–51
Lovelock CE, Adame MF, Bennion V, Hayes M, O'Mara J, et al. 2014. Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of South East Queensland, Australia. *Estuaries Coasts* 37:763–71
Lovelock CE, Adame MF, Bennion V, Hayes M, Reef R, et al. 2015. Sea level and turbidity controls on mangrove soil surface elevation change. *Estuar. Coast. Shelf Sci.* 153:1–9
Lovelock CE, Bennion V, Grinham A, Cahoon DR. 2011a. The role of surface and subsurface processes in keeping pace with sea level rise in intertidal wetlands of Moreton Bay, Queensland, Australia. *Ecosystems* 14:745–57
Lovelock CE, Feller IC, Adame MF, Reef R, Penrose HM, et al. 2011b. Intense storms and the delivery of materials that relieve nutrient limitations in mangroves of an arid zone estuary. *Funct. Plant Biol.* 38:514–22
Lovelock CE, Ruess RW, Feller IC. 2011c. CO_2 efflux from cleared mangrove peat. *PLOS ONE* 6:e21279
Lovelock CE, Sorrell B, Hancock N, Hua Q, Swales A. 2010. Mangrove forest and soil development on a rapidly accreting shore in New Zealand. *Ecosystems* 13:437–51
Lucas RM, Mitchell AL, Rosenqvist A, Proisy C, Melius A, Ticehurst C. 2007. The potential of L-band SAR for quantifying mangrove characteristics and change: case studies from the tropics. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 17:245–64
Lugo AE, Snedaker SC. 1974. The ecology of mangroves. *Annu. Rev. Ecol. Syst.* 5:39–64
Macintyre IG, Toscano MA, Bond GB. 2004. Holocene history of the mangrove islands of Twin Cays, Belize, Central America. *Atoll Res. Bull.* 510:1–16
Mazda Y, Kanazawa K, Wolanski E. 1995. Tidal asymmetry in mangrove creeks. *Hydrobiologia* 295:51–58
McCloskey TA, Liu K-B. 2013. Sedimentary history of mangrove cays in Turneffe Islands, Belize: evidence for sudden environmental reversals. *J. Coast. Res.* 29:971–83
McIvor AL, Spencer T, Möller I, Spalding M. 2013. *The response of mangrove soil surface elevation to sea level rise.* Nat. Coast. Prot. Ser. Rep. 3, Cambridge Coast. Res. Unit Work. Pap. 3, Nat. Conserv., Arlington, VA, and Wetl. Int., Wageningen, Neth.
McKee KL. 1993. Soil physicochemical patterns and mangrove species distribution: reciprocal effects? *J. Ecol.* 81:477–87
McKee KL. 2011. Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuar. Coast. Shelf Sci.* 91:475–83
McKee KL, Cahoon DR, Feller IC. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Glob. Ecol. Biogeogr.* 16:545–56
McKee KL, Faulkner PL. 2000. Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize. *Atoll Res. Bull.* 468:46–58

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

McKee KL, Rogers K, Saintilan N. 2012. Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In *Global Change and the Function and Distribution of Wetlands*, ed. BA Middleton, pp. 63–96. New York: Springer

McKee KL, Vervaeke WC. 2009. Impacts of human disturbance on soil erosion potential and habitat stability of mangrove-dominated islands in the Pelican Cays and Twin Cays Ranges, Belize. *Smithson. Contrib. Mar. Sci.* 38:415–27

McLeod E, Chmura GL, Bouillon S, Salm R, Björk M, et al. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Front. Ecol. Environ.* 9:552–60

Mendelssohn IA, Morris JT. 2000. Ecophysiological controls on the growth of *Spartina alterniflora*. In *Concepts and Controversies in Tidal Marsh Ecology*, ed. NP Weinstein, DA Kreeger, pp. 59–80. Dordrecht, Neth.: Kluwer

Middleton BA, McKee KL. 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. *J. Ecol.* 89:818–28

Mulrennan ME, Woodroffe CD. 1998. Saltwater intrusion into coastal plains of the Lower Mary River, Northern Territory, Australia. *J. Environ. Manag.* 54:169–88

Nascimento WR, Souza Filho PWM, Proisy C, Lucas RM, Rosenqvist A. 2013. Mapping changes in the largest continuous Amazonian mangrove belt using object-based classification of multisensor satellite imagery. *Estuar. Coast. Shelf Sci.* 117:83–93

Nolte S, Koppenaal EC, Esselink P, Dijkema KS, Schuerch M, et al. 2013. Measuring sedimentation in tidal marshes: a review on methods and their applicability in biogeomorphological studies. *J. Coast. Conserv.* 17:301–25

Oliver TSN, Rogers K, Chafer CJ, Woodroffe CD. 2012. Measuring, mapping and modelling: an integrated approach to the management of mangrove and saltmarsh in the Minnamurra River estuary, southeast Australia. *Wetl. Ecol. Manag.* 20:353–71

Pendleton L, Donato DC, Murray BC, Crooks S, Jenkins WA, et al. 2012. Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *PLOS ONE* 7:e43542

Pethick J, Orford JD. 2013. Rapid rise in effective sea-level in southwest Bangladesh: its causes and contemporary rates. *Glob. Planet. Change* 111:237–45

Phan LK, van Thiel de Vries JSM, Stive MJF. 2015. Coastal mangrove squeeze in the Mekong Delta. *J. Coast. Res.* 31:233–43

Phan NH, Hoang TS. 1993. *Mangroves of Vietnam*. Bangkok: IUCN

Phien-wej N, Giao PH, Nutalaya P. 2006. Land subsidence in Bangkok. *Eng. Geol.* 82:187–201

Pomar L, Kendall CG. 2008. Architecture of carbonate platforms: a response to hydrodynamics and evolving ecology. In *Controls on Carbonate Platform and Reef Development*, ed. J Lukasik, JA Simo, pp. 187–216. Tulsa, OK: Soc. Sediment. Geol.

Proisy C, Gratiot N, Anthony EJ, Gardel A, Fromard F, Heuret P. 2009. Mud bank colonization by opportunistic mangroves: a case study from French Guiana using lidar data. *Cont. Shelf Res.* 29:632–41

Proske U, Hanebuth TJJ, Behling H, Nguyen VL, Ta TKO, Diem BP. 2010. The palaeoenvironmental development of the northeastern Vietnamese Mekong River Delta since the mid Holocene. *Holocene* 20:1257–68

Quartel S, Kroon A, Augustinus PGEF, Van Santen P, Tri NH. 2007. Wave attenuation in coastal mangroves in the Red River Delta, Vietnam. *J. Asian Earth Sci.* 29:576–84

Rogers K, Saintilan N. 2008. Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *J. Coast. Res.* 24A:63–69

Rogers K, Saintilan N, Cahoon D. 2005. Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetl. Ecol. Manag.* 13:587–98

Rogers K, Saintilan N, Copeland C. 2012. Modelling wetland surface elevation dynamics and its application to forecasting the effects of sea-level rise on estuarine wetlands. *Ecol. Model.* 244:148–57

Rogers K, Saintilan N, Copeland C. 2013a. Managed retreat of saline coastal wetlands: challenges and opportunities identified from the Hunter River Estuary, Australia. *Estuaries Coasts* 37:67–78

Rogers K, Saintilan N, Howe AJ, Rodriguez JF. 2013b. Sedimentation, elevation and marsh evolution in a southeastern Australian estuary during changing climatic conditions. *Estuar. Coast. Shelf Sci.* 133:172–81

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Rogers K, Saintilan N, Woodroffe CD. 2014. Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: implications for coastal wetland response to climate change. *Estuar. Coast. Shelf Sci.* 149:46–56

Rogers K, Wilton KM, Saintilan N. 2006. Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuar. Coast. Shelf Sci.* 66:559–69

Saintilan N, Rogers K, Mazumder D, Woodroffe CD. 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. *Estuar. Coast. Shelf Sci.* 128:84–92

Sanders CJ, Smoak JM, Naidu AS, Patchineelam SR. 2008. Recent sediment accumulation in a mangrove forest and its relevance to local sea-level rise (Ilha Grande, Brazil). *J. Coast. Res.* 24:533–36

Semeniuk V. 2013. Predicted response of coastal wetlands to climate changes: a Western Australian model. *Hydrobiologia* 708:23–43

Shearman PL. 2010. Recent change in the extent of mangroves in the Northern Gulf of Papua. *Ambio* 39:181–89

Siikamaki J, Sanchirico JN, Jardine SL. 2012. Global economic potential for reducing carbon dioxide emissions from mangrove loss. *PNAS* 109:14369–74

Smajgl A, Toan TQ, Nhan DK, Ward J, Trung NH, et al. 2015. Responding to rising sea levels in the Mekong Delta. *Nat. Clim. Change* 5:167–74

Smith TJ, Anderson GH, Balentine K, Tiling G, Ward GA, Whelan KR. 2009. Cumulative impacts of hurricanes on Florida mangrove ecosystems: sediment deposition, storm surges and vegetation. *Wetlands* 29:24–34

Smoak JM, Breithaupt JL, Smith TJ III, Sanders CJ. 2012. Sediment accretion and organic carbon burial relative to sea-level rise and storm events in two mangrove forests in Everglades National Park. *Catena* 104:58–66

Soares MLG. 2009. A conceptual model for the responses of mangrove forests to sea level rise. *J. Coast. Res.* Spec. Issue 56:267–71

Spalding M, Kainuma M, Collins L. 2010. *World Atlas of Mangroves*. Washington, DC: Earthscan

Swales A, Bentley SJ Sr, Lovelock CE. 2015. Mangrove-forest evolution in a sediment-rich estuarine system: opportunists or agents of geomorphic change? *Earth Surf. Process. Landf.* 40:1672–87

Syvitski JPM, Kettner AJ, Overeem I, Hutton EWH, Hannon MT, et al. 2009. Sinking deltas due to human activites. *Nat. Geosci.* 2:681–86

Ta TKO, Nguyen VL, Tateishi M, Kobayashi I, Tanabe S, Saito Y. 2002. Holocene delta evolution and sediment discharge of the Mekong River, southern Vietnam. *Quat. Sci. Rev.* 21:1807–19

Tamura T, Saito Y, Nguyen VL, Ta KO, Bateman MD, et al. 2012. Origin and evolution of interdistributary delta plains; insights from Mekong River delta. *Geology* 40:303–6

Tamura T, Saito Y, Sieng S, Ben B, Kong M, et al. 2009. Initiation of the Mekong River delta at 8 ka: evidence from the sedimentary succession in the Cambodian lowland. *Quat. Sci. Rev.* 28:327–44

Thom BG. 1967. Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. *J. Ecol.* 55:301–43

Thom BG. 1982. Mangrove ecology: a geomorphological perspective. In *Mangrove Ecosystems in Australia: Structure, Function and Management*, ed. BF Clough, pp. 3–17. Canberra: Aust. Natl. Univ. Press

Törnqvist TE, Wallace DJ, Storms JEA, Wallinga J, van Dam RL, et al. 2008. Mississippi delta subsidence primarily caused by compaction of Holocene strata. *Nat. Geosci.* 1:173–76

Toscano MA, Macintyre IG. 2003. Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated ^{14}C dates from *Acropora palmata* framework and intertidal mangrove peat. *Coral Reefs* 22:257–70

Traill LW, Perhans K, Lovelock CE, Prohaska A, McFallan S, et al. 2011. Managing for change: wetland transitions under sea-level rise and outcomes for threatened species. *Divers. Distrib.* 17:1225–33

Tue NT, Dung LV, Nhuan MT, Omori K. 2014. Carbon storage of a tropical mangrove forest in Mui Ca Mau National Park, Vietnam. *Catena* 121:119–26

Twilley RR. 1985. The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. *Estuar. Coast. Shelf Sci.* 20:543–57

Twilley RR, Chen RH, Hargis T. 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water Air Soil Pollut.* 64:265–88

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Twilley RR, Rivera-Monroy VH. 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. *J. Coast. Res.* Spec. Issue 40:79–93

Twilley RR, Rivera-Monroy VH. 2009. Ecogeomorphic models of nutrient biogeochemistry for mangrove wetlands. In *Coastal Wetlands: An Integrated Ecosystem Approach*, ed. GME Perillo, E Wolanski, DR Cahoon, MM Brinson, pp. 641–83. Amsterdam: Elsevier

van Loon AF, Dijksma R, Van Menswoort MEF. 2007. Hydrological classification in mangrove areas: a case study in Can Gio, Vietnam. *Aquat. Bot.* 87:80–82

Van Santen P, Augustinus PGEF, Janssen-Stelder BM, Quartel S, Tri NH. 2007. Sedimentation in an estuarine mangrove system. *J. Asian Earth Sci.* 29:566–75

Walsh JP, Nittrouer CA. 2004. Mangrove-bank sedimentation in a mesotidal environment with large sediment supply, Gulf of Papua. *Mar. Geol.* 208:225–48

Walsh JP, Nittrouer CA. 2009. Understanding fine-grained river-sediment dispersal on continental margins. *Mar. Geol.* 263:34–45

Watson JG. 1928. *Mangrove Forests of the Malay Peninsula*. Malay. For. Rec. 6. Singapore: Fraser & Neave

Webb EL, Friess DA, Krauss KW, Cahoon DR, Guntenspergen GR, Phelps J. 2013. A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. *Nat. Clim. Change* 3:458–65

Whelan KRT, Smith TJ, Cahoon DR, Lynch JC, Anderson GH. 2005. Groundwater control of mangrove surface elevation: Shrink and swell varies with soil depth. *Estuaries* 28:833–43

Wilson CA, Goodbred SL Jr. 2015. Construction and maintenance of the Ganges-Brahmaputra-Meghna Delta: linking process, morphology, and stratigraphy. *Annu. Rev. Mar. Sci.* 7:67–88

Winn KO, Saynor MJ, Eliot MJ, Eliot I. 2006. Saltwater intrusion and morphological change at the mouth of the East Alligator River, Northern Territory. *J. Coast. Res.* 22:137–49

Wolanski E. 2006. The sediment trapping efficiency of the macro-tidal Daly Estuary, tropical Australia. *Estuar. Coast. Shelf Sci.* 69:291–98

Wolanski E, Chappell J. 1996. The response of tropical Australian estuaries to a sea level rise. *J. Mar. Syst.* 7:267–79

Wolanski E, Mazda Y, Ridd PV. 1992. Mangrove hydrodynamics. In *Tropical Mangrove Ecosystems*, ed. AI Robertson, DM Alongi, pp. 43–62. Washington, DC: Am. Geophys. Union

Woodroffe CD. 1990. The impact of sea-level rise on mangrove shorelines. *Prog. Phys. Geogr.* 14:483–520

Woodroffe CD. 1992. Mangrove sediments and geomorphology. In *Tropical Mangrove Ecosystems*, ed. AI Robertson, DM Alongi, pp. 7–41. Washington, DC: Am. Geophys. Union

Woodroffe CD. 1993. Late Quaternary evolution of coastal and lowland riverine plains of Southeast Asia and northern Australia: an overview. *Sediment. Geol.* 83:163–73

Woodroffe CD. 1995. Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. *Earth Surf. Process. Landf.* 20:65–85

Woodroffe CD, Lovelock CE, Rogers K. 2014. Mangrove shorelines. In *Coastal Environments and Global Change*, ed. G Masselink, R Gehrels, pp. 251–67. Chichester, UK: Wiley & Sons

Woodroffe CD, Mulrennan ME, Chappell J. 1993. Estuarine infill and coastal progradation, southern van Diemen Gulf, northern Australia. *Sediment. Geol.* 83:257–75

Woodroffe CD, Saito Y. 2011. River-dominated coasts. In *Treatise on Estuarine and Coastal Science*, ed. E Wolanski, DS McLusky, pp. 117–35. Waltham, MA: Academic

Yang J, Gao J, Cheung A, Liu B, Schwendenmann L, Costello MJ. 2013. Vegetation and sediment characteristics in an expanding mangrove forest in New Zealand. *Estuar. Coast. Shelf Sci.* 134:11–18

Yang J, Gao J, Liu B, Zhang W. 2014. Sediment deposits and organic carbon sequestration along mangrove coasts of the Leizhou Peninsula, southern China. *Estuar. Coast. Shelf Sci.* 136:3–10

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Annual Review of Marine Science

Volume 8, 2016

Contents

Global Ocean Integrals and Means, with Trend Implications
Carl Wunsch 1

Visualizing and Quantifying Oceanic Motion
T. Rossby 35

Cross-Shelf Exchange
K.H. Brink 59

Effects of Southern Hemisphere Wind Changes on the Meridional Overturning Circulation in Ocean Models
Peter R. Gent 79

Near-Inertial Internal Gravity Waves in the Ocean
Matthew H. Alford, Jennifer A. MacKinnon, Harper L. Simmons, and Jonathan D. Nash 95

Mechanisms of Physical-Biological-Biogeochemical Interaction at the Oceanic Mesoscale
Dennis J. McGillicuddy Jr. 125

The Impact of Submesoscale Physics on Primary Productivity of Plankton
Amala Mahadevan 161

Changes in Ocean Heat, Carbon Content, and Ventilation: A Review of the First Decade of GO-SHIP Global Repeat Hydrography
L.D. Talley, R.A. Feely, B.M. Sloyan, R. Wanninkhof, M.O. Baringer, J.L. Bullister, C.A. Carlson, S.C. Doney, R.A. Fine, E. Firing, N. Gruber, D.A. Hansell, M. Ishii, G.C. Johnson, K. Katsumata, R.M. Key, M. Kramp, C. Langdon, A.M. Macdonald, J.T. Mathis, E.L. McDonagh, S. Mecking, F.J. Millero, C.W. Mordy, T. Nakano, C.L. Sabine, W.M. Smethie, J.H. Swift, T. Tanhua, A.M. Thurnherr, M.J. Warner, and J.-Z. Zhang 185

Characteristic Sizes of Life in the Oceans, from Bacteria to Whales
K.H. Andersen, T. Berge, R.J. Gonçalves, M. Hartvig, J. Heuschele, S. Hylander, N.S. Jacobsen, C. Lindemann, E.A. Martens, A.B. Neuheimer, K. Olsson, A. Palacz, A.E.F. Prowe, J. Sainmont, S.J. Traving, A.W. Visser, N. Wadhwa, and T. Kiørboe 217

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Mangrove Sedimentation and Response to Relative Sea-Level Rise
C.D. Woodroffe, K. Rogers, K.L. McKee, C.E. Lovelock, I.A. Mendelssohn, and N. Saintilan 243

The Great *Diadema antillarum* Die-Off: 30 Years Later
H.A. Lessios 267

Growth Rates of Microbes in the Oceans
David L. Kirchman 285

Slow Microbial Life in the Seabed
Bo Barker Jørgensen and Ian P.G. Marshall 311

The Thermodynamics of Marine Biogeochemical Cycles: Lotka Revisited
Joseph J. Vallino and Christopher K. Algar 333

Multiple Stressors in a Changing World: The Need for an Improved Perspective on Physiological Responses to the Dynamic Marine Environment
Alex R. Gunderson, Eric J. Armstrong, and Jonathon H. Stillman 357

Nitrogen and Oxygen Isotopic Studies of the Marine Nitrogen Cycle
Karen L. Casciotti 379

Sources, Ages, and Alteration of Organic Matter in Estuaries
Elizabeth A. Canuel and Amber K. Hardison 409

New Approaches to Marine Conservation Through the Scaling Up of Ecological Data
Graham J. Edgar, Amanda E. Bates, Tomas J. Bird, Alun H. Jones, Stuart Kininmonth, Rick D. Stuart-Smith, and Thomas J. Webb 435

Ecological Insights from Pelagic Habitats Acquired Using Active Acoustic Techniques
Kelly J. Benoit-Bird and Gareth L. Lawson 463

Ocean Data Assimilation in Support of Climate Applications: Status and Perspectives
D. Stammer, M. Balmaseda, P. Heimbach, A. Köhl, and A. Weaver 491

Ocean Research Enabled by Underwater Gliders
Daniel L. Rudnick 519

Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at http://www.annualreviews.org/errata/marine

Annu. Rev. Mar. Sci. 2016.8:243-266. Downloaded from www.annualreviews.org
Access provided by University of Wollongong on 09/08/16. For personal use only.

Relationships between Surface Elevation and Groundwater in Mangrove Forests of Southeast Australia

Author(s): Kerrylee Rogers and Neil Saintilan

Source: *Journal of Coastal Research*, Jan., 2008, Vol. 24, No. 1A, Supplement (Jan., 2008), pp. 63-69

Published by: Coastal Education & Research Foundation, Inc.

Stable URL: https://www.jstor.org/stable/30133721

REFERENCES
Linked references are available on JSTOR for this article:
https://www.jstor.org/stable/30133721?seq=1&cid=pdf-reference#references_tab_contents
You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at https://about.jstor.org/terms

is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Coastal Research*

This content downloaded from
123.243.247.113 on Sat, 29 Jun 2024 03:25:39 +00:00
All use subject to https://about.jstor.org/terms

Journal of Coastal Research	24	1A	63–69	West Palm Beach, Florida	January 2008

Relationships between Surface Elevation and Groundwater in Mangrove Forests of Southeast Australia

Kerrylee Rogers and Neil Saintilan*

Department of Environment and Conservation
P.O. Box A290
Sydney South, NSW, 1232
Australia
N.Saintlan@mackillop.acu.edu.au

ABSTRACT

ROGERS, K. and SAINTILAN, N., 2008. Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *Journal of Coastal Research,* 24(1A), 63–69. West Palm Beach (Florida), ISSN 0749-0208.

Mangrove surface elevation was measured by means of the Surface Elevation Table and Marker Horizon technique (SET-MH) in a range of settings in southeastern Australia. Despite sustained vertical accretion, surface elevation declined at most sites with the onset of an El Niño drought in 2001–2002. At these sites, the Southern Oscillation Index accounted for 70–85% of variability in surface elevation over a 3-year period. At deltaic island sites, this trend was not evident, an observation we attribute to lower terrestrial groundwater inputs. At one site (Homebush Bay), a high correlation was found between surface elevation and groundwater depth, monitored approximately every 2 weeks for 4 months. At the same site, the diurnal astronomical tide was also found to significantly affect mangrove surface elevation, although not to the extent of the El Niño drought. Models of the response of mangroves to sea-level rise on the basis of contemporary processes should account for short-term perturbations, such as climate variability at regional and local scales.

ADDITIONAL INDEX WORDS: *Mangrove, Australia, elevation, sea level, groundwater.*

INTRODUCTION

Global climate change and increased relative sea level are likely to pose a threat to coastal ecosystems, such as mangrove and salt marsh (WOODROFFE, 1990; SEMENIUK, 1994; FIELD, 1995; BLASCO, SAENGER, and JANODET, 1996; SIMAS, NUNES, and FERRERIA, 2001). Because the location of mangrove and salt marsh communities are controlled by tidal elevation, any changes in tidal heights or amplitude, through sea-level rise, will force these systems to either adapt by increasing their elevation through processes of vertical sedimentation (REED, 1990, 1995), by physically changing the vegetation structure (*e.g.,* higher pneumatophores), or by migrating horizontally upslope (ORSON, PANAGEOTOU, and LEATHERMAN, 1985; VANDERZEE, 1988). Without an adequate response to sea-level rise, erosion, flooding, and loss of these ecosystems may be inevitable (SIMAS, NUNES, and FERRERIA, 2001). This may be particularly evident in cases where sediment loads are insufficient or anthropogenic structures (*e.g.,* developments and coastal protection) or the natural environment (*e.g.,* steep slope or competition at marsh boundary) prevent upslope migration.

Despite these predictions, the response of these systems to gradual or rapid sea-level rise remains largely unknown, particularly because the capacity of a wetland to respond to sea-level rise is more complex than sedimentation or upslope ecosystem migration alone (CAHOON, DAY, and REED, 1999). Policy makers are aware of the need to consider sea-level rise in coastal planning and management. Yet our understanding of marsh elevation dynamics in relation to sea level and the impacts of projected sea-level rise on these environments is limited (WOODROFFE, 1990; CALLAWAY, DELAUNE, and PATRICK, 1997). This lack of knowledge on ecosystem response to sea-level rise provides little basis for planning for future ecosystem protection. Research into the relationship between marsh elevation, mangrove, and salt marsh distribution and sea-level change provides the first step toward modeling the response of coastal marshes to sea-level rise and the possibility of improved management of coastal wetlands for future sea-level increases.

The capacity of a wetland to keep pace with sea-level rise is defined by a greater range of factors than sedimentation alone (KAYE and BARGHOORN, 1964; REED and CAHOON, 1993; DELAUNE, BAUMANN, and GOSSELINK, 1983), because marsh surface elevation is also influenced by autocompaction, groundwater discharge, and plant productivity. Interactions between these factors and sea level are complex, and their relative contribution to surface elevation trends varies over a range of temporal scales (CAHOON *et al.,* in press).

The measurement of these factors has been simplified by the development of the Surface Elevation Table and Marker Horizon technique (SET-MH). SET is a benchmark against which surface elevation may be measured (BOUMANS and DAY, 1993; CAHOON *et al.,* 2002). SET is a powerful tool for not only documenting the elevation trends of a wetland with

DOI:10.2112/05-0519.1 received 5 September 2005; accepted in revision 7 September 2005.
*Corresponding author.

This content downloaded from
123.243.247.113 on Sat, 29 Jun 2024 03:25:39 +00:00
All use subject to https://about.jstor.org/terms

respect to sea level, but also, when used in conjunction with marker horizons, in distinguishing the factors contributing to these trends over a range of timescales. However, an accurate assessment of the elevation trajectory of a wetland requires a data set sufficiently complete to include most of the forcing factors.

Recent studies that used SET-MH have emphasized the importance of below-ground processes in contributing to soil volume and marsh surface elevation. Mass mangrove mortality has been linked to elevation decline through peat collapse (CAHOON, FORD, and HENSEL, 2004). Conversely, root volume expansion leads to measurable increases in mangrove surface elevation (ROGERS, SAINTILAN, and HEIJNIS, 2005; CAHOON *et al.*, in press).

Tidal flooding may significantly alter soil water storage and soil volume through shrink and swell. For example, as a result of rising tides, increases in salt marsh elevation were observed (HARRISON and BLOOM, 1977). This was probably caused by the infiltration of tidal waters within sediments, causing the sediments to swell as a result of increased water storage (NUTTLE, HEMOND, and STOLZENBACH, 1990). In addition, a recent study detected significant changes in marsh elevation as a result of variability in evapotranspiration and tidal flooding by comparing elevation measures taken at low tide in the middle of the day, when evapotranspiration was high, with measures taken late in the day, when soil water storage from the recent high tide was likely to remain high as a result of low evapotranspiration (PAQUETTE *et al.*, 2004).

Recent studies in the Everglades have also found a significant relationship between surface-water stage and marsh elevation (CAHOON *et al.*, 2003; SMITH and CAHOON, 2003). CAHOON, REED, and DAY (1995) argue that seasonal variation in mean water level and/or increases in the depth of inundations resulted in increased water storage and surface elevation increases. Similarly, decreases in marsh elevations during a summer without floodings likely caused shrinkage of thick subsurface clay layers in the marshes in Europe (VAN WIJNEN and BAKKER, 2001). It was evident that shrink-swell of sediments was mainly influenced by organic matter content (KNOTT, NUTTLE, and HEMOND, 1987; CAHOON, REED, and DAY, 1995) and bulk density (CAHOON, REED, and DAY, 1995; VAN WIJNEN and BAKKER, 2001).

Groundwater may also directly influence marsh elevation by altering the soil volume. Significant correlations between marsh elevation change and groundwater head pressure highlight the role of groundwater in altering marsh elevation (WHELAN *et al.*, 2005). It may be likely that the high rainfall event described by CAHOON and LYNCH (1997) infiltrated groundwaters and significantly increased soil volume. Subsurface drainage may also be responsible for marsh elevation changes in response to storms and hurricanes (CAHOON, 2003). In Australia, wetland reclamation was purported to have caused soil compaction as a result of artificial decreases in the water table (BELPERIO, 1993). However, the association between groundwater and coastal wetland elevation has never been measured in the region.

Here, we aim to document mangrove surface elevation change over three temporal scales. First, interannual variability in marsh surface elevations are explored at a range of sites in southeastern Australia before and during an El Niño drought. The El Niño Southern Oscillation is monitored using the Southern Oscillation Index (SOI) in the supposition that the SOI represents a range of factors (temperature, rainfall, tidal level) that autocorrelate to influence groundwater levels in coastal wetlands.

Second, surface elevation and groundwater levels in a representative mangrove forest are monitored approximately every 2 weeks to determine the relative contribution of terrestrial groundwater inputs on mangrove surface elevation. These measures are taken at low tide to control for the influence of hydroperiod. Finally, mangrove surface elevation in the same wetland is measured between a spring high and low tide at a range of elevations to determine the relative contribution of astronomical tides on wetland elevation.

METHODS

Marsh surface elevation change was measured with a SET (version IV; CAHOON *et al.*, 2002). SET measures changes in sediment surface elevation. SET consists of a vertical benchmark, an aluminium base support pipe driven 4–6 m into the marsh surface to the point of refusal, and a portable instrument from which measures are made. The portable component consists of a vertical arm that fits onto the support pipe, and an accurately leveled horizontal arm that extends across the marsh surface. From a plate at the end of the horizontal arm, pins may be lowered to the marsh surface, and the length of the pin above the horizontal plate is measured. Relative changes in mean pin length over time provide an estimate of marsh surface elevation change (CAHOON, REED, and DAY, 1995; DAY and LYNCH, 1997; CAHOON, DAY, and REED, 1999; FORD, CAHOON, and LYNCH, 1999).

Marsh surface elevation change is influenced by subsurface processes and surface processes (CAHOON, REED, and DAY, 1995). Surface processes were determined by measuring vertical accretion using MHs. These horizons served as markers against which vertical accretion was measured. To establish the vertical thickness of sediment accreted, the distance from the marsh surface to the marker horizon was measured from minicores taken from each MH site. The degree that subsurface processes influence marsh surface elevation was determined by the difference between surface elevation change and surface processes.

This article reports on results from sites with the longest time period of measurement (>24 months). Of these, two sites were deltaic islands, consisting entirely of coastal wetland, either mangrove, salt marsh, or Casuarina forest. These sites afforded the opportunity to study wetlands with negligible groundwater inputs from adjacent hinterlands. The remaining sites had the potential to receive groundwater flows from adjacent hills, these being Homebush Bay, Parramatta River; Currambene Creek, Jervis Bay; and French Island, Koo Wee Rup, and Rhyll, Western Port Bay (Figure 1). A replicate group of three SETs was established in each mangrove forest. At the time of SET installation, three 0.25-m^2 feldspar MHs were established on the marsh surface around the perimeter of each SET. SETs and MHs were sampled approximately every 6–12 months.

This content downloaded from
123.243.247.113 on Sat, 29 Jun 2024 03:25:39 +00:00
All use subject to https://about.jstor.org/terms

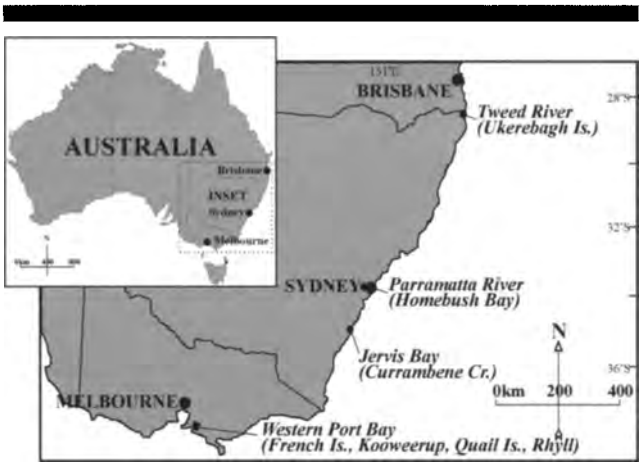


Figure 1. Location of study sites.

Cumulative graphs of surface elevation change and vertical accretion were produced for each study site. Where sufficient elevation change data was collected, graphs of the relationship between surface elevation change and the Southern Oscillation Index (SOI) (BUREAU OF METEOROLOGY, 2004a) were produced for each study site. Regression analyses were performed on mean rates of surface elevation change and SOI to determine whether the relationships were significant at each study site.

To examine the influence of groundwater height on marsh surface elevation, marsh surface elevation measures were taken in conjunction with measures of groundwater depth at five SETs at Homebush Bay, one in the salt marsh zone, one in the mixed zone, and three in the mangrove zone. Measurements were taken on 2 February 2004, 16 February 2004, 1 March 2004, 29 March 2004, and 31 May 2004.

To measure groundwater depth, perforated plastic pipes were inserted vertically into the marsh surface at approximately the same depth as SET aluminium poles. The groundwater height was then determined at the time of SET measurement by lowering a weighted string into the groundwater pipe until contact was made with the groundwater. The length of the weighted string was measured from the marsh surface to the groundwater.

Regression analysis was performed on mean incremental change in groundwater depth and marsh surface elevation to determine whether a significant relationship existed between changes in groundwater depth and marsh surface elevation.

Tidal flooding, water stage, and evapotranspiration have been identified in numerous studies as a potential driving force behind marsh elevation changes (NUTTLE, HEMOND, and STOLZENBACH, 1990; CAHOON, REED, and DAY, 1995; CAHOON and LYNCH, 1997; VAN WIJNEN and BAKKER, 2001; SMITH and CAHOON, 2003). Evapotranspiration and tidal flooding have also been implicated as a potential source of error for SETs (PAQUETTE *et al.*, 2004). SET measures in this study were consistently taken during low tides when marshes were not inundated. However, to ascertain whether exposure of marsh sediments after inundation led to significant decreases in marsh surface elevation, marsh elevation changes were investigated over an inundation cycle at Homebush Bay.

To examine the influence of tide height on surface elevation, SET measurements were repeated at Homebush Bay from peak high tide to low tide on 23 January 2004. SET measurements were taken continuously at one SET in the mangrove zone, mixed zone, and salt marsh zone. Measures of pin length were subtracted from the previous measurements to determine a relative change in surface elevation per pin per sampling period (*i.e.*, Sample 1 − Baseline; Sample 2 − Sample 1). Errors were estimated on the basis of the contribution of SET measurement error to the overall pin length.

RESULTS

Marsh Surface Elevation, El Niño, and SOI at Study Sites

Despite sustained vertical accretion, most sites exhibited a decrease in marsh surface elevation during the drought period of 2001–2002 (Figure 2). This decrease in surface elevation during the drought was not evident in the two sites situated on deltaic islands (Ukerebagh Island and Quail Island). For all sites not located on deltaic islands, positive correlations were evident between rates of surface elevation change and SOI in the mangrove zone (Figure 3). In the two sites situated on deltaic islands, the trend was not evident (Figure 4).

Marsh Surface Elevation and Groundwater

A significant positive relationship existed between incremental changes in marsh surface elevation and incremental changes in groundwater depth where both were measured at Homebush Bay ($r^2 = 0.7654$, $p = 0.0230$, Figure 5). Changes in groundwater depth reflected monthly rainfall between January and June 2004.

Marsh Surface Elevation and Inundation Stage

By taking repeated SET measures from peak high tide to low tide at Homebush Bay, the influence of inundation stage on marsh surface elevation was examined. Surface elevation increased in the salt marsh zone by a maximum of 0.83 mm over the tidal cycle and a maximum of 0.54 mm within a sampling interval (Figure 6). In the mixed zone, surface elevation decreased by a maximum of 1.75 mm over the tidal cycle and 1.10 mm between sampling intervals, while surface elevation decreased by a maximum of 3.72 mm in the mangrove zone over the tidal cycle and 1.49 mm between sampling periods.

Incremental changes in surface elevation between sampling periods did not exceed measurement errors reported by CAHOON *et al.* (2002). However, cumulative surface elevation change over the tidal cycle exceeded what may be attributed to measurement error within the mixed and mangrove zones. Surface elevation decrease in the mangrove zone by 1530 was significantly greater than the first sampling period ($p = 0.002$), while incremental rates of change were significantly greater in the final sampling period in the mangrove zone ($p < 0.001$).

This content downloaded from
123.243.247.113 on Sat, 29 Jun 2024 03:25:39 +00:00
All use subject to https://about.jstor.org/terms

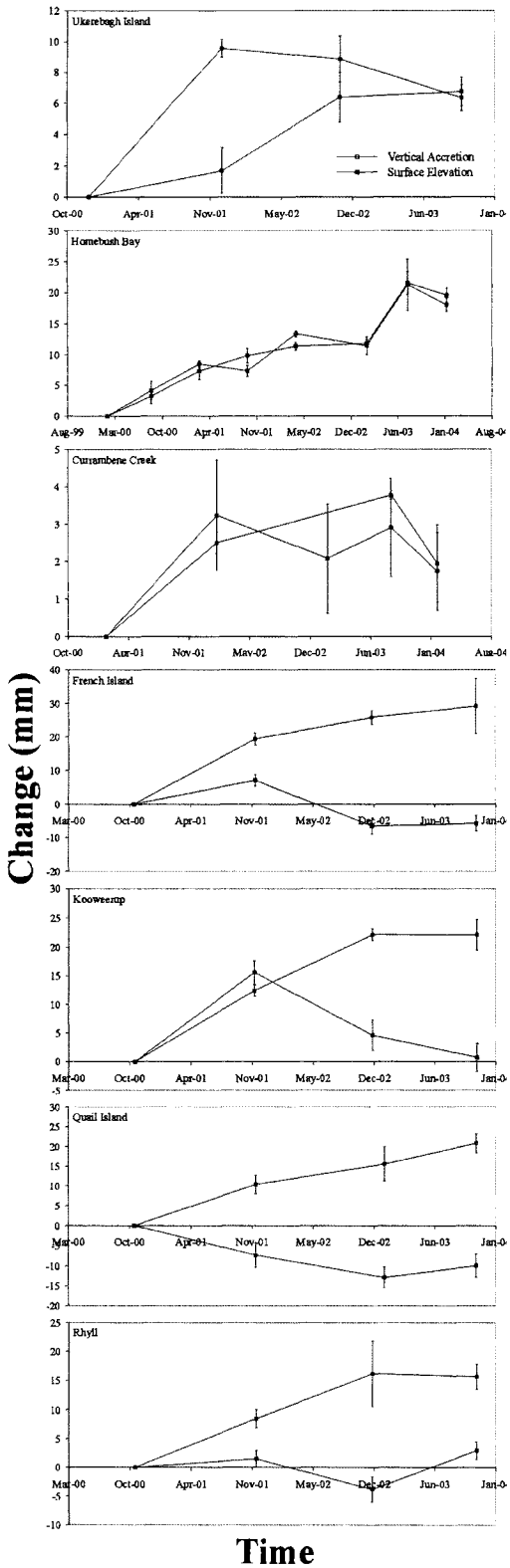


Figure 2. Cumulative surface elevation change and vertical accretion at study sites throughout Southeastern Australia.

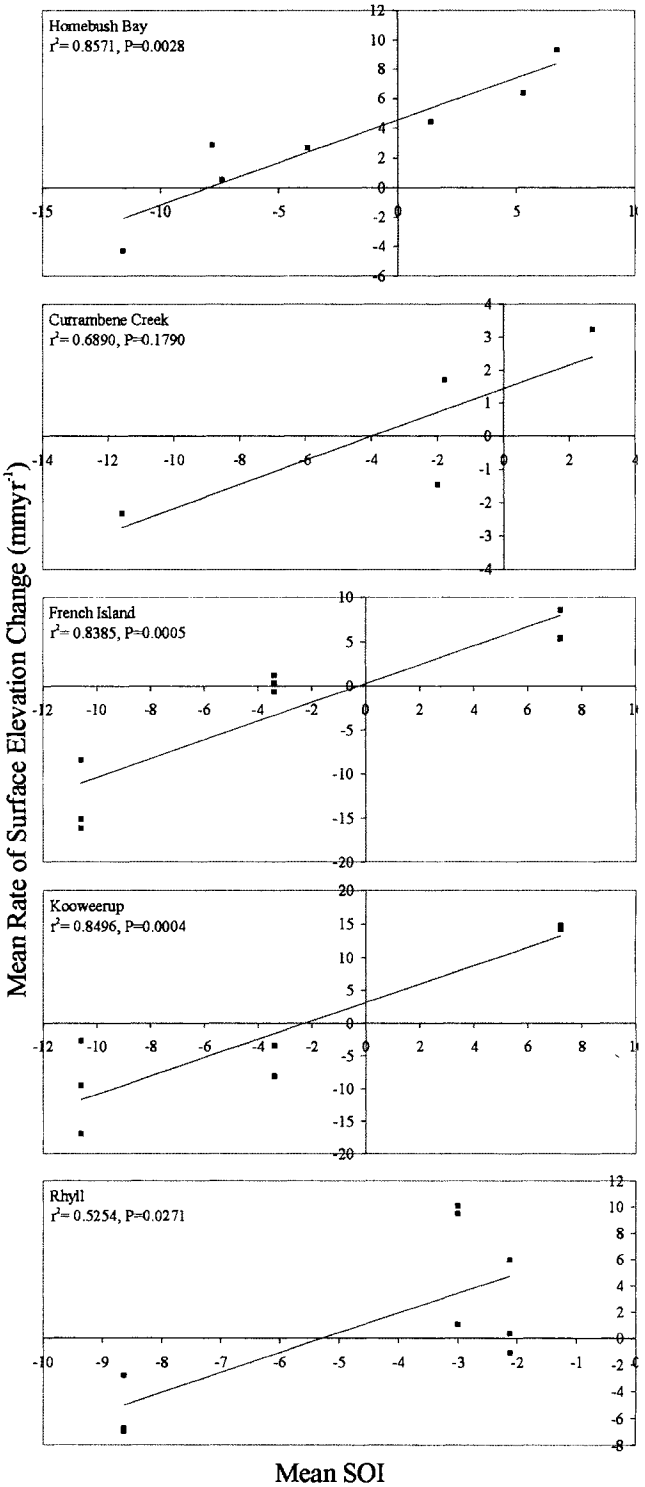


Figure 3. Relationship between mean monthly Southern Oscillation Index (SOI) and surface elevation change at four mangrove forests not located on deltaic islands. SOI provided by the Australian Bureau of Meteorology (2004a).

This content downloaded from
123.243.247.113 on Sat, 29 Jun 2024 03:25:39 +00:00
All use subject to https://about.jstor.org/terms

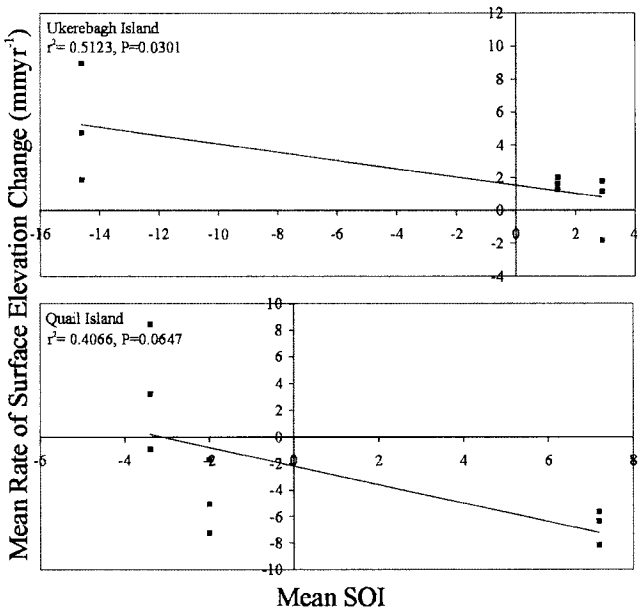


Figure 4. Relationship between mean monthly Southern Oscillation Index (SOI) and surface elevation change at two deltaic island mangrove forests.

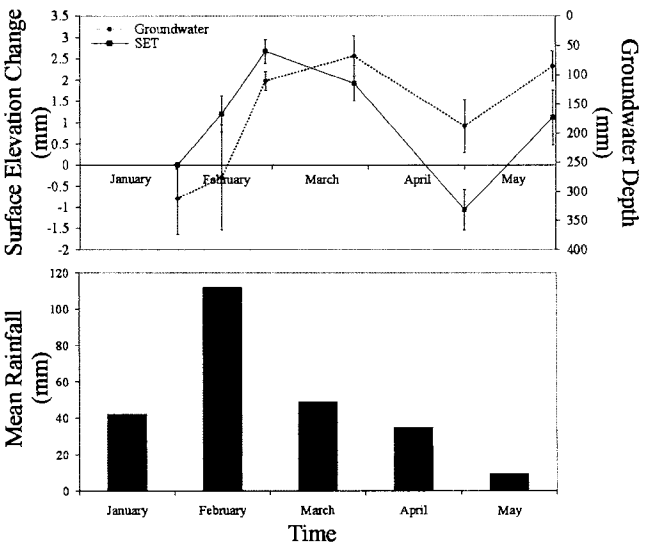


Figure 5. Cumulative mean (standard error) surface elevation change and groundwater depth at SETs at Homebush Bay. There is a positive relationship between surface elevation change and groundwater depth ($r^2 = 0.7654$, $p = 0.023$). The 2004 mean monthly rainfall is provided by the Australian Bureau of Meteorology (2004b).

DISCUSSION

At the broadest temporal scale, the SOI proved to be a useful indicator of marsh surface elevation in southeastern Australia, particularly for sites not located on deltaic islands. In three settings; French Island, Koo Wee Rup, and Homebush Bay, the SOI accounted for more than 80% of variability in marsh surface elevation. The deltaic islands presented a contrasting response. Subsidence in these settings proved independent of the El Niño drought, as might be expected with lesser terrestrial groundwater inputs.

Trend lines indicate a range of elevation change between pre-drought and drought conditions of 4 mm at Currambene Creek, 6 mm at Rhyll, 10 mm at Homebush Bay, 15 mm at French Island, and 25 mm at Koo Wee Rup. The degree to which rainfall and SOI influences groundwater and marsh surface elevation was variable between sites and may be dependent on the conductivity of surface sediments or local drainage conditions (HUGHES, BINNING, and WILLGOOSE, 1998; WHELAN *et al.*, 2005). On average, the degree of drought-induced subsidence corresponds well to measures taken in marshes in east Texas (10–15 mm: PEREZ and CAHOON, 2004) and in south Louisiana (20 mm: SWARZENSKI *et al.*, in press).

Over a period of 4 months, measures taken approximately every 2 weeks of surface elevation tracked closely with groundwater at Homebush Bay. Groundwater measures corresponded to monthly rainfall averages over the period. The amplitude of change was lower than that induced by the El Niño drought of the previous 2 years, with a range of less than 4 mm in surface elevation between high and low groundwater conditions.

Diurnal variability in surface elevation between spring high tide and low tide was measurable in the Homebush Bay mangrove, with the change of 3 mm corresponding to that attributed to evapotranspiration by PAQUETTE *et al.* (2004) in the Bay of Fundy and PEREZ *et al.* (2003) in a salt marsh in Louisiana. The trend was found only in mangrove and mixed mangrove–salt marsh habitats at Homebush Bay. The salt marsh SETs showed no significant change in surface elevation.

The magnitude of surface elevation change in this study is greatest at the scale of years, with the 2001–2002 El Niño drought depressing marsh surface elevations by up to 25 mm. Similar declines in water tables during El Niño droughts have been observed in mangrove forests of Micronesia (DREXLER and EWEL, 2001). At this scale, drought-induced subsi-

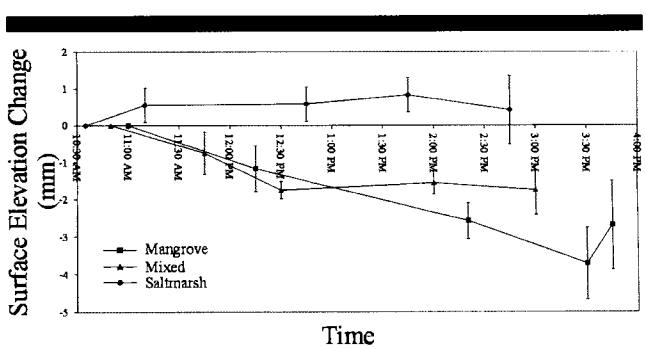


Figure 6. Cumulative mean (standard error) surface elevation change in the mangrove, mixed and salt marsh zones at Homebush Bay from peak high tide to low tide. Surface elevation change exceeded what may be attributed to measurement error in the mangrove zone in one measurement only.

This content downloaded from
123.243.247.113 on Sat, 29 Jun 2024 03:25:39 +00:00
All use subject to https://about.jstor.org/terms

dence might contribute to changes in relative sea level and hence inundation frequency.

Over longer time periods (decades to centuries), the capacity of mangroves to keep pace with sea-level rise might be expected to relate to accretion rates, both minerogenic and organic, judging by responses to the postglacial marine transgression (WOODROFFE, 1990; ELLISON and STODDART, 1991; WOODROFFE and GRINDROD, 1991; FUJIMOTO and MIYAGI, 1993; PARKINSON, DELAUNE, and WHITE, 1994). However, there is little relationship between surface elevation and sedimentation at smaller temporal scales, either in southeast Australia (ROGERS, SAINTILAN, and CAHOON, 2005; ROGERS, SAINTILAN, and HEIJNIS, 2005) or globally (CAHOON *et al.*, in press). At these scales, below-ground processes, primarily hydrological processes and soil organic matter accumulation (CAHOON *et al.* 2003; CAHOON, FORD, and HENSEL, 2004), explain most of the variability. Modeling of responses of mangroves to sea-level rise on the basis of contemporary processes therefore requires long-term readings and the removal of short-term perturbations from the data set. These perturbations include groundwater variability driven by climate variability at regional and local scales. The magnitude of these changes and their impacts of mangrove wetlands are beginning to be understood.

CONCLUSIONS

Changes in groundwater inputs, both terrestrial and tidal, exert a direct influence on surface elevation in the mangrove forests of southeast Australia. At most sites, the degree of change in surface elevation was observed to correlate with the SOI. At deltaic island sites, this trend was not evident, an observation we attribute to lower terrestrial groundwater inputs. The magnitude of change is greatest at the scale of years, as evident with the onset of an El Niño drought in 2001–2002. Because short-term perturbations exert a direct influence on surface elevation in mangrove forests, models of the response of mangroves to sea-level rise on the basis of contemporary processes should account for these perturbations.

ACKNOWLEDGMENTS

We acknowledge the financial contributions to this research made by the Coasts and Clean Seas Initiative, the Department of Infrastructure, Planning and Natural Resources (New South Wales), the Department of Sustainability and Environment (Victoria), Sydney Olympic Park Authority, and the Jervis Bay Marine Park Authority. We thank Don Cahoon and Jim Lynch, who assisted with the installation of SETs and the interpretation of results, Ron West for helpful suggestions on the direction of the research, and the many people who contributed to fieldwork, including Rebecca Allport, Laurie Ferns, David Rogers, and Kylee Wilton.

LITERATURE CITED

BELPERIO, A.P., 1993. Land subsidence and sea level rise in the Port Adelaide estuary: implications for monitoring the greenhouse effect. *Australian Journal of Earth Sciences,* 40, 359–368.

BLASCO, F.; SAENGER, P., and JANODET, E., 1996. Mangroves as indicators of coastal change. *Catena,* 27, 167–178.

BOUMANS, R. and DAY, J.W., JR., 1993. High precision measurements of sediment elevation in shallow coastal areas using a sedimentation-erosion table. *Estuaries,* 16, 375–380.

BUREAU OF METEOROLOGY, 2004a. SOI (Southern Oscillation Index) Archives: 1876–present. Australian Government, Bureau of Meteorology. http://www.bom.gov.au/climate/current/soihtm1.shtml (accessed June 30, 2006).

BUREAU OF METEOROLOGY, 2004b. Climate Averages Map. 2004 Mean monthly rainfall for Parramatta North, Station 66124. Australian Government, Bureau of Meteorology. http://www.bom.gov.au/climate/map/climate_avgs/clim_avg1.shtml (accessed June 30, 2006).

CAHOON, D.R., 2003. Storms as agents of wetland elevation change: their impact on surface and subsurface sediment processes. *In: Proceedings of the International Conference on Coastal Sediments 2003* (Clearwater Beach, Florida). CD-ROM. Corpus Christi, Texas: World Scientific Publishing and East Meets West Productions.

CAHOON, D.R.; REED, D.J., and DAY, J.W., JR., 1995. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. *Marine Geology,* 128, 1–9.

CAHOON, D.R. and LYNCH, J.C., 1997. Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, USA. *Mangroves and Salt Marshes,* 1, 173–186.

CAHOON, D.R.; DAY, J.W., JR., and REED, D.J., 1999. The influence of surface and shallow subsurface soil processes on wetland elevation: a synthesis. *Current Topics in Wetland Biogeochemistry,* 3, 72–88.

CAHOON, D.R.; LYNCH, J.C.; HENSEL, P.F.; BOUMANS, R.; PEREZ, B.C.; SEGURA, B., and DAY, J.W., JR., 2002. High precision measurement of wetland sediment elevation: I. Recent improvements to the sedimentation-erosion table. *Journal of Sedimentary Research,* 72(5), 730–733.

CAHOON, D.R.; HENSEL, P.; RYBCZYK, J.; MCKEE, K.L.; PROFFITT, C.E., and PEREZ, B.A., 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *Journal of Ecology,* 91, 1093–1105.

CAHOON, D.R.; FORD, M.A., and HENSEL, P.F., 2004. Ecogemorphology of *Spartina patens*–dominated tidal marshes: soil organic matter accumulation, marsh elevation dynamics, and disturbance. *In*: FAGHERAZZI, S., MARANI, M., and BLUM, L.K. (eds.), *The Ecogeomorphology of Tidal Marshes.* Coastal and Estuarine Studies 59. Washington, D.C.: American Geophysical Union, pp. 247–266.

CAHOON, D.; HENSEL P.F.; MCKEE K.; REED D.J.; SAINTILAN N., and SPENCER T., in press. Coastal wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. *In:* VERHOEVEN, J., WHIGHAM, D., BOBBINK, R., and BELTMAN, B. (eds.) *Wetlands as a Natural Resource.* Springer Ecological Studies. New York: Springer.

CALLAWAY, J.C.; DELAUNE, R.D., and PATRICK, W.H., JR., 1997. Sediment accumulation rates from four coastal wetlands along the Gulf of Mexico. *Journal of Coastal Research,* 13, 181–191.

DELAUNE, R.D.; BAUMANN, R.H., and GOSSELINK, J.G., 1983. Relationships among vertical accretion, coastal submergence and erosion in a Louisiana Gulf coast marsh. *Journal of Sedimentary Petrology,* 53, 147–157.

DREXLER, J.Z. and EWEL, K.C., 2001. Effects of the 1997–1998 ENSO-related drought on hydrology and salinity in a Micronesian wetland complex. *Estuaries,* 24, 347–356.

ELLISON, J.C. and STODDART, D.R., 1991. Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *Journal of Coastal Research,* 7, 151–165.

FIELD, C.D., 1995. Impact of expected climate change on mangroves. *Hydrobiologia,* 295, 75–81.

FORD, M.A.; CAHOON, D.R.; and LYNCH, J.C., 1999. Restoring marsh elevation in a rapidly subsiding salt marsh by thin-layer deposition of dredged material. *Ecological Engineering,* 12, 189–205.

FUJIMOTO, K. and MIYAGI, T., 1993. Development process of tidal-flat type mangrove habitats and their zonation in the Pacific Ocean. *Vegetatio,* 106, 137–146.

This content downloaded from
123.243.247.113 on Sat, 29 Jun 2024 03:25:39 +00:00
All use subject to https://about.jstor.org/terms

HARRISON, E.A. and BLOOM, A.L., 1977. Sedimentation rates on tidal salt marshes in Connecticut. *Journal of Sedimentary Petrology,* 47, 1484–1490.

HUGHES, C.E.; BINNING, P., and WILLGOOSE, G.R., 1998. Characterisation of the hydrology of an estuarine wetland. *Journal of Hydrology,* 211, 34–39.

KAYE, C.A. and BARGHOORN, E.S., 1964. Late Quaternary sea level change and crustal rise at Boston, Massachusetts with notes on the autocompaction of peat. *Bulletin of the Geological Society of America,* 75, 63–80.

KNOTT, J.F.; NUTTLE, W.K., and HEMOND, H.F., 1987. Hydrological parameters of salt marsh peat. *Hydrological Processes,* 1, 211–220.

NUTTLE, W.K.; HEMOND, H.F., and STOLZENBACH, K.D., 1990. Mechanisms of water storage in salt marsh sediments: the importance of dilation. *Hydrological Processes,* 4, 1–13.

ORSON, R.; PANAGEOTOU, W., and LEATHERMAN, S.P., 1985. Response of tidal salt marshes of the U.S. Atlantic and Gulf Coasts to rising sea-levels. *Journal of Coastal Research,* 1, 29–37.

PAQUETTE, C.H.; SUNDBERG, K.L.; BOUMANS, R.M.J., and CHMURA, G.L., 2004. Changes in salt marsh surface elevation due to variability in evapotranspiration and tidal flooding. *Estuaries,* 27, 82–89.

PARKINSON, R.W.; DELAUNE, R.D., and WHITE, J.R., 1994. Holocene sea-level rise and the fate of mangrove forests within the wider Caribbean region. *Journal of Coastal Research,* 10, 1077–1086.

PEREZ, B.; CAHOON, D.; SEGURA, B.; LYNCH, J., and OLNEY, T., 2003. Marsh elevation dynamics over various depth profiles in a Louisiana salt marsh. *In: Abstracts of the 17th Biennial Conference of the Estuarine Research Federation Conference* (Seattle, Washington), p. 103.

PEREZ, B.C. and CAHOON, D.R., 2004. Marsh Vertical Accretion and Elevation Change in Hydrologically Managed and Unmanaged Marshes within the McFaddin National Wildlife Refuge, Texas. Final Report to U.S. Fish and Wildlife Service, McFaddin National Wildlife Refuge, Sabine Pass, Texas.

REED, D.J., 1990. The impact of sea-level rise on coastal salt marshes. *Progress in Physical Geography,* 14, 24–40.

REED, D.J., 1995. The response of coastal marshes to sea-level rise: survival or submergence? *Earth Surface Processes and Landforms,* 20, 39–48.

REED, D.J. and CAHOON, D.R., 1993. Marsh submergence vs. marsh accretion: interpreting accretion defecit data in coastal Louisiana. *Coastal Zone '93.* New Orleans, Louisiana: American Shore and Beach Preservation Association, pp. 243–257.

Rogers, K.; Saintilan, N., and CAHOON, D.R., 2005. Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetlands Ecology and Management,* 13, 587–598.

ROGERS, K.; SAINTILAN, N., and HEIJNIS, H., 2005. Mangrove and salt marsh monitoring at Westernport Bay, Victoria. *Estuaries,* 28, 551–559.

SEMENIUK, V., 1994. Predicting the effect of sea-level rise on mangroves in north-western Australia. *Journal of Coastal Research,* 10, 1050–1076.

SIMAS T.; NUNES, J.P., and FERRERIA, J.G., 2001. Effects of global climate change on coastal salt marshes. *Ecological Modelling,* 139, 1–15.

SMITH, T.J., III, and CAHOON, D.R., 2003. Wetland sediment elevation in the Florida Everglades: response to surface water stage variation. *In: Proceedings of the International Conference on Coastal Sediments 2003* (Clearwater Beach, Florida). CD-ROM. Corpus Christi, Texas: World Scientific Publishing and East Meets West Productions.

SWARZENSKI, C.; PEREZ, B.C.; FAULKNER, S.; GAMBRELL, R.; MICHOT, T., and CAHOON, D.R., in press. A Field Investigation into Causes and Potential Consequences of Widespread Salt Marsh Dieback in Coastal Louisiana in 2000: Task #2.3. Final Report. Baton Rouge: Louisiana Department of Natural Resources.

VAN WIJNEN, H.J.; and BAKKER, J.P., 2001. Long-term surface elevation change in salt marshes: a prediction of marsh response to future sea-level rise. *Estuarine Coastal and Shelf Science,* 52, 381–390.

VANDERZEE, M.P., 1988. Changes in salt marsh vegetation as an early indicator of sea-level rise. *In*: PEARMAN, G.I. (ed.), *Greenhouse: Planning for Climate Change.* Melbourne: CSIRO, pp. 147–159.

WHELAN, K.R.T.; SMITH T.J., III; CAHOON, D.R.; LYNCH, J.C., and ANDERSON, G.H., 2005. Groundwater control of mangrove surface elevation: shrink-swell of mangrove soils varies with depth. *Estuaries,* 28, 833–843.

WOODROFFE, C.D., 1990. The impact of sea-level rise on mangrove shorelines. *Progress in Physical Geography,* 14, 483–520.

WOODROFFE, C.D. and GRINDROD, J., 1991. Mangrove biogeography: the role of Quaternary environmental and sea-level change. *Journal of Biogeography,* 18, 479–192.

This content downloaded from
123.243.247.113 on Sat, 29 Jun 2024 03:25:39 +00:00
All use subject to https://about.jstor.org/terms

Available online at www.sciencedirect.com
SCIENCE DIRECT®
Estuarine, Coastal and Shelf Science 66 (2006) 559–569
ESTUARINE COASTAL AND SHELF SCIENCE
www.elsevier.com/locate/ecss

Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia

K. Rogers [a], K.M. Wilton [b], N. Saintilan [a,*]

[a] *ACU National, PO Box 968, North Sydney, NSW 2059, Australia*
[b] *Water Management Division, NSW Department of Infrastructure, Planning and Natural Resources, GPO Box 39, Sydney, NSW 2001, Australia*

Received 2 April 2005; accepted 14 November 2005
Available online 28 December 2005

Abstract

Vertical accretion and surface elevation trends were studied in mangrove and saltmarsh wetlands in southeast Australia. A total of 69 surface elevation tables, each associated with three feldspar marker horizons, was deployed in 10 wetlands across 7 estuaries, and monitored for three years. Saltmarsh and mangrove vegetation distributions were mapped for the same estuaries, and elevation characteristics of the wetlands were modelled. Rates of vertical accretion were found to correlate with tidal range. No relationship was found between rates of vertical accretion and surface elevation increase. A positive relationship was demonstrated between contemporary rates of saltmarsh surface elevation change and longer-term rates of mangrove encroachment into saltmarsh. We conclude that landward mangrove encroachment may be facilitated by local factors contributing to saltmarsh compaction during drought conditions.
© 2005 Elsevier Ltd. All rights reserved.

Keywords: mangrove; saltmarsh; sea-level rise; autocompaction; Australia; vertical accretion

1. Introduction

The expansion in area covered by mangroves in estuaries in southeast Australia since the time of European settlement is now a well established trend (Saintilan and Williams, 1999; McLoughlin, 2000; Harty, 2004). Historical records point to a continuous increase in the area along estuarine shorelines occupied by mangroves (McLoughlin, 1988, 2000) and historical aerial photographs extending back to the 1930s show the landward encroachment of mangroves into saltmarsh in numerous estuaries (for example, McTainsh et al., 1988; Morton, 1994; Williams and Watford, 1997; Williams et al., 1999). Corresponding saltmarsh decline throughout southeast Australia is also well documented, with most estuaries losing over 25% of their saltmarsh in the past five decades and as much as 80% in some estuaries (Saintilan and Williams, 1999). While some of this decline has been attributed to land reclamation, the trend of mangrove encroachment into saltmarsh has been the predominant cause of saltmarsh decline (Saintilan and Williams, 2000).

Numerous hypotheses have been advanced explaining this trend, including transport of propagules along mosquito runnels (Breitfuss et al., 2003), increased precipitation (Morton, 1994), recolonisation of land after the cessation of agricultural activities (Mitchell and Adam, 1989; Morton, 1994), elevated sea level (Saintilan and Hashimoto, 1999), altered tidal regimes (Morton, 1994), increased sedimentation rates (Wilton, 1997; McLoughlin, 2000), elevated nutrient levels (McLoughlin, 1988; Wilton, 1997; McLoughlin, 2000), and marsh subsidence (Burton, 1982; Vanderzee, 1988; Saintilan, 1998).

Studies by Hennessy et al. (1999) and Pittock (1975, 1983) show large-scale regional changes in rainfall patterns, with an increase of 15–18% in New South Wales for the period 1910–1995 (Hennessy et al., 1999). Changes in rainfall regimes have been linked to changes in soil salinity, surface

* Corresponding author.
E-mail address: n.saintilan@mackillop.acu.edu.au (N. Saintilan).

0272-7714/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2005.11.004

water salinity, and mangrove survivorship, and may be implicated in the expansion of mangroves into saltmarsh (Clarke and Hannon, 1967). However, in a study of 7 NSW estuaries which analysed decadal patterns in rainfall and habitat change, a clear link between rainfall patterns and mangrove expansion into saltmarsh was not established (Wilton, 2002). Furthermore, no correlations were found in temperate Australian estuaries between rainfall and the proportion of mangrove and saltmarsh (Saintilan, 2004), in contrast to sub-tropical and tropical Australian estuaries (Bucher and Saenger, 1994).

Since European settlement, urban development has increased nutrient availability within estuaries because of agricultural and industrial activities that increase nutrients within catchments and higher run-off potential. Elevated nutrient levels may aid mangrove growth and health (Lugo et al., 1976; Onuf et al., 1977; Boto, 1983; Boto and Wellington, 1983, 1984). However, nutrient addition may only contribute by increasing luxuriance of the mangrove seedlings and does not contribute to mangrove establishment (Saintilan, 2003). Fertilised plots did not show a significant rate of establishment at the boundary between mangrove and saltmarsh.

Changes in the relationship between marsh elevation and water level, facilitated either by eustatic sea-level rise, marsh compaction/subsidence or vertical accretion, may have significant effects on the distribution of mangrove and saltmarsh throughout Australia and threaten the survival of these environments (Woodroffe, 1990). While studies of the changes in distribution of mangroves and saltmarsh in southeast Australia are numerous, our understanding of marsh sedimentary and elevation dynamics in relation to sea level and, ultimately, of the impacts of sea-level rise on these environments is limited (Woodroffe, 1990; Callaway et al., 1997). Studies of marsh vertical accretion are few, and no published studies exist on the relationships between vertical accretion and surface elevation for the region.

Studies indicate that various processes act on soil volume causing marsh elevation to change (Kaye and Barghoorn, 1964; DeLaune et al., 1983; Nuttle et al., 1990; Reed and Cahoon, 1993; Cahoon et al., 1995, 1999, 2000; Whelan et al., 2005). Marsh elevations do not remain static due to vertical accretion and the influence of below-ground processes, such as subsidence, autocompaction, groundwater, dilation, water stage and plant processes. Processes that cause compaction or subsidence act to decrease the soil volume so that elevation change is less than may be attributed to accretion alone. Alternatively processes that increase the soil volume, such as groundwater and plant processes may increase the soil elevation in excess of that attributable to accretion. When considering the role of eustatic sea-level rise and its effect on the expansion of mangroves into saltmarsh it is important to account for processes that influence marsh elevations. Changes in mangrove and saltmarsh extent may be more accurately explained by relative sea-level rise, which incorporates the eustatic component of sea-level rise and changes in surface elevation.

The influence of vertical accretion and below-ground processes on marsh elevation has been investigated through the use of surface elevation tables (SETs, Cahoon et al., 2002), previously known as sedimentation–erosion tables (Boumans and Day, 1993). SETs are a precise and non-destructive method for measuring changes in marsh elevation in shallow coastal environments. SET studies typically involve the establishment of replicated stable benchmarks in structurally similar vegetation. Changes in marsh elevation can then be tracked over time against the reference benchmark. When accompanied with measures of vertical accretion, typically using feldspar marker horizons (Cahoon and Turner, 1989), the component of surface elevation change that is attributable to accretion or autocompaction/subsidence may be differentiated. This paper reports the first comprehensive data on marsh vertical accretion and surface elevation in southeast Australia, and explores the influence of vertical accretion, and subsidence/autocompaction on changes in mangrove and saltmarsh distribution throughout the region.

1.1. Study location

Study sites encompassed 7 estuaries and 10 individual locations distributed over approximately 1000 km of coastline between the Tweed River, NSW and Western Port Bay, Victoria (Fig. 1). Study sites were included from a number of representative geomorphic settings, as described by Roy et al. (2001), including a drowned river valley (Parramatta River), a coastal embayment (Western Port Bay) and barrier estuaries (Tweed River, Hunter River, Minnamurra River, Cararma Inlet and Currambene Creek). All study sites are underlain by Quaternary alluvial deposits, are subject to the effects of *El Niño* cycles and have temperate climates, with the exception of Ukerebagh Island on the Tweed River, which has a sub-tropical climate. Each site exhibits a mesotidal regime and with the exception of the Tweed River and Minnamurra River, water level data indicate that sea level has increased prior to the commencement of study (Table 1).

Mangroves and saltmarsh are the typical intertidal vegetation for these study sites. In southeast Australia, species diversity is low due to the influence of environmental gradients affecting their distribution (Duke et al., 1998). Mangrove species diversity declines with increasing latitude. The Tweed River is colonised by six mangrove species: *Avicennia marina* (Forssk.) Vierh., *Aegiceras corniculatum* (L.) Blanco, *Rhizophora stylosa* Griff., *Exoecaria agallochoa* L., *Ceriops tagal* var. *australis* and *Brugiera gymnorhiza* (L.) Lamk. This reduces to two species: *A. marina* and *A. corniculatum* south of the Manning River and *A. marina* alone south of Pambula River (West et al., 1984). *Avicennia marina* is nearing its southernmost limit in Western Port Bay, with Corner Inlet supporting the most southerly mangroves (Hogarth, 1999). Frosts have a little influence on the distribution of mangroves in Southeast Australia.

Unlike mangroves, as latitude increases from tropical to temperate Australia, saltmarshes become more complex in structure and comprise greater species diversity (Adam

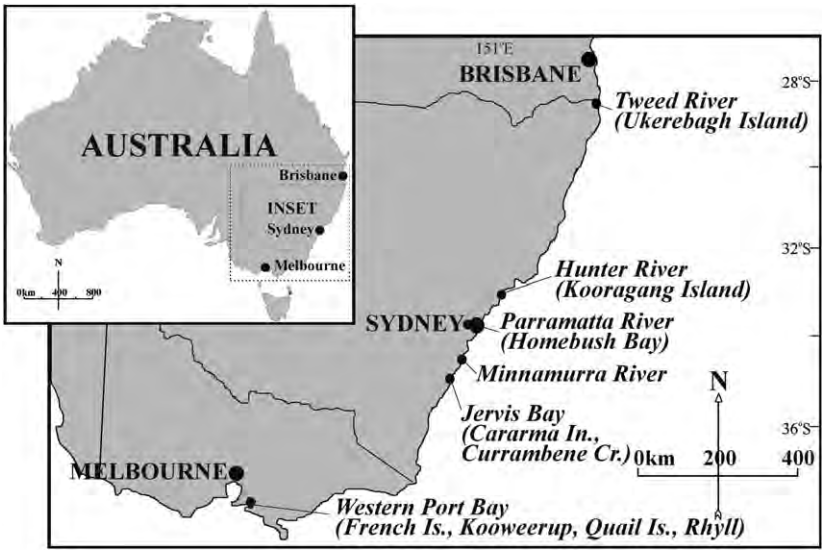


Fig. 1. Locality map of study sites, southeast Australia.

et al., 1988). Saltmarshes in tropical northern Australia support a maximum of 7 species, with more than 250 species of saltmarsh and fringe vegetation observed in NSW (Adam et al., 1988). Some common saltmarsh species observed at study sites include *Sporobolus virginicus* (Linnaeus) Kunth, *Sarcocornia quinqueflora* (Bunge ex Ungen-Sternberg) AJ Scott, *Juncus krausii* Hochestetter, *Samolus repens* (G and JR Forster) Persoon, *Sueada australis* (R Brown) Moquin-Tandon, and *Trigolchin striata* Ruiz and Pavon, while *Sclerostegia arbuscula*, *Wilsonia backhousei* JD Hooker and *Halosarcia pergranulata* (J Black) PG Wilson are common in the more floristically rich southern sites.

2. Methods

2.1. GIS-based aerial photograph interpretation and mapping

Historical and contemporary aerial photographs of each study site were scanned and imported into an ArcView Geographic Information System (GIS) (ESRI Inc. version 3.2) as digital images at a resolution greater than 150 dots per inch. All digital images were georectified using a minimum of six ground control points. Mangrove and saltmarsh community boundaries were delineated in accordance with the protocols of Wilton and Saintilan (2000). The area of vegetation units was determined and changes in extent over the period of aerial photography were analysed (see Table 2 for period of aerial photography). Rates of change in mangrove and saltmarsh extent were estimated as a percentage increase per year between the earliest and most recent mapping periods. Rates of change at Kooragang Island and Minnamurra River were determined on the basis of the previous studies of Williams et al. (1999) and Chafer (1998).

2.2. Surface elevation and vertical accretion

Surface elevation tables (SET version IV, Cahoon et al., 2002) were installed in order to determine surface elevation trends. The SET reportedly has a confidence interval of 1.4 mm (Cahoon et al., 2002). The SET version IV utilises a benchmark pole driven 4–6 m into the marsh. A detachable arm extends parallel to the marsh, with sliding vertical pins used to measure changes in the marsh surface elevation to an accuracy of 1.2 mm (Boumans and Day, 1993). SET stations were established according to two layout strategies; either in replicated sets of three within both mangrove and saltmarsh zones (Ukerebagh Island, Minamurra River, Cararma Inlet, French Island, Rhyll, Kooweerup and Quail Island), or within mangrove, mixed mangrove and saltmarsh zones where mangrove encroachment had given rise to a wide ecotone (Kooragang Island, Currambene Creek, and Homebush Bay). Surface elevation measures were taken at low tide to reduce the variability in surface elevation that may be attributed to dilation. Surface elevation measurements were taken at least once a year from 2000 to 2003.

Vertical accretion was also measured at each SET site. At the time of SET installation, three 0.25 m^2 feldspar marker horizons were established on the marsh surface around the perimeter of each SET, 207 horizons in total. These horizons served as markers against which vertical accretion was measured. Mini cores were taken from each feldspar horizon annually. The distance from the marsh surface to the marker horizon was measured in order to establish the vertical thickness of sediment accreted.

Elevation and vertical accretion trends were established and rates of surface elevation change and vertical accretion were estimated for mangrove and saltmarsh zones or mangrove, saltmarsh and mixed zones at each study site. Randomised block design analysis of variance was used to determine whether surface elevation change and vertical accretion varied consistently within sites and between zones within sites.

Table 1
Study sites and descriptive features of each study site including the river system on which the study site is located, the geographic location, estuarine setting as described by Roy et al. (2001), catchment area, mean daily temperature range, mean monthly rainfall range, long-term sea-level change, sea-level change over the study period, dominant mangrove vegetation and dominant saltmarsh vegetation

Study site	River system	Geographic location	Estuarine setting	Catchment area (km^2)	Mean daily temperature range (°C)	Mean monthly rainfall range (mm)	Long-term sea-level change (mm) (location, period in yrs)	Sea-level change over the study period (mm)	Dominant mangrove vegetation	Dominant saltmarsh vegetation
Ukerebagh Island	Tweed River	153°33′E, 28°10′S	Barrier Estuary (III/5)	1114[a]	8.5–29.6	40.5–230.9	−0.40 (Letitia Spit, 16)	−0.47	*Rhizophora stylosa* *Avicennia marina*	*Sporobolus virginicus*
Kooragang Island	Hunter River	151°48′E, 32°55′S	Barrier Estuary (III/5)	22 000[a]	8.4–25.6	69.5–121.9	+0.33 (Hexham, 19)	−0.55	*Avicennia marina* *Aegiceras corniculatum*	*Sporobolus virginicus* *Sarcocornia quinqueflora* *Juncus krausii*
Berowra Creek	Hawkesbury River	151°15′E, 33°30′S	Drowned River Valley (II/3)	310[b]	6.0–26.8	71.1–147.4	+0.69 (Spencer, 12)	+25.91	*Avicennia marina* *Aegiceras corniculatum*	*Juncus krausii* *Sarcocornia quinqueflora* *Sporobolus virginicus* *Samolus repens*
Marramarra Creek	Hawkesbury River	151°03′E, 33°31′S	Drowned River Valley (II/3)	310[b]	6.0–26.8	71.1–147.4	+0.69 (Spencer, 12)	+25.91	*Avicennia marina* *Aegiceras corniculatum*	*Juncus krausii* *Sarcocornia quinqueflora* *Sporobolus virginicus* *Samolus repens*
Homebush Bay	Parramatta River		Drowned River Valley (II/3)	130[c]	6.2–28.2	46.2–124.7	+0.91 (Fort Denison, 90)	−9.52	*Avicennia marina*	*Sarcocornia quinqueflora* *Sporobolus virginicus* *Sueada australis* *Juncus krausii*
Minnamurra River	Minnamurra River	150°52′E, 34°39′S	Barrier Estuary (III/5)	110[a]	8.4–25.1	75.2–144.9	−0.47 (Macquarie Rivulet, 19)	−6.17	*Avicennia marina* *Aegiceras corniculatum*	*Sporobolus virginicus* *Sarcocornia quinqueflora* *Samolus repens* *Sueada australis* *Juncus krausii*
Cararma Inlet	Jervis Bay	150°49′E, 35°1′S)	Barrier Estuary (III/5)	3[c]	9.2–23.9	79.5–134.2	+4.12 (Creswell, 10)	−34.93	*Avicennia marina* *Aegiceras corniculatum*	*Sclerostegia arbuscula* *Sporobolus virginicus* *Sarcocornia quinqueflora* *Samolus repens* *Sueada australis* *Juncus krausii* *Baumea juncea*
Currambene Creek	Jervis Bay	150°40′E, 35°3′S	Barrier Estuary (III/5)	165[c]	9.2–23.9	79.5–134.2	+4.12 (Creswell, 10)	−27.48	*Avicennia marina* *Aegiceras corniculatum*	*Sporobolus virginicus* *Sarcocornia quinqueflora* *Samolus repens* *Sueada australis* *Juncus krausii* *Baumea juncea*
French Island	Western Port Bay	145°18′E, 38°13′S	Coastal Embayment (I/1)	3433[a]	7.0–24.4	42.8–79.1	+2.66 (Stony Point, 10)	−4.05	*Avicennia marina*	*Sclerostegia arbuscula* *Halosarcia pergranulata* *Sporobolus virginicus* *Sarcocornia quinqueflora* *Samolus repens* *Sueada australis* *Juncus krausii* *Baumea juncea*

Kooweerup	Western Port Bay	145°23′E, 38°13′S	Coastal Embayment (I/1)	3433[a]	7.0–24.4	42.8–79.1	+2.66 (Stony Point, 10)	−4.05	*Avicennia marina*	Same as French Island
Quail Island	Western Port Bay	145°18′E, 38°13′S	Coastal Embayment (I/1)	3433[a]	7.0–24.4	42.8–79.1	+2.66 (Stony Point, 10)	−4.05	*Avicennia marina*	Same as French Island
Rhyll	Western Port Bay	145°18′E, 38°28′S	Coastal Embayment (I/1)	3433[a]	7.0–24.4	42.8–79.1	+2.66 (Stony Point, 10)	−4.05	*Avicennia marina*	Same as French Island

[a] Catchment area of entire river system.
[b] Catchment area of Berowra Creek and Marramarra Creek combined.
[c] Catchment area of individual study site.

2.3. Regression analyses

To determine the contribution of autocompaction to changes in wetland vegetation extent, regression analyses compared rates of wetland vegetation extent change, estimated using GIS-based aerial photograph interpretation and mapping, and rates of surface elevation change in mangrove and saltmarsh zones, estimated using SETs. Regression analyses comparing rates of wetland vegetation change and rates of vertical accretion in mangrove and saltmarsh zones, estimated using feldspar marker horizons, were also completed to determine the contribution of vertical accretion to changes in wetland vegetation extent. No comparisons were made with rates of change in mixed zones.

3. Results

3.1. GIS-based aerial photograph interpretation and mapping

A general trend of saltmarsh decline and mangrove increase over the period of aerial photography (Table 2) was observed at all study sites. Rates of change in mangrove extent ranged between increases at 2.85% yr^{-1} and 0.07% yr^{-1}, while saltmarsh extent declined at rates between 1.43% yr^{-1} and 0.17% yr^{-1} (Table 2).

3.2. Surface elevation and vertical accretion

At most study sites, rates of vertical accretion exceeded rates of surface elevation change, indicating that autocompaction was a significant contributor to marsh surface elevation

Table 2
Area of mangrove and saltmarsh vegetation over the period of aerial photography and estimated changes (as percent and rate) in extent at study sites throughout southeast Australia

Study site	Study period (time 1–2)	Vegetation type	Area at time 1 (ha)	Area at time 2 (ha)	Change (%)	Rate of change (% yr^{-1})
Ukerebagh Island	1961–1998	Mangrove	37.7	45.2	+19.89	+0.54
		Saltmarsh	13.8	11.1	−19.57	−0.53
Kooragang Island[a]	1954–1994	Mangrove	532	636	+19.55	+0.49
		Saltmarsh	930	422	−54.62	−1.37
Homebush Bay	1930–2000	Mangrove	22.28	36.75	+64.92	+0.93
		Saltmarsh	64.61	3.99	−93.83	−1.34
Minnamurra River[b]	1938–1997	Mangrove	56.5	95.4	+68.85	+1.17
		Saltmarsh	58.9	28.9	−50.93	−0.86
Cararma Inlet	1948–1999	Mangrove	25.5	62.6	+145.49	+2.85
		Saltmarsh	181.7	79.0	−56.52	−1.11
Currambene Creek	1961–1993	Mangrove	58.5	76.6	+30.94	+0.97
		Saltmarsh	43.3	26.4	−39.03	−1.22
French Island	1967–1999	Mangrove	185.16	189.23	+2.20	+0.07
		Saltmarsh	518.63	490.63	−5.40	−0.17
Kooweerup	1939–1999	Mangrove	11.32	18.13	+60.16	+1.00
		Saltmarsh	41.57	23.02	−44.62	−0.74
Quail Island	1973–1999	Mangrove	73.84	97.47	+32.00	+1.23
		Saltmarsh	157.52	138.71	−11.94	−0.46
Rhyll	1939–1999	Mangrove	40.04	62.28	+55.54	+0.93
		Saltmarsh	174.27	139.83	−19.76	−0.33

[a] Sourced from Williams et al. (1999).
[b] Sourced from Chafer (1998).

Table 3
Mean (standard error) rates of surface elevation change, vertical accretion and subsidence within the mangrove, mixed and saltmarsh zones at study sites throughout southeast Australia. *P*-values indicating whether rates of vertical accretion were significantly different from rates of surface elevation change at study sites throughout Southeast Australia

Site	Zone	Mean surface elevation change (mm yr^{-1})	Mean vertical accretion (mm yr^{-1})	Mean compaction (mm yr^{-1})	Differences between accretion and elevation (within sites)	Differences between accretion and elevation (within zones)
Ukerebagh Island	Mangrove	2.40 ± 1.39	2.21 ± 0.30	0.19	$P = 0.014$	$P = 0.030$
	Saltmarsh	0.49 ± 0.68	0.50 ± 0.23	−0.01		$P = 0.100$
Kooragang Island	Mangrove	1.98 ± 0.54	4.72 ± 0.05	−2.74	$P < 0.001$	$P < 0.001$
	Mixed	2.05 ± 0.63	4.19 ± 1.25	−2.14		$P < 0.001$
	Saltmarsh	1.92 ± 0.98	2.03 ± 0.38	−0.11		$P = 0.281$
Homebush Bay	Mangrove	5.64 ± 2.15	4.58 ± 0.28	1.06	$P = 0.723$	$P = 0.840$
	Mixed	4.66 ± 1.16	3.33 ± 0.81	1.33		$P = 0.654$
	Saltmarsh	2.92 ± 1.59	2.20 ± 0.29	0.72		$P = 0.905$
Minnamurra River	Mangrove	0.61 ± 0.44	6.64 ± 0.52	−6.03	$P < 0.001$	$P < 0.001$
	Saltmarsh	0.26 ± 0.87	5.93 ± 1.21	−5.67		$P < 0.001$
Cararma Inlet	Mangrove	-0.81 ± 1.00	3.03 ± 0.41	−3.84	$P = 0.071$	$P < 0.001$
	Saltmarsh	3.25 ± 0.71	1.27 ± 0.13	1.98		$P = 0.004$
Currambene Creek	Mangrove	0.29 ± 2.02	0.65 ± 0.34	−0.36	$P = 0.041$	$P = 0.105$
	Mixed	0.07 ± 1.49	1.37 ± 0.48	−1.30		$P = 0.287$
	Saltmarsh	0.14 ± 1.48	0.33 ± 0.11	−0.19		$P = 0.429$
French Island	Mangrove	-2.13 ± 1.66	9.49 ± 2.69	−11.62	$P < 0.001$	$P < 0.001$
	Saltmarsh	5.27 ± 0.96	4.07 ± 0.25	1.20		$P = 0.176$
Kooweerup	Mangrove	-0.03 ± 2.23	7.20 ± 0.85	−7.23	$P = 0.001$	$P = 0.002$
	Saltmarsh	-0.16 ± 0.94	2.03 ± 0.32	−2.19		$P = 0.022$
Quail Island	Mangrove	-2.60 ± 2.07	6.77 ± 0.79	−9.37	$P < 0.001$	$P < 0.001$
	Saltmarsh	-0.68 ± 1.18	2.35 ± 0.96	−3.03		$P < 0.001$
Rhyll	Mangrove	0.92 ± 1.87	5.10 ± 0.72	−4.18	$P = 0.001$	$P = 0.003$
	Saltmarsh	0.64 ± 0.75	1.59 ± 0.19	−0.95		$P = 0.110$

(Table 3, Fig. 2). Within study sites there was a significant difference between surface elevation change and vertical accretion at all study sites except Cararma Inlet and Homebush Bay where vertical accretion was the primary contributor to surface elevation change (Table 3, Figs. 3 and 4).

3.3. Regression analyses

A significant and positive relationship was found between rates of mangrove vertical accretion and tidal range ($R^2 = 0.6023$, $P = 0.0050$; Fig. 5). No relationship was found between rates of vertical accretion and surface elevation change ($P = 0.5998$). Rates of mangrove increase were negatively correlated with mean rates of marsh surface elevation increase in the saltmarsh zone ($R^2 = 0.68$, $P = 0.001$; Fig. 6).

Rates of mangrove increase did not correlate well with contemporary rates of vertical accretion in the mangrove zone ($R^2 = 0.0180$, $P = 0.6940$) and saltmarsh zone ($R^2 < 0.001$, $P = 0.9965$).

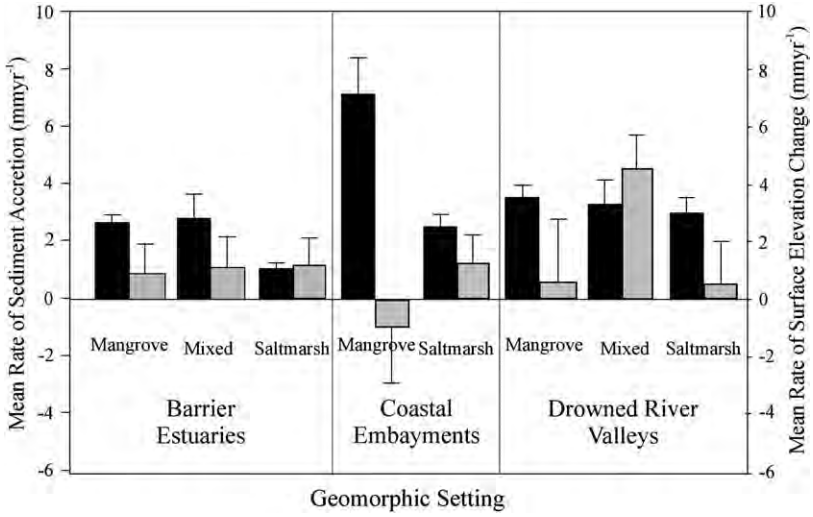


Fig. 2. Rates of sedimentation and surface elevation change in mangrove, saltmarsh and mixed mangrove–saltmarsh environments in southeast Australia, by estuary type. Average and standard deviation.

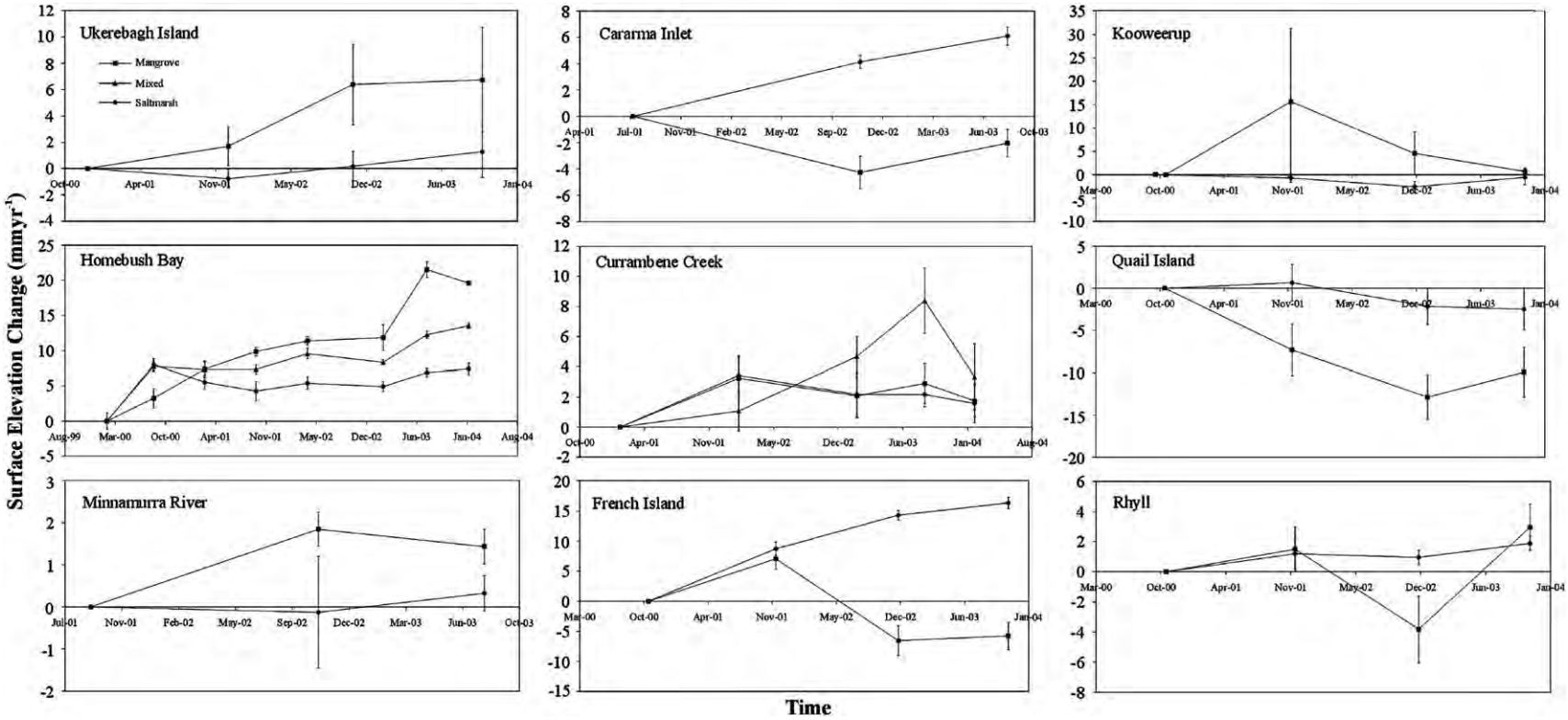


Fig. 3. Surface elevation change at study sites throughout southeast Australia.

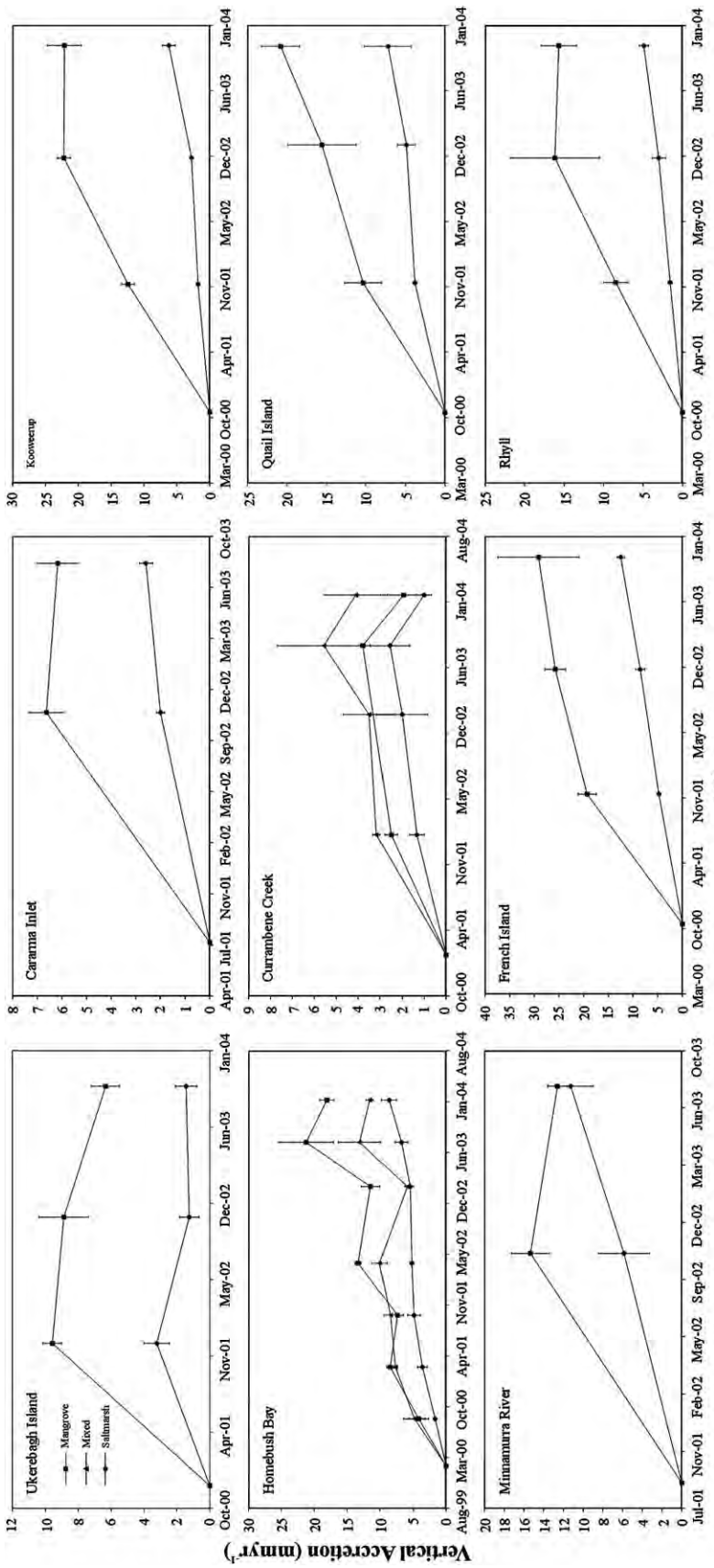


Fig. 4. Vertical accretion at study sites throughout southeast Australia.

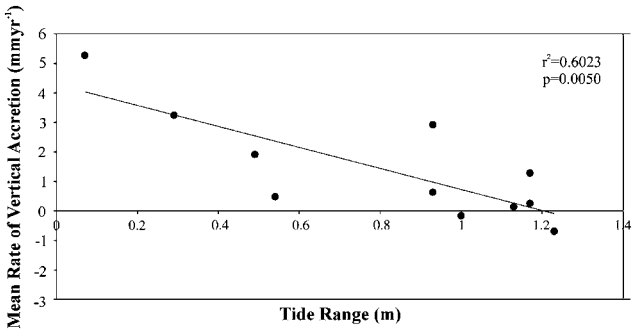


Fig. 5. Correlation between sedimentation rate and tidal range in mangroves of southeast Australia.

4. Discussion

4.1. Mangrove encroachment and saltmarsh decline

Mangrove encroachment into saltmarsh and consequent saltmarsh decline were evident at all study sites, following the regional trend reported by Saintilan and Williams (1999). Rates of saltmarsh decline were generally lower at study sites in Victoria than at sites in NSW. Temperature may be a contributing factor to lower rates of saltmarsh decline in Western Port Bay. *Avicennia marina* reaches its southern limit in nearby Corner Inlet, colder air temperatures and frosts produce slower growth rates in mangroves (McMillan, 1975; Saenger and Moverley, 1985). Furthermore, the dense stands of saltbush genera (*Halosarcia* and *Sclerostegia*), which are characteristic of saltmarshes in Western Port Bay, may play an inhibitive role by shading seedlings of *A. marina*. Similar competition has been reported between mangroves and *Spartina* in marshes in Louisiana (McKee and Rooth, 2003) and *Phragmites* and *Spartina* in Maryland (Rooth and Stevenson, 2000).

4.2. Vertical accretion and surface elevation

Measures of rates of vertical accretion cannot be used as a surrogate for elevation change (Kaye and Barghoorn, 1964; Cahoon et al., 1995). Although lengths of records for many sites were limited (3–4 years), clearly factors other than vertical accretion strongly influence surface elevation over inter-annual time periods. Elevation gains through vertical accretion may be quickly lost to surface autocompaction, as evidenced by the large discrepancy between vertical accretion and surface elevation increase at most sites. However, subsurface processes of groundwater flux and organic productivity are likely to have influenced the results of this study (Rogers and Saintilan, in press).

The relationship between vertical accretion and tidal amplitude corresponds to similar findings in saltmarsh systems (Harrison and Bloom, 1977; Stevenson et al., 1986), where strong tidal currents in open waters re-suspend sediments and facilitate deposition within wetlands.

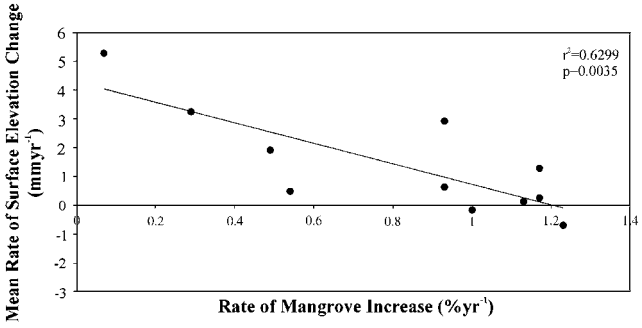


Fig. 6. Relationship between the rate of mangrove increase and the rate of saltmarsh subsidence in southeast Australian estuaries.

4.3. Vertical accretion, autocompaction and mangrove encroachment

A role for upper-level autocompaction in mangrove encroachment into saltmarsh is supported by the results of this study. A significant relationship exists between mean rates of saltmarsh surface elevation change and rates of mangrove increase ($R^2 = 0.6299$, $P = 0.035$). Relatively stable sites, where there was minimal mangrove expansion, were generally those where vertical accretion translated directly into net saltmarsh elevation increase (eg. French Island, Cararma Inlet, Kooragang Island, Ukerebagh Island). Sites showing high rates of mangrove encroachment were also those in which the rates of vertical accretion, even though they may be high, did not lead to a net increase in the elevation of the saltmarsh surface (eg. Quail Island, Minnamurra River, Kooweerup, Currambene Creek). In the context of rising sea levels this would translate into a net saltmarsh surface elevation decline with respect to sea level, increasing the inundation frequency, and promoting upslope mangrove expansion.

Previous studies (Saintilan and Wilton, 2001; Wilton, 2002) questioned the role of eustatic sea-level rise in mangrove encroachment on a decadal scale, as the gradient of encroachment, or the vertical increase in the mangrove–saltmarsh boundary over time exceeded the vertical increase in sea level over the same period. However, rates of subsidence/autocompaction may vary from site to site in accordance with site-specific factors such as soil bulk density (Cahoon et al., 1995; van Wijnen and Bakker, 2001), mineral and organic matter content of soil (Knott et al., 1987; Cahoon et al., 1995), rainfall (Rogers et al., in press) and plant productivity (Rooth and Stevenson, 2000; Morris et al., 2002). These influences may become particularly apparent during drought years, which occur periodically in the region due to the *El Niño* Southern Oscillation. Acid soils are present within estuaries throughout Southeast Australia and agricultural drainage and drought has reportedly caused irreversible soil shrinkage leading to compaction (White et al., 1997). An *El Niño* Southern Oscillation related drought corresponded to our period of sampling and significant autocompaction of sediments was attributed to the drought (Rogers and Saintilan, in press).

References

Adam, P., Wilson, N.C., Huntley, B., 1988. The phytosociology of coastal saltmarsh vegetation in New South Wales. Wetlands (Australia) 7, 35–84.

Boto, K.G., 1983. Nutrient status and other soil factors affecting mangrove productivity in North-East Australia. Wetlands (Australia) 3, 45–49.

Boto, K.G., Wellington, J.T., 1983. Phosphorus and nitrogen nutritional status of a northern Australian mangrove forest. Marine Ecology Progress Series 11, 63–69.

Boto, K.G., Wellington, J.T., 1984. Soil characteristics and nutrient status in a Northern Australian mangrove forest. Estuaries 7, 61–69.

Boumans, R.M.J., Day Jr., J.W., 1993. High precision measurements of sediment elevation in shallow coastal areas using a sedimentation–erosion table. Estuaries 16, 375–380.

Breitfuss, M.J., Connolly, R.M., Dale, P.E.R., 2003. Mangrove distribution and mosquito control: transport of *Avicennia marina* propagules by mosquito-control runnels in southeast Queensland saltmarshes. Estuarine, Coastal and Shelf Science 56, 573–579.

Bucher, D., Saenger, P., 1994. A classification of tropical and subtropical Australian estuaries. Aquatic Conservation: Marine and Freshwater Ecosystems 4, 1–119.

Burton, T., 1982. Mangrove changes recorded north of Adelaide. Safic 6, 8–12.

Cahoon, D.R., Turner, R.E., 1989. Accretion and canal impacts in a rapidly subsiding wetland: II. Feldspar marker horizon technique. Estuaries 12, 260–268.

Cahoon, D.R., Reed, D.J., Day Jr., J.W., 1995. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. Marine Geology 128, 1–9.

Cahoon, D.R., Day Jr., J.W., Reed, D.J., 1999. The influence of surface and shallow subsurface soil processes on wetland elevation: a synthesis. Current Topics in Wetland Biogeochemistry 3, 72–88.

Cahoon, D.R., French, J.R., Spencer, T., Reed, D., Möller, I., 2000. Vertical accretion versus elevational adjustment in UK saltmarshes: an evaluation of alternative methodologies. In: Pye, K., Allen, J.R.L. (Eds.), Coastal and Estuarine Environments: Sedimentology, Geomorphology and Geoarchaeology. Geological Society of London, London, pp. 223–238 (special publications).

Cahoon, D.R., Lynch, J.C., Hensel, P., Boumans, R., Perez, B.C., Segura, B., Day Jr., J.W., 2002. High-precision measurements of wetland sediment elevation: I. Recent improvements to the sedimentation–erosion table. Journal of Sedimentary Research 72, 730–733.

Callaway, J.C., DeLaune, R.D., Patrick Jr., W.H., 1997. Sediment accumulation rates from four coastal wetlands along the Gulf of Mexico. Journal of Coastal Research 13, 181–191.

Chafer, C.J., 1998. A Spatio-temporal Analysis of Estuarine Vegetation Change in the Minnamurra River 1938–1997. 47 pp., plus appendices.

Clarke, L.D., Hannon, N., 1967. The mangrove swamp and salt marsh communities of the Sydney district, Part I: Soils and vegetation. Journal of Ecology 55, 753–771.

DeLaune, R.D., Baumann, R.H., Gosselink, J.G., 1983. Relationships among vertical accretion, coastal submergence and erosion in a Louisiana Gulf coast marsh. Journal of Sedimentary Petrology 53, 147–157.

Duke, N.C., Ball, M.C., Ellison, J.C., 1998. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecology and Biogeography Letters 7, 27–47.

Harrison, E.A., Bloom, A.L., 1977. Sedimentation rates on tidal salt marshes in Connecticut. Journal of Sedimentary Petrology 47, 1484–1490.

Harty, C., 2004. Planning strategies for mangrove and saltmarsh changes in southeast Australia. Coastal Management 32 (4), 405–415.

Hennessy, K.J., Suppiah, R., Page, C.M., 1999. Australian rainfall changes, 1910–1995. Australian Meteorological Magazine 48, 1–13.

Hogarth, P.J., 1999. The biology of mangroves. Oxford University Press, New York.

Kaye, C.A., Barghoorn, E.S., 1964. Late Quaternary sea level change and crustal rise at Boston, Massachusetts with notes on the autocompaction of peat. Bulletin of the Geological Society of America 75, 63–80.

Knott, J.F., Nuttle, W.K., Hemond, H.F., 1987. Hydrological parameters of salt marsh peat. Hydrological Processes 1, 211–220.

Lugo, A.E., Sell, M., Snedaker, S.C., 1976. Mangrove ecosystem analysis. In: Patten, B.C. (Ed.), Systems Analysis and Simulation Ecology. Academic Press, New York, pp. 113–145.

McKee, K.L., Rooth, J.E., 2003. Impacts of elevated CO_2 and nutrients on biomass production and allocation in a mangrove–saltmarsh community. Society of Wetland Scientists 24th Annual Meeting, New Orleans, Louisiana.

McLoughlin, L., 1988. Mangroves and grass swamps: changes in the shoreline vegetation of the Middle Lane Cover River, Sydney, 1780's–1880's. Wetlands (Australia) 7, 13–24.

McLoughlin, L., 2000. Estuarine wetlands distribution along the Parramatta River, Sydney, 1788–1940: implications for planning and conservation. Cunninghamia 6, 579–610.

McMillan, C., 1975. Adaptive differentiation in chilling in mangrove populations. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (Eds.), Proceedings of the International Symposium on Biology and Management of Mangroves. University of Florida, Florida.

McTainsh, G., Iles, B., Saffinga, P., 1988. Spatial and temporal patterns of mangroves at Oyster Point Bay, South East Queensland, 1944–1983. Proceedings of the Royal Society of Queensland 99, 83–91.

Mitchell, M.L., Adam, P., 1989. The decline of saltmarsh in Botany Bay. Wetlands (Australia) 8, 55–60.

Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea level. Ecology 83, 2869–2877.

Morton, R.M., 1994. Fluctuations in wetland extent in southern Moreton Bay. In: Greenwood, J.G., Hall, N.J. (Eds.), Future Marine Science in Moreton Bay. School of Marine Science, University of Queensland, Brisbane, pp. 145–150.

Nuttle, W.K., Hemond, H.F., Stolvenback, H.D., 1990. Mechanisms of water storage in salt marsh sediments: The importance of dilation. Hydrological Processes 4, 1–13.

Onuf, C.P., Teal, J.M., Valiela, I., 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology 58, 514–526.

Pittock, A.B., 1975. Climatic change and the patterns of variation in Australian rainfall. Search 6 (11–12), 498–504.

Pittock, A.B., 1983. Recent climatic change in Australia: implications for a CO_2-warmed earth. Climatic Change 5, 321–340.

Reed, D.J., Cahoon, D.R., 1993. Marsh submergence vs. marsh accretion: interpreting accretion deficit data in coastal Louisiana. Coastal Zone '93. American Shore and Beach Preservation Association, New Orleans, Louisiana, pp. 243–257.

Rogers, K., Saintilan, N. Relationships between surface elevation and groundwater in mangrove forests of SE Australia. Journal of Coastal Research, in press.

Rogers, K., Saintilan, N., Cahoon, D.R., 2005. Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. Wetlands Ecology and Management 13, 587–598.

Rooth, J.E., Stevenson, J.C., 2000. Sediment deposition patterns in *Phragmites australis* communities: implications for coastal areas threatened by rising sea-level. Wetlands Ecology and Management 8, 173–183.

Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of south-east Australia estuaries. Estuarine, Coastal and Shelf Science 53, 351–384.

Saenger, P., Moverley, J., 1985. Vegetative phenology of mangroves along the Queensland coastline. Proceedings of the Ecological Society of Australia 13, 257–265.

Saintilan, N., 1998. Photogrammetric survey of the Tweed River wetlands. Wetlands (Australia) 17, 74–82.

Saintilan, N., 2003. The influence of nutrient enrichment upon mangrove seedling establishment and growth in the Hawkesbury River estuary, New South Wales, Australia. Wetlands (Australia) 21, 29–35.

Saintilan, N., 2004. Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. Estuarine, Coastal and Shelf Science 61, 591–601.

Saintilan, N., Hashimoto, T.R., 1999. Mangrove–saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia. Hydrobiologia 413, 95–102.

Saintilan, N., Williams, R.J., 2000. The decline of saltmarshes in Southeast Australia: results of recent surveys. Wetlands (Australia) 18, 49–54.

Saintilan, N., Williams, R.J., 1999. Mangrove transgression into saltmarsh environments in south-east Australia. Global Ecology and Biogeography Letters 8, 117–124.

Saintilan, N., Wilton, K., 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetlands Ecology and Management 9, 409–420.

Stevenson, J.C., Ward, L.G., Kearney, M.S., 1986. Vertical accretion in marshes with varying rates of sea-level rise. In: Wolfe, D.A., Champ, M.A., Flemer, D.A., Mearns, A.J. (Eds.), Estuarine Variability. Academic Press, New York, pp. 241–259.

Vanderzee, M.P., 1988. Changes in saltmarsh vegetation as an early indicator of sea-level rise. In: Pearmen, G.I. (Ed.), Greenhouse: Planning for Climate Change. CSIRO, Melbourne.

van Wijnen, H.J., Bakker, J.P., 2001. Long-term surface elevation change in salt marshes: a prediction of marsh response to future sea-level rise. Estuarine, Coastal and Shelf Science 52, 381–390.

West, R.J., Thorogood, C.A., Walford, T.R., Williams, R.J., 1984. Mangrove distribution in New South Wales. Wetlands (Australia) 4, 2–6.

Williams, R.J., Watford, F.A., 1997. Changes in the distribution of mangrove and saltmarsh in Berowra and Marramarra Creeks, 1941–1991. NSW Fisheries, Fisheries Research Institute, Cronulla, 21pp.

White, I., Melville, M.D., Wilson, B.P., Sammut, J., 1997. Reducing acidic discharges from coastal wetlands in eastern Australia. Wetlands Ecology and Management 5, 55–72.

Whelan, K.R.T., Smith III, T.J., Cahoon, D.R., Lynch, J.C., Anderson, G.H., 2005. Groundwater control of mangrove surface elevation: shrink-swell of mangrove soils varies with depth. Estuaries, in press.

Williams, R.J., Watford, F.A., Balashov, V., 1999. Kooragang Wetland Rehabilitation Project: Changes in Wetland Fish Habitats of the Lower Hunter River. NSW Fisheries, Office of Conservation, Fisheries Research Institute, Cronulla.

Wilton, K., 1997. Changes in mangrove (*Avicennia marina*) and saltmarsh (*Sarcocornia quinqueflora*) habitats in the Sydney area, with specific reference to Careel Bay, Pittwater. The Ecology of Estuaries and Soft Sediment Habitats. Published conference abstracts, Deakin University, Warrnambool, Victoria.

Wilton, K., 2002. Coastal wetland habitat dynamics in selected New South Wales estuaries. PhD thesis, Australian Catholic University, 329 pp., plus appendices.

Wilton, K.M., Saintilan, N., 2000. Protocols for mangrove and saltmarsh habitat mapping. Australian Catholic University Coastal Wetlands Unit Technical Report 2000/01. Produced for the Estuaries Branch, NSW Department of Land and Water Conservation, Sydney.

Woodroffe, C.D., 1990. The impact of sea-level rise on mangrove shorelines. Progress in Physical Geography 14, 483–520.

Estuaries Vol. 28, No. 4, p. 551–559 August 2005

Mangrove Encroachment of Salt Marsh in Western Port Bay, Victoria: The Role of Sedimentation, Subsidence, and Sea Level Rise

K. ROGERS[1,*], N. SAINTILAN[1], and H. HEIJNIS[2]

[1] *School of Arts and Sciences, Australian Catholic University, Post Office Box 968, North Sydney, NSW 2059, Australia*
[2] *Environment Division, Australian Nuclear Science and Technology Organisation, PMB1, Menai, NSW 2234, Australia*

ABSTRACT: Surface elevation tables, feldspar marker horizons, and ^{210}Pb analysis of core profiles were implemented at four sites in Western Port Bay, Victoria, Australia, to provide information on the role of sedimentation, subsidence or compaction, and enhanced sea-level rise in contributing to salt marsh decline. Photogrammetric surveys indicate that the rate of salt marsh decline that is attributable to mangrove encroachment is lower in Western Port Bay than in comparable sites in New South Wales. Differences in the rate of mangrove encroachment at Western Port Bay may be attributed to the inverse relationship found between the degree of mangrove encroachment and surface elevation increase. While sedimentation contributes to surface elevation changes, surface elevation is not solely explained by sedimentation; factors including auto-compaction and changes in the water table also play a significant role in Western Port Bay. Historic sedimentation rates measured using ^{210}Pb dating techniques corresponded to contemporary sedimentation rates determined from feldspar marker horizons. Core sediment profiles show no change in sedimentation rates at three sites. A fourth site (French Island) was the only site that exhibited high rates of sedimentation, which appears to be related to local land-use changes in the area. All sites maintained their elevation with respect to sea level over the study period. Historic sedimentation exceeded sea-level rise for the past 32 yr, but it is difficult to determine the extent to which belowground processes affect surface elevation, causing deviations between surface elevation and sedimentation over longer periods.

Introduction

Mangroves and salt marshes are an important component of the estuarine ecosystem of Western Port Bay, Victoria, Australia. Although the grey mangrove (*Avicennia marina* var. *australisica* (Forssk.) Vierh.) nears its southern limit of distribution, it is able to sustain a biomass of 20 kg m^{-2}, cover over 40% of the shoreline, and provide significant levels of detritus to intertidal and nearshore communities (Clough and Attiwill 1975). It is these communities that are the most productive and diverse of the coastal inlets of Victoria (Chapman 1974). The salt marsh habitat supports a greater floristic diversity than comparable salt marshes elsewhere in mainland Australia (Adam 1990) and is an important roosting habitat for migratory birds, rare species of parrots, and fish (Zann 1997).

Salt marshes are vulnerable to pressures of development and estuary modification. In southeastern Australia, mangrove encroachment of salt marshes has contributed to salt marsh decline over the last five decades (Saintilan and Williams 1999, 2000). The results from 28 photogrammetric surveys published since 1982 reveal that the loss of salt marsh is in excess of 30% in over 70% of the estuaries studied. These changes may be the result of elevated sea levels, changes to the tidal prism, or the response of these systems to changes in the quantity and nutrient level of tideborne sediments.

This research is part of a comprehensive mangrove and salt marsh monitoring program commenced by the Victorian Department of Natural Resources and Environment in its assessment of the marine resources of Western Port Bay. The purpose of the study is to provide quantitative information on the dynamics of mangrove and salt marsh vegetation and changes in rates of sedimentation and surface elevation within mangrove and salt marsh habitats. These changes were examined in the context of sea-level rise throughout southeastern Australia over the past century. The study incorporates sites of varying degrees of catchment development including sites where direct human effects upon wetlands were anticipated, and significantly less affected sites in more remote locations. The preliminary results of a 3-yr baseline study are discussed.

* Corresponding author; tele: +61 2 9739 2874; fax: +61 2 9739 2009; e-mail: k.rogers@mackillop.acu.edu.au

© 2005 Estuarine Research Federation

Study Location

Western Port Bay (38°21′00″S, 145°13′00″E) is east of Melbourne, Australia. The climate of Western Port Bay is described as a cool temperate climate with mean daily temperatures at Stony Point ranging between 7.1°C and 24.1°C and annual rainfall averaging 763.8 mm yr^{-1}. Annual rainfall between April 2002 and April 2003, the height of a drought, totalled 598.3 mm at Cranbourne (38°06′S, 145°16′E).

The saline coastal wetlands of Western Port Bay primarily comprise of mangrove forests and salt marsh plains. *A. marina* is the only mangrove species occurring south of Merimbula, New South Wales, and is close to its southern limit in Corner Inlet (38°46′S, 146°20′E). The salt marsh plains are floristically rich, supporting approximately 30 species including a number species endemic to this region. Following a process of literature review, photogrammetric and LANDSAT survey, and community consultation estuarine wetlands at French Island, Kooweerup, Quail Island, and Rhyll were selected as the primary study sites (Fig. 1).

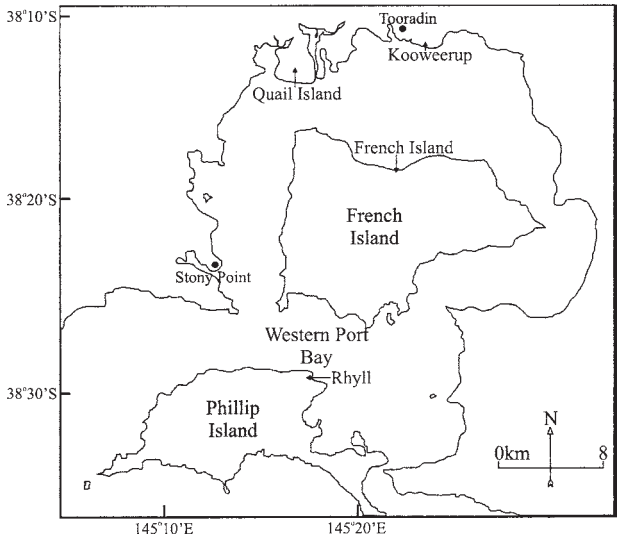


Fig. 1. Location of French Island, Kooweerup, Quail Island, and Rhyll study sites within Western Port Bay.

Materials and Methods

To analyse changes in estuarine wetland vegetation and sedimentation at Western Port Bay, photogrammetric mapping, surface elevation, and sedimentation studies were employed at each study site.

Photogrammetric Mapping

Historical aerial photographs of each study site dated 1939, 1967, 1973, and 1999, were scanned and imported into the ArcView Geographic Information System (ESRI Inc. version 3.2) as digital images. All digital images were georectified using a minimum of six ground control points. Vegetation community boundaries were delineated in accordance with the protocols of Wilton and Saintilan (2000). The area of vegetation units was determined and the changes in extent analyzed to determine whether they occurred at the seaward or landward boundary of mangrove and salt marsh.

Surface Elevation and Sediment Accretion

To analyze surface elevation, version IV of Surface Elevation Tables (SETs) were installed (Cahoon et al. 2002a). SETs enable detection of change in surface elevation of intertidal and shallow subtidal environments by taking high precision measurements of surface elevation (Boumans and Day 1993). A total of 24 SET monitoring stations were installed at Western Port Bay. At each site, 3 SETs were established in the salt marsh and 3 in the mangrove, to characterize the sedimentation and elevation properties of these vegetation units. Initial measurements were taken in October 2000 and additional measurements taken in November 2001, December 2002, and November 2003.

Sediment accretion was measured in conjunction with each SET monitoring station. At the time of SET installation, three 0.25-m^2 feldspar marker horizons were established on the marsh surface at the perimeter of each SET monitoring station. These horizons served as sedimentation markers against which sediment accretion was measured. Mini cores were taken from each feldspar horizon in November 2001, December 2002, and November 2003, and the distance from the marsh surface to the marker horizon was measured.

Analysis of variance was used to determine whether surface elevation change and vertical accretion varied consistently over the study period and between mangrove and salt marsh environments.

Continuous cores, with dimensions of approximately 10 cm diameter and 0.5–1 m length, were extracted from the muddy sediments of the salt marsh at Kooweerup, Quail Island, French Island, and Rhyll, Western Port Bay. Cores were taken to the Australian Nuclear Science and Technology Organisation, where the length and compaction of the core was recorded. The sediments were divided into 1 cm slices and a selection of slices was analyzed using standard ^{210}Pb dating techniques.

Results

Photogrammetric Mapping

Photogrammetric mapping of the estuarine wetlands at Western Port Bay indicate that despite varying degrees of development, the loss of salt

TABLE 1. Total area (hectares) and change in area (percent change over study period) of mangrove and salt marsh at study sites in Western Port Bay between 1939 and 1999.

Site	Vegetation Type	Vegetation Extent				Percent Change
		1939	1967	1973	1999	
Kooweerup	Mangrove	11.32		14.40	18.13	60.09
	Salt marsh	41.57		31.96	23.02	−44.61
Rhyll	Mangrove	40.04		57.86	62.28	55.54
	Salt marsh	174.27		153.72	139.83	−19.76
Quail Island	Mangrove			73.84	97.47	32.00
	Salt marsh			157.52	138.71	−11.94
French Island	Mangrove		185.16	178.32	189.23	2.20
	Salt marsh		518.63	510.92	490.63	−5.40

marsh due to mangrove transgression is apparent at each site (Table 1). Mangrove is primarily replacing salt marsh by extending along tidal creeks draining the salt marsh and expanding into the salt marsh interior.

Surface Elevation

Marsh surface elevation did not increase consistently at all sites in Western Port Bay (Table 2). Rhyll exhibited a net elevation gain in both the mangrove and salt marsh zones, while there was no net elevation gain in both mangrove and salt marsh zones at Kooweerup (Fig. 2). Both French Island and Quail Island exhibited an elevation increase in the salt marsh zone and an elevation decrease in the mangrove zone over the study period. Annual rates of surface elevation change did not differ significantly between mangrove and salt marsh zones at Kooweerup ($p = 0.983$), Quail Island ($p = 0.244$), and Rhyll ($p = 0.540$), but was significantly greater in the salt marsh zone at French Island ($p < 0.001$). Rates of surface elevation increase or decrease differed significantly ($p < 0.001$) over time at French Island, Kooweerup, and Rhyll, but not at Quail Island ($p = 0.131$).

Contemporary Sediment Accretion

Sediment accretion was consistently higher in the mangrove zone at all sites (Fig. 3 and Table 2). Differences between the rate of sediment accretion in the mangrove and salt marsh zones was significant ($p < 0.001$) at French Island, Kooweerup, Quail Island, and Rhyll. The rate of sediment accretion was consistent over the period of analysis at Kooweerup ($p = 0.122$) and Quail Island ($p = 0.099$); the rate of sediment accretion was significantly different over time at French Island ($p < 0.001$) and Rhyll ($p = 0.018$).

Sediment accretion over the period of analysis exceeded marsh surface elevation change at all sites and in all zones except French Island where surface elevation increase exceeded sediment accretion in the salt marsh zone. Differences in the rate of surface elevation change and the rate of sediment accretion were significant at all sites ($p < 0.001$).

TABLE 2. Mean (±SE) rates of surface elevation change (mm) and sediment accretion (mm) in the mangrove and salt marsh zones at study sites in Western Port Bay. * At Quail Island only Period 2 extends from November 2001 to January 2003 and Period 3 from January 2003 to November 2003.

Site	Zone	Measurement	Period 1	Period 2*	Period 3*
			October 2000 to November 2001	November 2001 to November 2002	November 2002 to November 2003
French Island	Mangrove	Elevation	6.69 (1.80)	−13.98 (2.06)	1.15 (1.92)
		Accretion	16.75 (2.65)	12.08 (0.99)	9.49 (2.69)
	Salt marsh	Elevation	8.79 (1.04)	5.10 (1.19)	1.73 (1.14)
		Accretion	4.39 (0.37)	4.01 (0.43)	4.37 (0.51)
Kooweerup	Mangrove	Elevation	15.65 (2.30)	−9.62 (3.21)	−6.76 (2.19)
		Accretion	11.62 (0.92)	10.41 (0.48)	7.20 (0.85)
	Salt marsh	Elevation	−0.28 (1.12)	−2.80 (1.03)	2.24 (1.42)
		Accretion	1.87 (0.36)	1.51 (0.26)	2.03 (0.32)
Quail Island	Mangrove	Elevation	−5.70 (3.38)	−4.92 (1.59)	4.77 (2.23)
		Accretion	9.48 (2.14)	6.92 (1.93)	6.77 (0.79)
	Salt marsh	Elevation	4.43 (4.68)	−1.93 (1.06)	−0.64 (1.07)
		Accretion	3.52 (0.23)	2.18 (0.50)	2.35 (0.96)
Rhyll	Mangrove	Elevation	2.78 (1.61)	−6.69 (1.98)	8.44 (3.15)
		Accretion	8.79 (1.63)	7.58 (2.65)	5.10 (0.72)
	Salt marsh	Elevation	1.02 (1.14)	−0.25 (0.95)	1.08 (0.57)
		Accretion	1.94 (0.27)	1.41 (0.41)	1.59 (0.19)

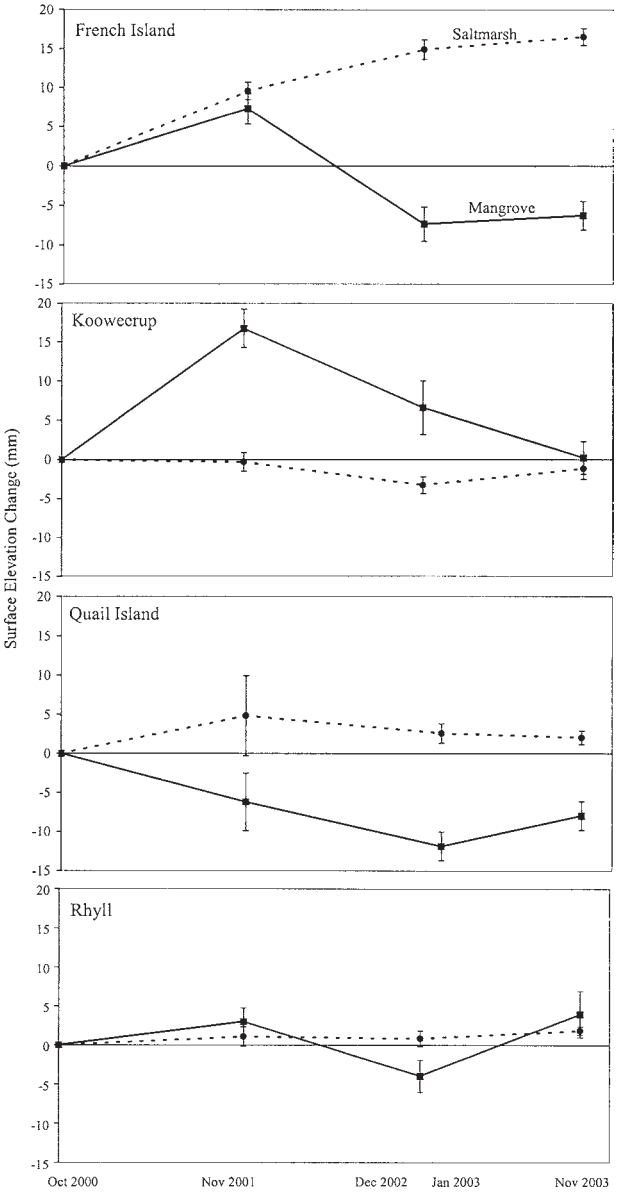


Fig. 2. Surface elevation change at study sites in Western Port Bay between October 2000 and November 2003.

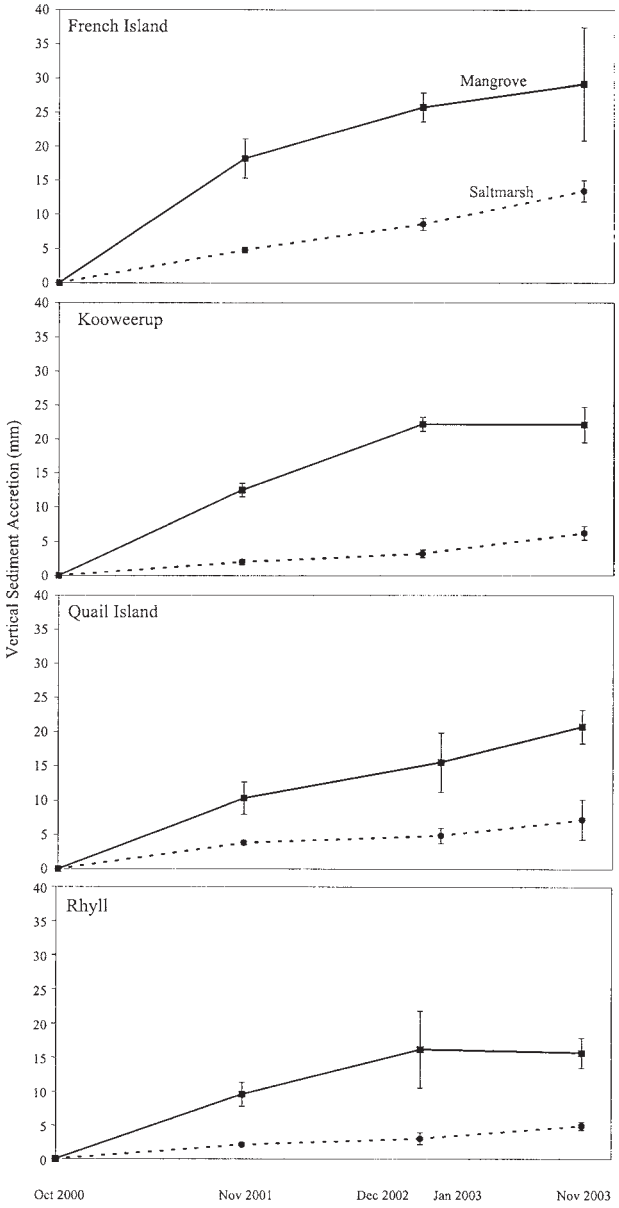


Fig. 3. Sediment accretion at study sites in Western Port Bay between October 2000 and November 2003.

Historic Sedimentation Rates

Analysis of excess ^{210}Pb activity (Fig. 4) in the cores extracted from the salt marsh at Kooweerup indicate that sediment is accreting at a mean rate of 1.63 ± 0.16 mm yr^{-1} for the past 150 yr, while at Quail Island and Rhyll sediment is accreting at 1.4 ± 0.2 and 2.5 ± 0.1 mm yr^{-1}, respectively, for the past 100 yr (Fig. 5). The best estimate of historic sedimentation corresponds closely with the contemporary sediment accretion rates estimated using feldspar marker horizons (Table 3). The upper mixing zone was excluded from estimates and may reflect the high degree of bioturbation and mixing of sediments.

Excess ^{210}Pb activity in the French Island salt marsh core does not reflect contemporary sediment accretion. A high sedimentation event occurred approximately 15 yr ago, accreting sediment on the marsh surface at a rate of 20 ± 8 mm yr^{-1}. Prior to this, the historic sedimentation rate is low (1.4 ± 0.2 mm yr^{-1}) compared to contemporary estimates.

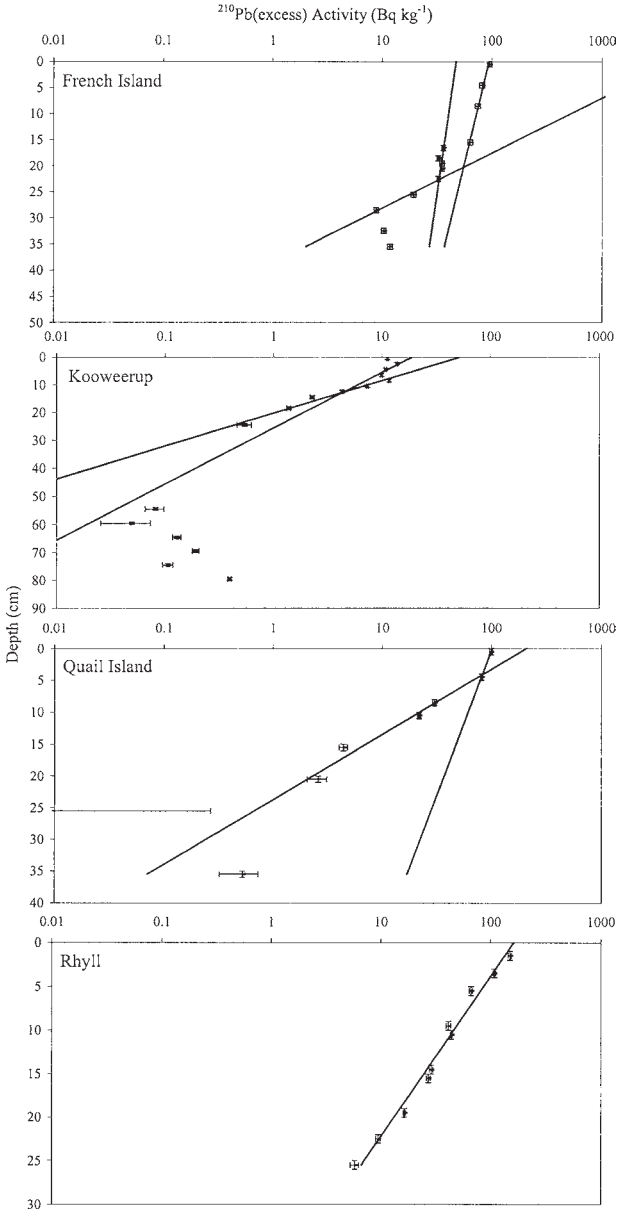


Fig. 4. Excess ^{210}Pb activity in sediments at various depths from cores extracted from the salt marsh at French Island, Kooweerup, Quail Island, and Rhyll, Western Port Bay.

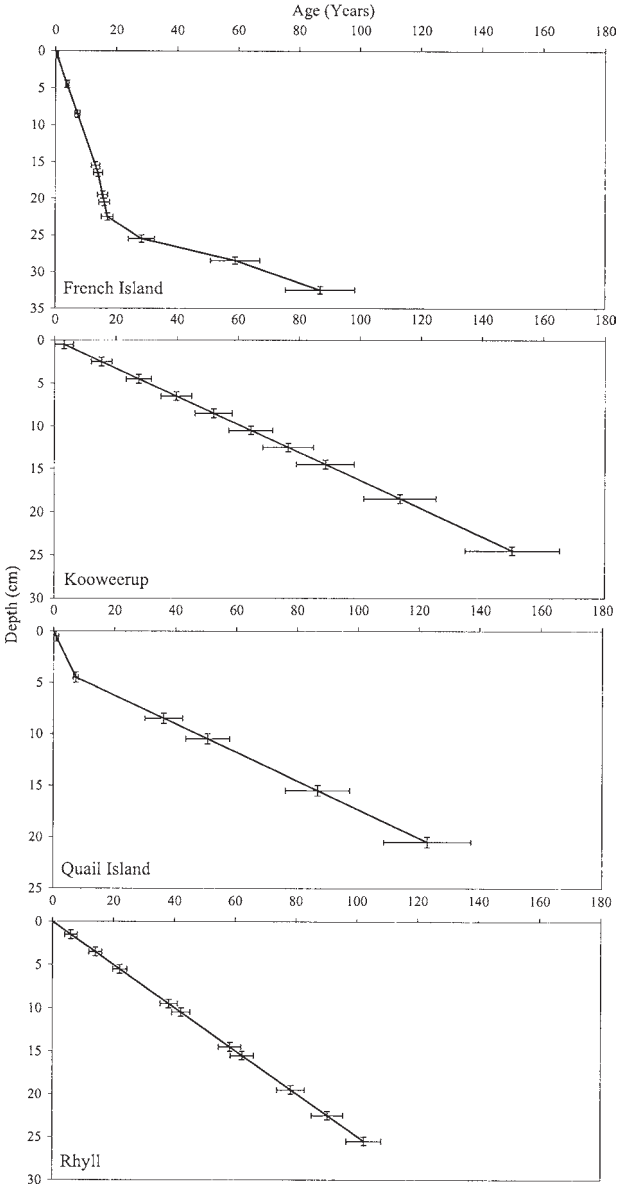


Fig. 5. Age of sediments at various depths from cores extracted from the salt marsh at French Island, Kooweerup, Quail Island, and Rhyll, Western Port Bay.

Discussion

Mangrove Encroachment in Western Port Bay

Detailed photogrammetric mapping of the *A. marina* community showed a pattern of greater change in the more developed sites. Salt marsh decline at all sites primarily occurred along tidal creeks draining the salt marsh where mangrove juveniles were observed encroaching along these creeks. Diminished horizontal movement of propagules by tides (Patterson et al. 1997) and favorable salinity, light, and sediment factors (Clarke and Allaway 1993) may enhance mangrove establishment along tidal drainage creeks.

It is evident that salt marsh decline was proportional to catchment development. The heavily affected site of Kooweerup, which is the northernmost site within Western Port Bay, exhibited the highest degree of mangrove expansion and salt marsh decline. Much of the earlier decline in salt marsh at this site can be attributed to the construction of the airport at Tooradin between 1939 and 1973, though since this time salt marsh

TABLE 3. Historic and contemporary sedimentation rates (±SE), determined from ^{210}Pb-dating of sediments and feldspar marker horizons, for study sites in Western Port Bay.

	Mean Contemporary Sedimentation		Upper Mixing Zone Sedimentation		Best Estimate of Historic Sedimentation		Other Sedimentation Events	
Site	Rate (mm yr^{-1})	Period (yr prior)	Rate (mm yr^{-1})	Period (yr prior)	Rate (mm yr^{-1})	Period (yr prior)	Rate (mm yr^{-1})	Period (yr prior)
French Island	4.26 (0.43)	0–3	12 (1) $r^2 = 0.9806$	0–13	1.4 (0.2) $r^2 = 0.9867$	16–58	20 (8) $r^2 = 0.7671$	13–16
Kooweerup	1.80 (0.31)	0–3	25.04 (42.05) $r^2 = 0.1081$	0–3	1.63 (0.16) $r^2 = 0.975$	3–52		
Quail Island	2.69 (0.56)	0–3	6.0 r^2 = na	0–4	1.4 (0.2) $r^2 = 0.975$	4–120		
Rhyll	1.65 (0.29)	0–3			2.5 (0.1) $r^2 = 0.9830$	0–100		

has continued to decline by 28% (between 1973 and 1999), while mangrove increased by 26%. The French Island site, located on the remote northern shore of the French Island National Park, exhibited the smallest degree of decline between 1973 and 1999 with salt marsh decreasing by 4% and mangrove increasing by 6%. The lower rate of mangrove encroachment on French Island may in part be attributed to a levee constructed between the mangrove and salt marsh in the 19th century as part of a salt works.

Quail Island, selected as a significantly less affected site due to the isolation of the island within a Nature Reserve, exhibited the second highest degree of decline with salt marsh decreasing by 12% and mangrove increasing by 32% between 1973 and 1999. Salt marsh decline at the Rhyll site, on the northern side of Phillip Island was in the order of 9% between 1973 and 1999, while mangrove increased by 8%.

When excluding the decrease in salt marsh that can be attributed to reclamation for the airport at Kooweerup and farmland at Rhyll, the rates of salt marsh decline in Western Port Bay are low compared to rates reported by Saintilan and Williams (1999, 2000) for estuaries in New South Wales. The median rate of decline in salt marsh due to mangrove encroachment over the same period in New South Wales estuaries was 30%.

Possible Causes of Mangrove Encroachment

There are a number of possible explanations for lower rates of mangrove encroachment in Western Port Bay than for estuaries in New South Wales. Temperature may be a factor since *A. marina* reaches its southern limit in nearby Corner Inlet, and colder air temperatures and frosts produce slower growth rates in mangroves (McMillan 1975; Saenger and Moverley 1985). The dense stands of saltbush species (*Halosarcia* and *Sclerostegia* spp.) is a characteristic of salt marshes in Western Port Bay. Saltbush may play an inhibitive role by either shading seedlings of *A. marina* or collecting sediments and building up the marsh surface to exclude mangroves. These species are absent in New South Wales except for a limited distribution of Halosarcia at Cararma Inlet and Homebush Bay. Similar competition has been reported between mangroves and *Spartina* sp. in marshes in Louisiana (McKee and Rooth 2003; Patterson et al. 1993) and *Phragmites* and *Spartina* spp. in Maryland (Rooth and Stevenson 2000).

Variation in the rate of encroachment between sites in Western Port Bay may be related to trends in marsh surface elevation. Changes in salt marsh relative elevation may play a significant role by increasing tidal inundation and creating environments suitable for mangrove establishment and habitation. A strong relationship exists between the rate of mangrove increase and the rate of salt marsh surface elevation change ($r^2 = 0.817$). Sites with large salt marsh surface elevation increases exhibit low rates of mangrove increase, while sites with salt marsh elevation deficits exhibit high rates of mangrove increase.

Factors Influencing Surface Elevation

Rates of sediment accretion commonly have been used as an estimate for marsh elevation. While it may be suitable to assume that accretion is the primary process controlling marsh elevation at some sites, this is not always appropriate. Recent literature featuring SETs document subsurface processes of autocompaction and subsidence of marsh sediments (Cahoon et al. 1995; Cahoon and Lynch 1997; Cahoon et al. 2000), decomposition of organic matter, root growth and increases in productivity (Cahoon et al. 1999), water storage in sediments (Cahoon et al. 1995; Cahoon and Lynch 1997; Cahoon et al. 1999), changes in the water table (Rogers et al. in press), and tidal flooding (Paquette et al. 2004) that may cause marsh elevation to differ significantly from accretion.

Rates of surface elevation change did not differ significantly from rates of sediment accretion in the salt marsh zone at French Island ($p = 0.316$), Quail

Island ($p = 0.541$), and Rhyll ($p = 0.106$). Marsh elevation in the salt marsh zone at these sites can be primarily explained by sediment buildup on the marsh surface. Since surface elevation does not differ from sediment accretion at these sites, the vulnerability of these salt marshes may be expressed as a deficit between sediment accretion and sea-level rise.

Since mangroves generally establish at lower tidal elevations and have higher inundation frequencies than salt marsh at Western Port Bay, sediment accretion was consistently higher in the mangrove zone than the salt marsh at all sites. Surface elevation change in the mangrove zone did not consistently exceed surface elevation change in the salt marsh. Sediment accretion significantly exceeded surface elevation change in the mangrove zone at all sites and the salt marsh zone at Kooweerup, indicating that marsh elevations at these sites is not solely explained by sediment accretion alone and that processes of autocompaction or subsurface subsidence are evident. A marked drop in surface elevation became evident from November 2001 to December 2002 at all sites except the salt marsh zone at French Island. This trend was particularly noticeable in all mangrove sites. A subsequent increase in surface elevation was evident at all sites with the exception of the Kooweerup salt marsh, which may have been affected by earth moving works in the vicinity.

The drop in marsh surface elevation corresponds to the period of the El Niño drought of 2002 to 2003 in southeastern Australia and was also observed at Homebush Bay, New South Wales (Rogers et al. in press) and Jervis Bay, Minnamurra River, Hawkesbury River, and Hunter River (Rogers et al. 2002). Current SET research highlights the role of belowground processes of water accumulation in maintaining marsh surface elevation. Correlations have been found between marsh surface elevation change and mean water table depth (Cahoon et al. 2002b) and marsh surface elevation change and total monthly rainfall (Rogers et al. in press). This study and SET research in southeastern Australia suggests that rainfall and subsequent groundwater recharge plays a significant role in determining interannual variability in surface elevation with respect to sea level.

Comparison of Contemporary and Historic Rates of Sedimentation

Several authors have commented on an elevated rate of sedimentation in Western Port Bay since the 1970s (Wilk et al. 1979; Hancock et al. 2001). The dieback of extensive seagrass beds on the eastern side of the bay has been attributed to this sediment. With the exception of the French Island site, there is no evidence in the salt marsh cores of any change in sedimentation rate over the past 60–100 yr. Unlike cores retrieved from the open bay by Hanckock et al. (2000), the cores presented in this paper show a consistent decline in excess ^{210}Pb after a shallow mixing zone. The cores imply that salt marshes are potentially a useful source of sediment chronology, given low biological activity and consequently low rates of bioturbation. Due to the high tidal elevation of salt marshes in Western Port Bay, sedimentation primarily occurs during spring tide events only, and may miss short-term pulses of sediment during neap tide phases.

The ^{210}Pb chronology for French Island suggests an increase in sedimentation rate beginning in approximately 1985. There is also a relatively deep surface mixing zone in this core. While corresponding to the suggested increased sedimentation within the bay, the result more likely reflects local changes in land use following the closure of market gardens on the northern shore of the island and inclusion of this area in the French Island National Park or the infilling of ponds used in salt manufacture in the 1880s.

Current rates of sedimentation measured by feldspar marker horizons correspond broadly with rates of sedimentation measured by the ^{210}Pb profiles. Since sedimentation rates measured by excess ^{210}Pb account for soil compaction, discrepancies between sedimentation measured by feldspar marker horizons and ^{210}Pb concentrations may be related to compaction of sediments over time and errors inherent in each measurement technique. These rates are high compared with salt marshes of similar geomorphology and catchment development in New South Wales (Rogers et al. 2002). Perhaps lower rates of encroachment is in part related to overall higher rates of sedimentation in the salt marsh at Western Port Bay.

Sedimentation, Surface Elevation, and Sea Level

Hancock et al. (2000) applied a 2-layer mixing model to interpret ^{210}Pb profiles from sediments in Western Port Bay by assuming that mixing was absent below the upper mixing zone and that excess ^{210}Pb in the lower layer decays according to its half-life. By applying these assumptions to the core at Kooweerup it is evident that sedimentation for the past 150 yr (1.63 mm yr^{-1}) closely correlates with contemporary sediment accretion. Assuming there has been no subsidence of sediments below the core extracted from Kooweerup and based on a long-term (32 yr) sea-level rise estimate from nearby Williamstown, sedimentation in the salt marsh at Kooweerup has exceeded sea-level rise, implying a buildup of the marsh surface relative to mean sea level. The same is true for the Rhyll and Quail

Island sites, where according to the 2-layer mixing model, sedimentation exceeds sea-level rise for the past 125 yr.

In the mangrove zone at French Island the rate of sediment accretion exceeded the rate of surface elevation change with the mangrove marsh elevation decreasing by 6.27 mm over the study period. Shallow compaction, being the deficit between sediment accretion and surface elevation change, was in the order of 11.53 mm yr^{-1}. The accumulative effects of high marsh compaction rates, low sedimentation rates, marsh surface elevation change, and an average sea-level rise of 0.26 mm yr^{-1} at nearby Williamstown (Mitchell et al. 2000) suggest that the mangrove forest at French Island is not sustainable under current sedimentation regimes, climate conditions, and long-term sea-level rise trends (32 yr of data at Williamstown).

Statistical analysis of surface elevation change in the mangrove zone at French Island indicates that rates of surface elevation change varied significantly over time ($p < 0.001$) and do not represent consistent trends, primarily due to the relationship between marsh surface elevation and the El Niño related drought. Sea level at nearby Stony Point has decreased by 21.8 mm yr^{-1} over the study period. When comparing short-term surface elevation change with long-term sea-level rise, there is a deficit between the rate of marsh surface elevation increase (22.0 mm yr^{-1}) and sea-level rise (+0.26 mm yr^{-1}) in the order of 22.26 mm yr^{-1}. When comparing the short-term rates of surface elevation change (22.0 mm yr^{-1}) with short-term changes in mean sea level over the study period (221.8 mm yr^{-1}), there is a marsh elevation increase relative to mean sea level in the order of 19.8 mm yr^{-1}. Since a consistent trend of marsh elevation change is not evident at French Island and is not sustainable when compared to long-term sea-level rise data, we suggest that it is more appropriate to compare short-term rates of surface elevation change with short-term changes in means sea level. The same is true for Kooweerup where the rate of surface elevation change relative to mean sea level over the study period was 21.6 mm yr^{-1} in the mangrove zone and 21.5 mm yr^{-1} in the salt marsh zone.

The salt marsh zone at French Island was the only site that exhibited a consistent trend of marsh surface elevation increase over the study period, increasing at a mean rate of 5.21 mm yr^{-1}. While there was no net surface elevation decrease in correlation with the recent drought, the rate of surface elevation increase was significantly less ($p < 0.001$) increasing at a rate of 8.79 mm yr^{-1} during October 2000 to November 2001 and 1.73 mm yr^{-1} during December 2002 to November 2003. This may be partly related to the accumulation of water in abandoned salt evaporation ponds at the site. Comparisons of mean rates of salt marsh surface elevation increase with long-term sea-level trends indicates that under current sedimentation and hydrological conditions, the marsh elevation has increased relative to mean sea level in the order of 4.95 mm yr^{-1}. It is difficult to determine the extent to which surface elevation may correspond to sedimentation history over the longer period when belowground processes are not measured. Analysis of foraminiferan assemblages within the profile would go some way to resolving this issue, in that the elevation with respect to sea level could be estimated through the core (Edwards and Horton 2000; Horton et al. 2003).

Acknowledgments

The authors wish to acknowledge the financial assistance provided by the Victorian Department of Sustainability and Environment, and the Australian Institute of Nuclear Science and Engineering. Field assistance from Angus King, Nick Sporyalich, Angus Kerr, Jason Caitlin, and Lawrence Ferns is also kindly acknowledged.

Literature Cited

Adam, P. 1990. Saltmarsh Ecology, 1st edition. Cambridge University Press, Cambridge, Massachusetts.

Boumans, R. M. J. and J. W. Day, Jr. 1993. High precision measurements of sediment elevation in shallow coastal areas using a sedimentation-erosion table. *Estuaries* 16:375–380.

Cahoon, D. R., J. W. Day, and D. J. Reed. 1999. The influence of surface and shallow subsurface soil processes on wetland elevation: A synthesis. *Current Topics in Wetland Biogeochemistry* 3:72–88.

Cahoon, D. R., J. French, T. Spencer, D. J. Reed, and I. Moller. 2000. Vertical accretion versus elevational adjustment in U.K. saltmarshes: An evaluation of alternative methodologies, p. 223–238. *In* K. Pye and J. R. L. Allen (eds.), Coastal and Estuarine Environments: Sedimentology, Geomorphology, and Geoarchaeology. Special Publications 175. Geological Society, London, U.K.

Cahoon, D. R. and J. C. Lynch. 1997. Vertical accretion and shallow subsidence in Southwestern Florida, U.S.A. *Mangroves and Salt Marshes* 1:173–186.

Cahoon, D. R., J. C. Lynch, H. Phillippe, R. Boumans, B. C. Perez, B. Segura, and J. W. Day. 2002a. High precision measurements of wetland sediment elevation: I. Recent improvements to the sedimentation-erosion table. *Journal of Sedimentary Research* 72:730–733.

Cahoon, D. R., J. C. Lynch, T. J. Smith , Iii, K. R. T. Whelan, G. H. Anderson, and C. Walker. 2002b. Do surface and groundwater fluctuations influence sediment surface elevation in the coastal Everglades wetlands?, p. 29–30. *In* A. E. Torres, A. L. Higer, H. S. Henkel, P. R. Mixson, V. R. Eggleston, T. L. Embry, and G. Clement (eds.), U.S. Geological Survey Greater Everglades Science Program: 2002 Biennial Report. U.S. Geological Survey Open File 03-54, Palm Harbor, Florida.

Cahoon, D. R., D. J. Reed, and J. W. Day. 1995. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. *Marine Geology* 128:1–9.

Chapman, R. 1974. Western Port region conservation survey: A report to the Western Port Region Planning Authority. Conservation Council of Victoria, Melbourne, Australia.

CLARKE, P. J. AND W. G. ALLAWAY. 1993. The regeneration niche of the grey mangrove (*Avicennia marina*): Effects of salinity, light, and sediment factors on establishment, growth and survival in the field. *Oecologia* 93:548–556.

CLOUGH, B. F. AND P. M. ATTIWILL. 1975. Nutrient cycling in a community of *Avicennia marina* in a temperate region of Australia, p. 137–146. *In* G. E. Walsh, S. C. Snedaker, and H. J. Teas (eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, Volume 1. University of Florida, Gainesville, Florida.

EDWARDS, R. J. AND B. P. HORTON. 2000. Reconstructing relative sea-level change using U.K. salt-marsh formainifera. *Marine Geology* 169:41–56.

HANCOCK, G. J., J. M. OLLEY, AND P. J. WALLBRINK. 2001. Sediment transport and accumulation in Western Port. CSIRO Land and Water technical report 47/01, Canberra, Australia.

HANCOCK, G. J., I. T. WEBSTER, P. F. FORD, AND W. S. MOORE. 2000. Using Ra isotopes to examine transport processes controlling benthic fluxes into a shallow estuarine lagoon. *Geochimica et Cosmochimica Acta* 64:3685–3699.

HORTON, B. P., P. LARCOMBE, S. A. WOODROFFE, J. E. WHITTAKER, M. R. WRIGHT, AND C. WYNN. 2003. Contemporary foraminiferal distributions of a mangrove environment, Great Barrier Reef coastline, Australia; Implications of sea-level reconstructions. *Marine Geology* 198:225–243.

MCKEE, K. L. AND J. E. ROOTH. 2003. Impacts of elevated CO_2 and nutrients on biomass production and allocation in a mangrove-saltmarsh community. *In* Proceedings of Society of Wetland Scientists 24th Annual Meeting, New Orleans, Louisiana.

MCMILLAN, C. 1975. Adaptive differentiation to chilling in mangrove populations, p. 62–70. *In* G. E. Walsh, S. C. Snedaker, and H. J. Teas (eds.), Proceedings of the International Symposium on Biology and Management of Mangroves, Volume 1. University of Florida, Gainesville, Florida.

MITCHELL, W., J. CHITTLEBOROUGH, B. RONAI, AND G. W. LENNON. 2000. Sea level rise in Australia and the Pacific. *Climate Change Newsletter* 12:7–10.

PAQUETTE, C., K. L. SUNDBERG, R. M. J. BOUMANS, AND G. L. CHMURA. 2004. Changes in saltmarsh surface elevation due to variability in evapotranspiration and tidal flooding. *Estuaries* 27:70–89.

PATTERSON, S., K. L. MCKEE, AND I. A. MENDELSSOHN. 1997. Effects of tidal inundation and predation on *Avicennia germinans* seedling establishment and survival in a sub-tropical mangal/salt marsh community. *Mangroves and Salt Marshes* 1:103–111.

PATTERSON, C. S., I. A. MENDELSSOHN, AND E. M. SWENSON. 1993. Growth and survival of *Avicennia germinans* seedlings in a mangal salt marsh community in Louisiana, U.S.A. *Journal of Coastal Research* 9:801–810.

ROGERS, K., N. SAINTILAN, AND D. CAHOON. in press. Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetlands Ecology and Management.*

ROGERS, K., N. SAINTILAN, AND K. M. WILTON. 2002. Monitoring the loss of saltmarsh in South East Australia. Report prepared for Environment Australia by the Centre for Environmental Restoration and Stewardship, Australian Catholic University National, Sydney, Australia.

ROOTH, J. E. AND J. C. STEVENSON. 2000. Sediment deposition in *Phragmites australis* communities: Implications for coastal areas threatened by rising sea-level. *Wetlands Ecology and Management* 8:173–183.

SAENGER, P. AND J. MOVERLEY. 1985. Vegetative phenology of mangroves along the Queensland coastline. *Proceedings of the Ecological Society of Australia* 13:257–265.

SAINTILAN, N. AND R. J. WILLIAMS. 1999. Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography* 8:117–124.

SAINTILAN, N. AND R. J. WILLIAMS. 2000. Short note: The decline of saltmarsh in southeast Australia: Results of recent surveys. *Wetlands (Australia)* 18:49–54.

WILK, R. R., J. B. KEENE, AND M. A. H. MARDEN. 1979. Sediment characteristics in the embayment head of Western Port: The impact of swamp drainage and erosion on sedimentation and seagrass distribution. Ministry of Conservation, Environmental Studies Series Publication No. 24. Melbourne, Australia.

WILTON, K. M. AND N. SAINTILAN. 2000. Protocols for mangrove and saltmarsh habitat mapping. Australian Catholic University National Coastal Wetlands Unit Technical Report 2000/01, Sydney, Australia.

ZANN, L. P. 1997. Our Sea, Our Future: Major findings of the State of the Marine Environment Report for Australia. Ocean Rescue 2000, Department of Environment, Sport and Territories, Canberra, Australia.

Received, June 15, 2004
Revised, March 14, 2005
Accepted, April 11, 2005

Estuarine, Coastal and Shelf Science 149 (2014) 46–56

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: Implications for coastal wetland response to climate change

Kerrylee Rogers [a, *], Neil Saintilan [a, b], Colin D. Woodroffe [a]

[a] GeoQuest Research Centre, School of Earth and Environmental Sciences, University of Wollongong, Wollongong 2522, Australia
[b] Water Wetland and Coastal Science NSW Office of Environment and Heritage, Australia

ARTICLE INFO

Article history:
Received 12 February 2014
Accepted 15 July 2014
Available online 27 July 2014

Keywords:
mangrove expansion
salt marsh decline
surface elevation
sea-level rise
climate variability

ABSTRACT

The response of coastal wetlands to sea-level rise is receiving global attention and observed changes in the distribution of mangrove and salt marsh are increasingly associated with global climate change, particularly sea-level and temperature rise, and potentially elevated carbon dioxide. Processes operating over smaller-spatial scales, such as rainfall variability and nutrient enrichment are also proposed as possible short-term drivers of changes in the distribution of mangrove and salt marsh. We consider the response of mangrove and salt marsh in a subtropical estuary to changes in environmental variables over a 12 year period by comparing rates of surface elevation change and vegetation distribution dynamics to hydrological and climatic variables, specifically water level and rainfall. This period of analysis captured inter-annual variability in sea level and rainfall associated with different phases of the El Niño Southern Oscillation (ENSO). We found that the mangrove and salt marsh trend of increasing elevation was primarily controlled by position within the tidal prism, in this case defined by inundation depth and distance to the tidal channel. Rainfall was not a primary driver of elevation trends in mangrove and salt marsh, but rainfall and water level variability did influence variability in elevation over the study period, though cross-correlation of these factors confounds identification of a single process driving this variability. These results highlight the scale-dependence of coastal wetland vegetation distribution dynamics; the longer-term trend of surface elevation increase and mangrove encroachment of salt marsh correlated with global sea-level trends, while short-term variability in surface elevation was related to local variability in water level and rainfall. Rates of surface elevation increase were found to lag behind rates of water level change within the Tweed River, which may facilitate further expansion of mangrove into salt marsh. This study advocates integration of ecological and geomorphic techniques to understand the response of coastal wetlands to sea-level rise and climatic perturbations.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

The response of coastal wetlands to sea-level rise is of global concern (Reed, 1995; Cahoon et al., 2006; Day et al., 2008; McKee et al., 2012). However, relationships between sea level and wetland surface elevation are complex with many biophysical feedbacks between water level, inundation depth, duration and frequency of inundation, groundwater levels, sedimentation, and plant productivity; all of which potentially influence wetland surface elevation relative to sea level (Whelan et al., 2005; Cahoon et al., 2006; Rogers and Saintilan, 2009; McKee et al., 2012). Wetlands are reported to keep pace with sea-level rise when integrated over long periods of time, through the accumulation of allochthonous or autochthonous sediment (Saintilan et al., 2013; Krauss et al., 2014). Investigations appear to have confirmed continuous wetland vertical accretion during the decelerating stage of transgressive sea-level phases, with rates of aggradation of delta substrates comparable to reported rates of sea-level rise during the Holocene (Woodroffe, 1990; Hashimoto et al., 2006).

The maintenance of tidal wetlands over millennial and decadal timescales has given rise to theoretical treatments of wetland accretion and elevation adjusting according to the degree of tidal inundation (Pethick, 1981; Allen, 2000; Kirwan and Murray, 2007; Fagherazzi et al., 2012). For example, Morris et al. (2002) used field

* Corresponding author.
E-mail address: Kerrylee@uow.edu.au (K. Rogers).

http://dx.doi.org/10.1016/j.ecss.2014.07.009
0272-7714/© 2014 Elsevier Ltd. All rights reserved.

observations of wetland productivity and surface elevation responses to sea-level rise and nutrient enrichment to model a dynamic relationship between production, accretion and surface elevation whereby wetland elevation is constantly adjusted to balance rates of sea-level rise. Inundation-dependent accretion models increasingly presume that at higher rates of sea-level rise, wetland productivity decreases due to anoxic stress leading to rapid vegetation loss, and a threshold of wetland survival can be crossed (Kirwan et al., 2008, 2010), as confirmed by field observations in several settings (Kearney and Stevenson, 1991; Day et al., 2000; Reed, 2002; Kirwan et al., 2008). In these circumstances, the terms 'accretion deficit' or 'elevation deficit' have been applied to the long-term difference between water levels and vertical accretion or elevation trends (Cahoon et al., 1995).

Longer-term time-series elevation records are particularly useful for validating models of the response of coastal wetlands to projected sea-level rise. Landscape-scale spatial models incorporating drivers of surface elevation trends (sedimentation, plant productivity) and their varying responses to sea level are emerging, such as the 'sea-level affecting marshes model' (SLAMM; Akumu et al., 2011; Traill et al., 2011) and statistical models derived from local empirical data (Oliver et al., 2012; Rogers et al., 2012). These models are useful for exploring the relative vulnerability of coastal wetlands to varying sea-level rise scenarios, and options for accommodating landward retreat.

However, while long-term surface elevation and sea-level trends are of importance in predicting the fate of coastal wetlands, there is a growing body of work suggesting that short-term vegetation dynamics may be driven by relative sea-level changes of high amplitude operating over shorter time periods. Saintilan and Hashimoto (1999) suggested that mangrove incursion upon salt marsh on the Hawkesbury River, NSW, could not be explained by long-term accretion trends, and suggested that shorter-term (decadal-scale) sea-level fluctuations provided a better explanation of the timing and degree of mangrove expansion in that system. More recently, Kim et al. (2011) in a study of vegetation dynamics in the Skallingen salt marsh, Denmark, concluded that short-term increases in the frequency of over-marsh high water events associated with increased storminess and wind tides explained the dominance of species associated with frequent flooding. Long-term accretion trends in the Skallingen salt marsh did not indicate an accretion deficit.

Inter-annual and inter-decadal variability in water level and rainfall is strongly linked to phases in large-scale ocean-atmosphere oscillations. For example, the Skallingen salt marsh studied by Kim et al. (2011) is microtidal, and over-marsh high water events were associated with the positive phase of the North Atlantic Oscillation, which sets up frequent westerly gales and short-term wind tides in the North Sea. In SE Australia, inter-annual and inter-decadal variability in sea level is strongly linked to the El Niño Southern Oscillation (ENSO) and the Inter-decadal Pacific Oscillation (IPO), respectively (Zhang and Church, 2012). Saintilan and Hashimoto's (1999) observation of mangrove incursion upon salt marsh on the Hawkesbury corresponds with the onset of a negative phase of the ENSO in the 1970's. During these periods, sea-level rise is comparatively rapid, and the Australian monsoon is strengthened leading to increased rainfall over northern and eastern Australia, providing an additional, albeit cross-correlated driver of mangrove encroachment. Several studies in the region have suggested a role for rainfall as a potential driver (Saintilan and Wilton, 2001; Eslami-Andargoli et al., 2009, 2010).

Identifying the relative contribution of short and long-term drivers of geomorphic change in coastal wetlands is important for several reasons. Periods of sea-level stability, as recently experienced in SE Australia during an extended El Niño-related drought (2000–2009), can give a false impression of the resilience of coastal wetlands to longer-term sea-level trends. Rogers and Saintilan (2009) caution using short-term elevation data sets for modelling the response of wetlands to sea-level rise for this reason. Change in these systems may be concentrated in pulses of higher rates of rise associated with shifts in climatic phases. Furthermore, the coincidence of short and long-term drivers of change during climatic phases; such as riverine flooding, storm set-up and elevated water levels associated with the La Niña phase; may have a compounding effect on coastal wetland stability.

The Surface Elevation Table (SET) is a powerful tool for investigating relationships between coastal wetland surface elevation and drivers over multiple time-scales (Cahoon et al., 2002a, 2002b; Webb et al., 2013). The SET comprises a benchmark rod driven into the wetland surface against which relative surface elevation can be measured. The potential importance of ENSO in driving wetland surface elevation variability has been demonstrated in SE Australia (Rogers and Saintilan, 2009); in this case wetland surface elevation decreased with the onset of drought and elevation was correlated with rainfall, SOI and water table depth (Rogers et al., 2005, 2006; Rogers and Saintilan, 2009). However, only by repeated measurements over extended periods can the influence of different phases of ENSO on accretion or elevation deficits be determined. This paper provides a long-term (12 year) assessment of surface elevation changes in relation to sea level and rainfall trends through a full ENSO cycle. We analyse mangrove and salt marsh surface elevation data generated from a network of SETs established on the Tweed River estuary in 2000 and vegetation distribution dynamics derived from aerial photograph interpretation to investigate the drivers of wetland surface elevation dynamics. We specifically tested whether:

I. Surface elevation trends were influenced by climatic or hydrological variables including rainfall, ENSO phase (based on the Southern Oscillation Index), or water levels within the estuary; and
II. Surface elevation variability, derived by removing the trend from surface elevation data, was influenced by climatic or hydrological variables.

2. Methods

2.1. Study site

The Tweed River (Fig. 1) is located near the border of New South Wales and Queensland, Australia (28°11′S, 153°33′E) and drains a catchment of approximately 1000 km^2 that traverses the border. The estuary is classified as a wave-dominated barrier estuary that is relatively mature in the scheme of Roy et al. (2001). Low elevation alluvial plains are situated behind a prominent coastal barrier and are affected by urban development associated with the township of Tweed Heads. The estuary is semi-diurnal, with a tidal range of approximately 2.1 m and supports approximately 475 ha of saline coastal wetlands (mangrove and salt marsh) at intertidal elevations of approximately 0–1.5 m AHD (Australian Height Datum).

The focal study area was Ukerebagh Island, a low relief island primarily composed of marine sands deposited as part of the tidal delta of the Tweed River. Mangroves occur in the lower intertidal zone and include five species: *Aegiceras corniculatum*, *Avicennia marina*, *Bruguiera gymnorrhiza*, *Excoecaria agallocha* and *Rhizophora stylosa*. Salt marsh occupies the upper intertidal zone and diversity is largely limited to *Sporobolus virginicus*, though some *Juncus kraussii* occurs at the highest elevations. *Casuarina glauca* grows at elevations exceeding approximately 1.2 m AHD.

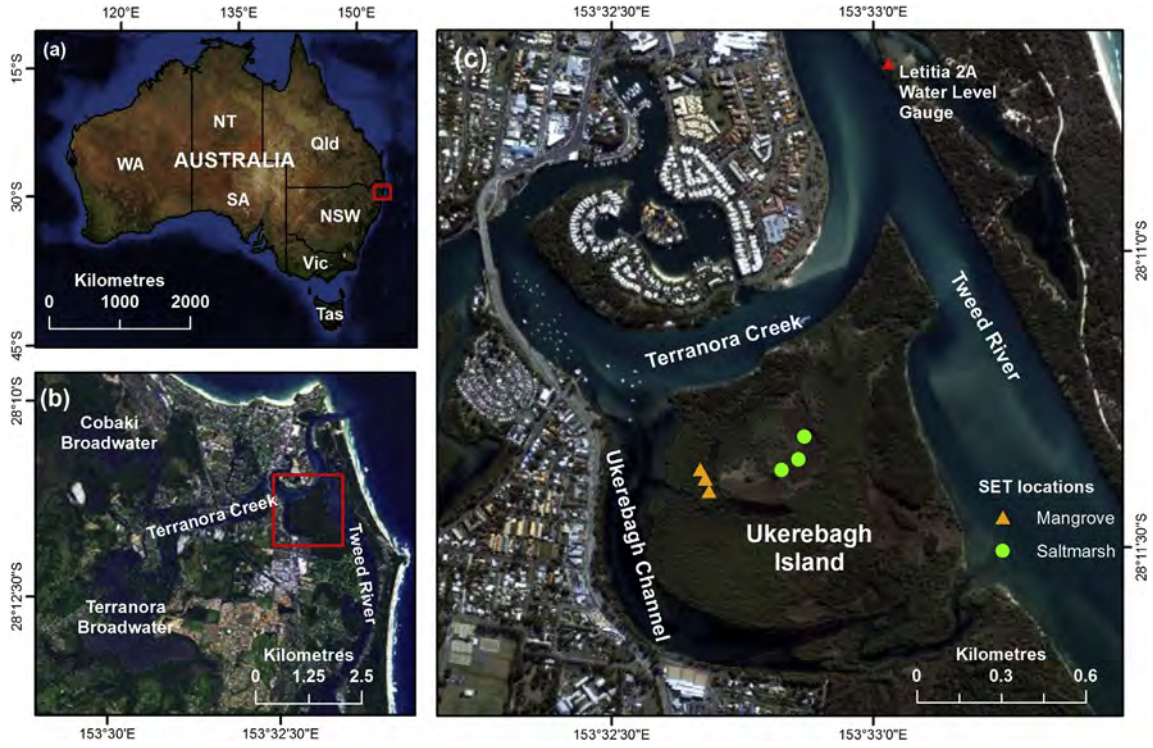


Fig. 1. Location of the Tweed River and the focal study site of Ukerebagh Island. SET locations are indicated within mangrove and saltmarsh, respectively.

2.2. Vegetation distribution dynamics

Changes in mangrove and salt marsh extent on the Tweed River have been mapped by Saintilan (1998) for the period 1930–1994 by aerial photograph interpretation using a stereo plotter. Ukerebagh Island is located within the 'tidal channel' section of this mapping and Saintilan (1998) notes expansion of mangrove on Ukerebagh Island into distributary channels of the Tweed River between 1930 and 1994, as well as some landward expansion into salt marsh. Landward expansion into salt marsh is dominated by *Avicennia marina* and is consistent with regional trends in SE Australia (Saintilan and Williams, 1999, 2000). Mangrove extent increased by 33 ha or 75% in the period 1930–1994; and while the distribution of salt marsh was similar in 1930 and 1994, there was a 5 ha gain between 1930 and 1948, which was subsequently lost due to mangrove incursions.

We augmented this mapping with higher frequency mapping using aerial photograph interpretation for the years of 2000, 2002, 2003, 2005, 2007, 2010 and 2012. Aerial photographs were scanned and georectified in ArcView (version 3.1); and mangrove and salt marsh were delineated as polygons for each map period. The area of each vegetation type was summarised for each map period for further analysis.

2.3. Surface elevation change dynamics

To analyse potential drivers of surface elevation trends we utilised a network of SETs (version IV, Cahoon et al., 2002a) installed on Ukerebagh Island in November 2000. SETs comprise a stable benchmark against which relative rates of surface elevation change can be determined in intertidal environments (Cahoon et al., 2002a). The technique can be used to establish longer-term elevation trends; and when coupled with measurements of vertical accretion enables the disaggregation of surface processes of sediment accretion and below-ground processes that influence the soil volume, such as shrink and swell of sediments, plant productivity or subsidence. The zone of influence of below-ground processes detected by the technique is limited to the base of SET benchmark poles, which was installed to a depth of approximately 4 m at Ukerebagh Island. SET benchmark poles were installed in replicates of three within both mangrove and salt marsh sites on 20 November 2000. Mangrove SETs were established at an approximate elevation of 0.17 m, 0.12 m and 0.12 m AHD respectively; salt marsh SETs were established at 0.63 m, 0.63 m and 0.74 m AHD. The portable component of the SET instrument consists of a horizontal arm with a horizontal plate at one end, and can be positioned onto benchmark poles in up to eight positions. The horizontal arm is levelled using a spirit level and nine fibreglass pins are lowered to the wetland surface through pin holes on the horizontal plate. Relative changes in the surface elevation over time can be detected for each pin by taking measurements of the length of pins above the levelled horizontal plate and repeating the procedure at specified time intervals. Initial measurements of the nine pins were taken in four arm directions for each monitoring station on 30 November 2000, and the procedure was repeated on 8 December 2001, 4 November 2002, 13 October 2003, 19 January 2006, 4 September 2007, 31 August 2009, 28 June 2010 and 19 October 2012.

To quantify sedimentation over the study period feldspar marker horizons (MHs) were laid on the wetland surface in three replicated quadrats of 0.25 m^2 at the margin of each SET monitoring station on 30 November 2000. Feldspar MHs are an artificial horizon against which sediment accumulates. After sediment has accumulated over the MH, the MH is visible within cores extracted from quadrats and the degree of sediment accumulation above the MH can be quantified using a ruler (Cahoon and Turner, 1989). Mini-cores were extracted from each MH when SETs were sampled and the vertical depth of sediment accumulation above the MH was determined. The MH is prone to loss due to bioturbation, mixing with other sediments, and removal or re-suspension by tides (Cahoon and Turner, 1989). Over the study period, the MH became

increasingly difficult to locate, particularly within the mangrove which is exposed to greater bioturbation and tidal influences. Hence, reported mean vertical accretion was derived only from MH that could be detected. We assumed that vertical accretion contributed to the observed surface elevation dynamics, and that accretion dynamics were captured in measurements of surface elevation, but did not include accretion in statistical analyses of factors influencing surface elevation.

2.4. Statistical analyses

SET measurements were standardised to rates of elevation change. Field notes were used to identify outliers associated with obstructions between the pins and the wetland surface, such as crab holes and pneumatophores; and these outliers were removed from further analyses. The corrected data were used to determine mean surface elevation and standard error for each arm direction at each SET benchmark, and mean surface elevation and standard error for mangrove and salt marsh at each measurement period. Mean relative surface elevation for mangrove and salt marsh was plotted against the measurement date and relative to the mean surface elevation at the first measurements (i.e. zero mean surface elevation at 30 November 2000). Linear regression analysis was applied to mean relative surface elevation to establish elevation trends for mangrove and salt marsh; rates of surface elevation increase were described on the basis of the slope of the linear trend.

The corrected data were standardised for time and converted to rates of surface elevation change. Repeated measures multivariate analysis of variance was employed to identify statistical differences between rates of surface elevation change over time and between sites in mangrove and those in salt marsh.

Rainfall and water level data that may influence mangrove and salt marsh surface elevation were compiled for each SET and for each month of SET sampling. This data set included different metrics for rainfall, water level and the southern oscillation index (SOI), and was supplemented by site specific information. Factors incorporated in the data set included:

- Rainfall metrics derived from monthly rainfall collated at the Tweed Heads rainfall gauge (Station number: 58506) including total monthly rainfall, mean rainfall for the previous three months, mean rainfall for the previous six months and antecedent rainfall. Antecedent rainfall was defined as mean rainfall for the period of three to six months prior to each month of SET sampling and is henceforth described as mean rainfall for three months with a three month lag.
- SOI metrics (BOM, 2013) including monthly SOI, mean SOI for the previous 3 months, mean SOI for the previous 6 months and antecedent SOI. Antecedent SOl was defined as mean SOI for the period of three to six months prior to each month of SET sampling and is henceforth described as mean SOI for three months with a three month lag.
- Water level metrics derived from monthly water level data extracted from the nearest water level gauge (Letitia 2A gauge; Station number: 201429; Fig. 1) including mean monthly water level, mean water level for the previous 3 months, mean water level for the previous 6 months, and antecedent water levels. Antecedent water levels was defined as mean water level for the period of three to six months prior to each month of SET sampling and is henceforth described as mean water level for three months with a three month lag.
- Time, which was characterised as the number of days since the first SET measurements on 30 November 2000.
- Hydrological distance, which was determined using a high resolution digital elevation model (DEM). The DEM was derived from a LiDAR survey conducted in June 2007 for Tweed Shire council by Fugro, Pty Ltd and reportedly has a vertical accuracy of ±15 cm. The ArcGIS hydrology toolset was utilised in conjunction with the DEM to establish the distance that tidal waters flow from the lower elevation wetland boundary to each SET. This technique differs from geometric measures as it more accurately captures the hydrological pathways through the wetland. We initially used the 'Sink' tool to identify cells in the input DEM that were lower elevation than neighbouring cells; these cells become problematic when determining flow direction and were subsequently filled using the 'Fill' tool. A total of 8402 cells of 2 m^2 resolution were identified using the 'Sink' tool, equating to approximately 4% of the total area of Ukerebagh Island. The resulting filled DEM layer was used as an input in the 'Flow Direction' tool; this tool creates a new layer that characterises the flow direction from each cell in the DEM to its steepest downslope neighbouring cell. The subsequent flow direction layer was then used as an input in the 'Flow Length' tool to determine the length of the upslope flow path from the low elevation boundary of the wetland. The flow length layer was queried to identify the flow length for each SET benchmark.
- Inundation depth, which was determined by the difference between the elevation of each SET and the mean monthly water level for each sampling period. The elevation of each SET was derived from a LiDAR derived DEM and the elevation of each SET was adjusted through time on the basis of the elevation change detected using the SETs.

To identify the drivers of surface elevation trends within mangrove and salt marsh, stepwise linear regression analyses were undertaken using this data set and surface elevation for each SET in the mangrove and salt marsh. To ensure that statistical analyses only applied to the intertidal component of Ukerebagh Island we assumed that surface elevation in the terrestrial vegetation community was stationary and included values in the data set that were supra-tidal.

Drivers of surface elevation trends were assumed to be evident in linear trends in elevation. To aid identification of the drivers of variability in elevation the linear trend was removed from the data set, or 'detrended'. We applied the prediction equation from linear regression analysis of surface elevation change for each SET within the mangrove and salt marsh to identify the predicted surface elevation for each SET over time; the difference between the observed and predicted surface elevation for each SET was regarded as the variable component of relative surface elevation. Stepwise linear regression analyses were applied to the detrended data, the compiled rainfall and water level data and site specific information to identify the drivers of surface elevation variability within mangrove and salt marsh at Ukerebagh Island.

3. Results

3.1. Vegetation distribution dynamics

Fig. 2 illustrates the trend of mangrove expansion into salt marsh between (a) May 2000 and (b) April 2012. The seaward mangrove boundary remained relatively stable over this period; however the northwestern salt marsh area diminished in extent due to both mangrove expansion and conversion to mudflat by the loss of salt marsh vegetation. Salt marsh area decreased by approximately 2 ha by displacement with mangrove (1 ha) and mudflats (1 ha) over the study period (Fig. 3). The total intertidal area (mangrove, salt marsh and mudflat) remained relatively stable over the study period, fluctuating between 58.8 ha and 59.1 ha.

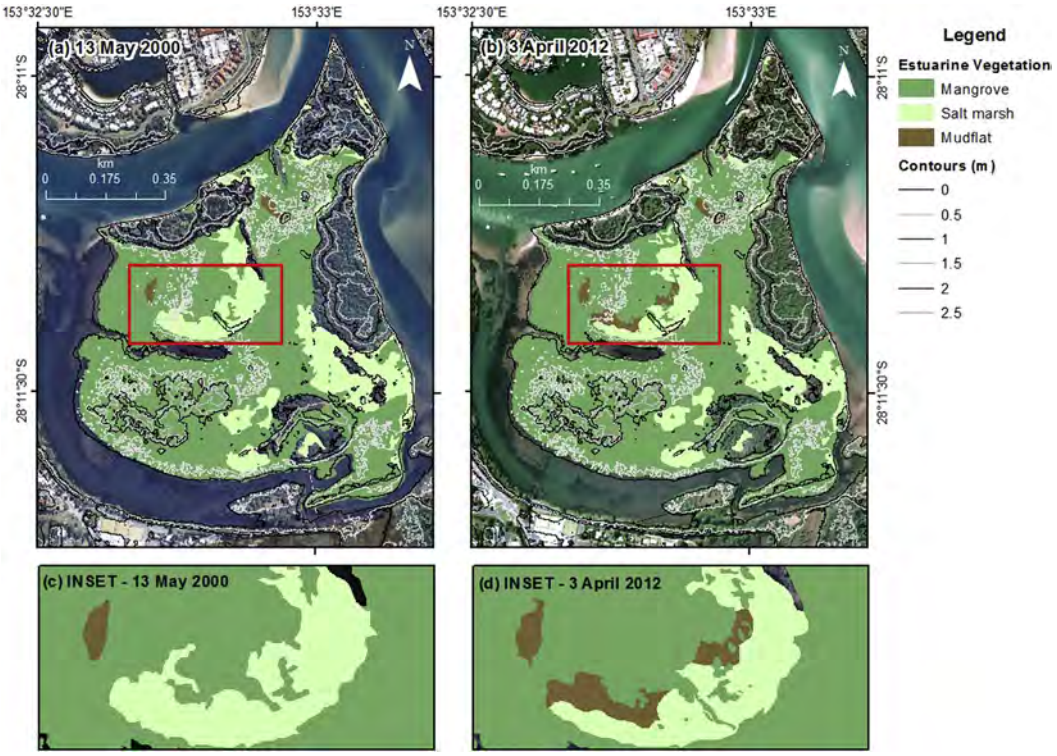


Fig. 2. Estuarine vegetation mapping from aerial photographs captured on (a) 13 May 2000, and (b) 3 April 2012. Vegetation mapping undertaken from aerial photography captured on 19 April 2002, 8 June 2003, 5 March 2005, 12 June 2007 and 5 April 2010 is not presented in Fig. 2; however the area of estuarine vegetation for these mapping periods are provided in Fig. 3. Insets of mudflat extent in (c) 13 May 2000, and (d) 3 April 2012.

3.2. Drivers of surface elevation trends

The rate of surface elevation increase was significantly greater in the mangrove than the salt marsh ($p = 0.0033$) and regression analyses indicated that mangrove surface elevation increased at a rate of 1.40 ± 0.03 mm y^{-1}, while the salt marsh increased at 0.17 ± 0.09 mm y^{-1} (Fig. 4, Table 1). Rates of surface elevation increase also varied over time ($p = 0.0040$) and a significant interaction effect was evident between vegetation type (mangrove or salt marsh) and time ($p = 0.0006$) indicating a complex relationship between processes influencing mangrove and salt marsh surface elevation over time.

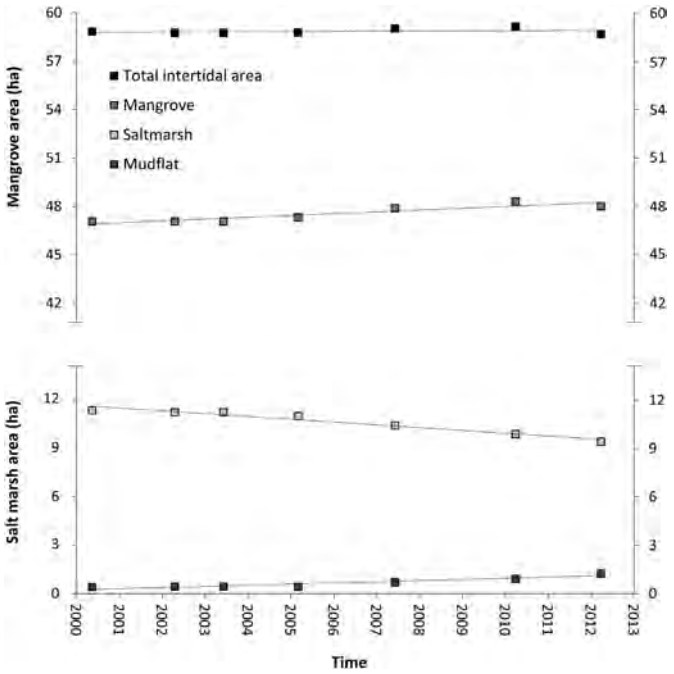


Fig. 3. Mangrove, salt marsh and mudflat extent on Ukerebagh Island between May 2000 and April 2012. Area defined by aerial photography captured on 13 May 2000, 19 April 2002, 8 June 2003, 5 March 2005, 12 June 2007, 5 April 2010, and 3 April 2012.

Stepwise linear regression analyses were undertaken to identify the drivers of surface elevation trends within mangrove and salt marsh. Factors that were incorporated in the mangrove model in descending t-ratio order were: time; inundation depth; antecedent water level; hydrological distance; antecedent rainfall; and SOI, with the first five factors being highly significant (Table 2: Model A). The resulting linear regression model was significant ($r^2 = 0.8041$, $p < 0.0001$).

Factors that were incorporated in the salt marsh model in descending t-ratio order were: antecedent rainfall; time; antecedent SOI; water level (6 month mean); hydrological distance; and inundation depth (Table 2: Model B). The model was significant ($p = 0.0242$), though the coefficient of determination was not high ($r^2 = 0.4428$).

When considering elevation trends throughout Ukerebagh Island by combining the empirical results for mangrove and salt marsh and incorporating stationary elevations within the terrestrial vegetation community, a strong and significant relationship ($r^2 = 0.6713$, $p < 0.0001$) was identified with time, hydrological distance and inundation depth (Table 2: Model C).

3.3. Drivers of surface elevation variability

Stepwise linear regression analyses of detrended rates of surface elevation change showed strong correlations between surface elevation variability and environmental variables. In particular,

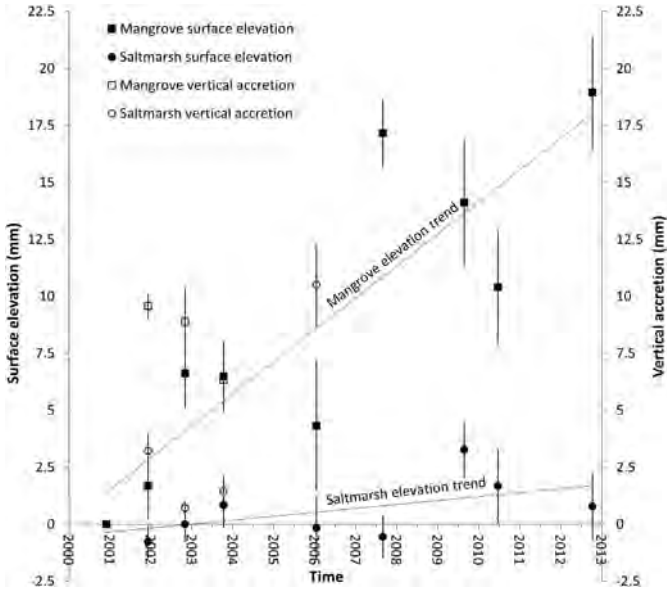


Fig. 4. Mangrove and salt marsh surface elevation between November 2000 and October 2012. Changes were detected using SETs and MHs established within mangrove and salt marsh at Ukerebagh Island and surface elevation is relative to the initial measurements in November 2000. MHs were not readily detected after January 2006 and were excluded from statistical analyses.

detrended mangrove surface elevation was partly explained by antecedent water levels and antecedent rainfall (Table 2: Model D, Fig. 5); while detrended salt marsh surface elevation was partly explained by antecedent rainfall (Table 2: Model E, Fig. 5). Both the mangrove and salt marsh models of elevation variability were significant and exhibited strong coefficients of determination (Table 3: Model D and E), though there was significant correlation of estimates for both models between variables of rainfall and water levels.

4. Discussion

4.1. Drivers of surface elevation trends and variability

A strong upward trend in elevation was evident within the mangrove at Ukerebagh Island (1.40 ± 0.03 mm y^{-1}; Fig. 4); multiple factors contributed to this trend, the most significant being time; the depth of the surface below water level; and antecedent water level (Table 2: Model A). With the exception of SOI and antecedent rainfall these drivers attest to a relationship between inundation and surface elevation that is compatible with concepts of feedback between elevation adjustment and inundation (Allen, 2000; Fagherazzi et al., 2012). Notwithstanding the positive trend, elevation gain in the mangrove lagged behind long-term water level trends from the nearest water level gauge (Letitia 2A gauge; Station number: 201429) between December 1987 and June 2013 (estimated to be increasing at 4.24 ± 0.16 mm y^{-1}), though we observed no signs of retreat or stress of the mangrove community during the study period. Elevation also increased in the salt marsh over the study period (0.17 ± 0.09 mm y^{-1}, Fig. 4), though lagged behind long-term water level trends. Multiple factors contributed to the model explaining salt marsh surface elevation change, though no single factor was significant (Table 2: Model B).

Detrended data highlighted the role of climatic and hydrological drivers on surface elevation variability in both the mangrove and salt marsh with significant relationships evident between detrended elevation data, antecedent rainfall and antecedent water level (Table 2: Model D and E). However we also demonstrated strong cross correlation between rainfall and water levels (Table 3), two factors noted to have strong connections with interannual climatic perturbations in SE Australia (Allan et al., 1990; Nerem et al., 1999; Zhang and Church, 2012). The cross correlation of these factors subsequently limits the identification of a single driver of surface elevation variability at interannual temporal scales. Fig. 6 illustrates the relationship between water level variability, in this case

Table 2
Stepwise linear regression results for analyses of the relationship between environmental variables, denoted in models as factors, and a) mangrove surface elevation; b) salt marsh surface elevation; c) mangrove and salt marsh surface elevation; d) detrended mangrove elevation; and e) detrended salt marsh elevation.

Model	Effect	Factor	t ratio (F ratio)	*p* value (r^2)
A	Mangrove surface elevation	Time	5.93	**<0.0001**
		Inundation depth	4.68	**0.0001**
		Antecedent water level	2.66	**0.0140**
		Hydrological distance	−2.35	**0.0275**
		Antecedent rainfall	−2.13	**0.0445**
		SOI	−1.77	**0.0908**
		Whole model	(15.7334)	**<0.0001 (0.8041)**
B	Salt marsh surface elevation	Antecedent rainfall	1.68	0.1059
		Time	1.23	0.2322
		Antecedent SOI	−1.23	0.2323
		Water level (6mo mean)	−0.35	0.7309
		Hydrological distance	0.24	0.8135
		Inundation depth	−0.02	0.9817
		Whole model	(3.0462)	**0.0242 (0.4428)**
C	Mangrove and salt marsh surface elevation	Time	4.65	**<0.0001**
		Hydrological distance	−4.57	**<0.0001**
		Inundation depth	4.02	**0.0002**
		Antecedent water level	1.44	0.1551
		SOI (3mo mean)	−0.99	0.3276
		Antecedent rainfall	−0.71	0.4834
		Whole model	(17.0214)	**<0.0001 (0.6713)**
D	Detrended mangrove elevation	Antecedent water level	2.33	**0.0674**
		Antecedent rainfall	−2.15	**0.0843**
		SOI	−1.40	0.2218
		Whole model	(2.6684)	0.1588 (0.6155)
E	Detrended salt marsh elevation	Antecedent rainfall	3.17	**0.0284**
		Antecedent water level	−1.78	0.1356
		SOI	0.53	0.6180
		Whole model	(4.8129)	**0.0617 (0.7428)**

Statistically significant *p* values at a significance level of 0.10 are denoted in bold.

Table 1
Repeated measures multivariate analysis of variance statistics comparing differences in surface elevation between zones (mangrove and salt marsh), over time and the interactions of time and zones.

Treatment effects	Treatments	Value	*F* ratio	Numerator degrees of freedom	Denominator degrees of freedom	*p* value
Between Subjects	Zone	0.4932	10.8498	1	22	0.0033
	Intercept	0.8868	19.5095	1	22	0.0002
Within subjects	Time	2.1515	2.1515	7	16	0.0040
	Time × Zone	3.0647	7.0050	7	16	0.0006

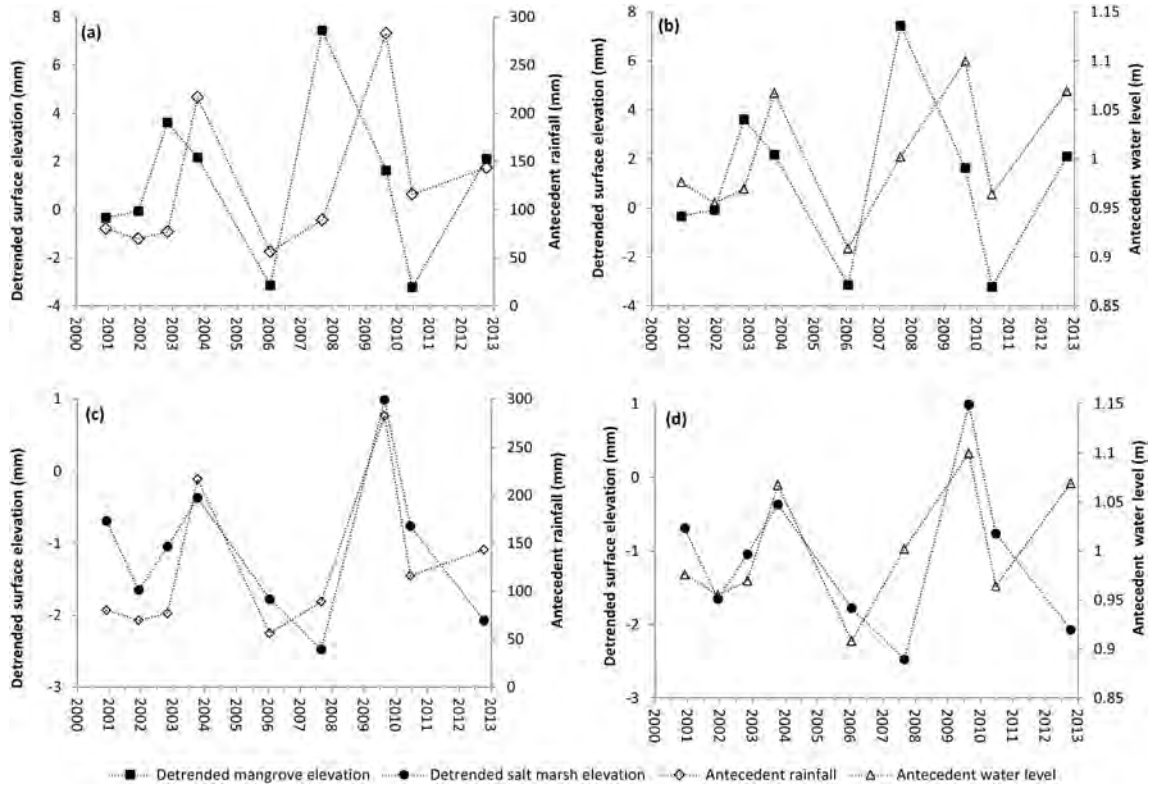


Fig. 5. Relationship between (a) detrended mangrove surface elevation and antecedent rainfall; (b) detrended mangrove surface elevation and antecedent water level; (c) detrended salt marsh surface elevation and antecedent rainfall; and (d) detrended salt marsh surface elevation and antecedent water level at Ukerebagh Island.

demonstrated by removing the linear upward trend in water level at the Letitia 2A tide gauge over the study period, and rainfall.

4.2. Role of surface elevation change in vegetation distribution dynamics

A consistent trend of mangrove expansion and salt marsh decline has been documented throughout SE Australia (Saintilan and Williams, 1999, 2000) and detailed analysis of vegetation distribution dynamics by Saintilan (1998) indicates that this trend has been occurring on Ukerebagh Island. Urbanisation in the catchment has influenced nutrient inputs into the Tweed River (Costanzo et al., 2003); however, Saintilan (2003) demonstrated that nutrient addition did not improve mangrove seedling survival for up to 16 months, and beyond this period nutrient addition only improved juvenile primary productivity; hence nutrient addition was not considered to influence the vegetation distribution dynamics observed on Ukerebagh Island. In this study, mangrove expansion was detected at a higher temporal resolution over a period exceeding a decade and expansion was observed to be preceded by the loss of salt marsh vegetation and the development of unvegetated mudflats between mangrove and salt marsh (Fig. 2). The factors causing the transition from salt marsh to mudflat to mangrove warrant further investigation of the salinity and waterlogging tolerance of *Sporobolus virginicus* and *Avicennia marina*; the dominant species involved in this transition. Mangrove expansion into salt marsh is a trend that is receiving wider global recognition with expansion of mangrove into salt marsh and poleward range extension of mangrove increasingly observed (Saintilan et al., 2014; Cavanaugh et al., 2014). Relative sea-level rise, resulting from eustatic and isostatic processes, and localised factors influencing land and water elevations, have been associated with landward mangrove expansion during the Holocene (Woodroffe, 1990; Wolanski and Chappell, 1996) and the 20th century (Rogers et al., 2006; Gilman et al., 2007; Williamson et al., 2011); however other factors such as changing rainfall patterns (Eslami-Andargoli et al., 2009, 2010), elevated atmospheric carbon dioxide (Williamson et al., 2011), changing frequency of extreme events such as freezes (Stevens et al., 2006) and nutrient availability (McLoughlin, 1988; Simpson et al., 2013) have also been proposed as drivers. In SE Australia, Rogers et al. (2006) correlate these changes with surface elevation trends and water level changes. Eslami-Andargoli et al. (2009) propose that mangrove and salt marsh dynamics in nearby Moreton Bay, Queensland, are largely driven by the prevailing rainfall patterns, which control soil water salinity, reduce exposure to sulphates and potentially increase nutrient and sediment loads via runoff.

In this study we demonstrate the cross-correlation of rainfall and water-level trends in an estuary immediately south of that studied by Eslami-Andargoli et al. (2009), suggesting that the influence of rainfall on mangrove expansion into salt marsh might equally be mediated through water level increases or variability. Our observations, which covered both positive and negative ENSO phases, demonstrate a strong relationship between position within the tidal prism, a factor represented in our analyses by inundation depth, distance from open water and surface elevation increase. Longer-term water levels in the estuary have been rising at 4.24 mm y^{-1} over the past 25 years (Letitia 2A gauge, located approximately 200 m from Ukerebagh Island). While this exceeds observed global mean sea-level rise of 3.2 mm y^{-1} for the period 1993–2010 (Church et al., 2013), the trajectories are similar and differences are associated with factors influencing hydrology at a local scale. Thus the observed relationship between elevation, water levels and inundation provides insight into the elevation

Table 3
Correlation of estimates for each factor included in stepwise linear regression models detailed in Table 2.

Factors	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Model A	Hydrological distance	Time	Inundation depth	SOI (3mo mean)	Antecedent rainfall	Antecedent water level
Hydrological distance	1.00	−0.05	−0.03	0.04	0.14	−0.10
Time	−0.05	1.00	0.02	0.21	0.00	−0.15
Inundation depth	−0.03	0.02	1.00	−0.09	−0.32	0.27
SOI (3mo mean)	0.04	0.21	−0.09	1.00	0.23	0.02
Antecedent rainfall	0.14	0.00	−0.32	0.23	1.00	**−0.84**
Antecedent water level	−0.10	−0.15	0.27	0.02	**−0.84**	1.00

Factors	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Model B	Hydrological distance	Time	Inundation depth	Water level (6 mo mean)	Antecedent SOI	Antecedent rainfall
Hydrological distance	1.00	0.16	−0.84	−0.13	−0.17	0.13
Time	0.16	1.00	−0.28	−0.88	−0.17	0.64
Inundation depth	−0.84	−0.28	1.00	0.28	0.26	−0.30
Water level (6 mo mean)	−0.13	−0.88	0.28	1.00	0.21	**−0.83**
Antecedent SOI	−0.17	−0.17	0.26	0.21	1.00	−0.20
Antecedent rainfall	0.13	0.64	−0.30	**−0.83**	−0.20	1.00

Factors	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Model C	Hydrological distance	Time	Inundation depth	SOI (3mo mean)	Antecedent rainfall	Antecedent water level
Hydrological distance	1.00	−0.02	0.39	−0.02	−0.08	0.07
Time	−0.02	1.00	−0.05	−0.04	−0.04	−0.17
Inundation depth	0.39	−0.05	1.00	−0.06	−0.21	0.19
SOI (3mo mean)	−0.02	−0.04	−0.06	1.00	−0.04	0.18
Antecedent rainfall	−0.08	−0.04	−0.21	−0.04	1.00	**−0.86**
Antecedent water level	0.07	−0.17	0.19	0.18	**−0.86**	1.00

Model D	Antecedent rainfall	Antecedent water level	SOI
Antecedent rainfall	1.00	**−0.85**	0.24
Antecedent water level	**−0.85**	1.00	0.05
SOI	0.24	0.05	1.00

Model E	Antecedent rainfall	Antecedent water level	SOI
Antecedent rainfall	1.00	**−0.85**	0.24
Antecedent water level	**−0.85**	1.00	0.05
SOI	0.24	0.05	1.00

Highly correlated values are denoted in bold.

response of coastal wetlands to past and projected sea-level rise. Rates of elevation gain in the mangrove and salt marsh over the 12 year study period lagged behind water level trends within the estuary, and the combined influence of long-term water-level trends and short-term phases of water level increase would provide opportunities for mangrove expansion into salt marsh co-incident with rainfall patterns.

Past coastal changes provide valuable information that can be applied to research related to current and future change; an approach advocated by Woodroffe and Murray-Wallace (2012) who emphasise the importance of spatial and temporal scale for coastal ecosystem adaptation research. We propose that vegetation distribution dynamics is an ecological indicator of the alteration of processes that may be operating at a range of spatial and temporal scales. Large-scale geomorphic change in coastal wetlands typically operate over longer timescales; for example, coastal wetland evolution globally commenced or resumed when eustatic sea level decelerated and began to stabilise approximately 7000 years ago (Allen, 2000). At intermediate scales geomorphic change operating over decades to centuries may have regionally significant implications for coastal wetland vegetation; for example human activities in the 20th century that altered channel morphology and hydrology of the Mississippi River have limited the supply of sediment to the Mississippi Delta Plain, and in conjunction with sea-level rise and

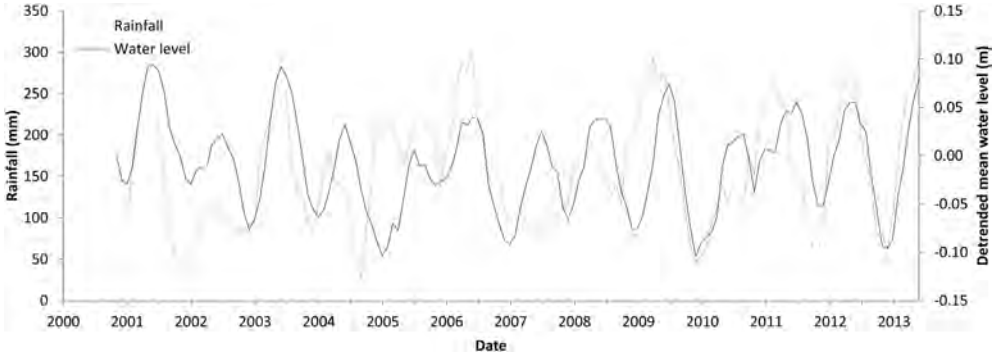


Fig. 6. Correlation between water level variability at the Letitia 2A gauge (Station number: 201429), illustrated here by removing the upward linear trend in water level, and rainfall from the Tweed Heads gauge (Station number: 58056) over the study period.

storm effects has caused significant interior wetland loss associated with subsidence, and seaward edge wetland loss due to erosion (Day et al., 2007).

At smaller spatial scales, such as Ukerebagh Island, recent vegetation distribution dynamics may be an indicator of changes operating at larger spatial and temporal scales, or may be associated with smaller perturbations, such as local rainfall and water level variability. Kim et al. (2010) in their study of salt marsh distribution in Skallingen, verified this premise by observing vegetation loss due to headward erosion and expansion of tidal creeks associated with eustatic sea-level rise effects on hydrology, and spatially different vegetation composition associated with short-term fluvial processes. Consequently, we do not dismiss the role of rainfall in mangrove expansion into salt marsh, particularly over inter-annual and inter-decadal timescales at which climatic perturbations operate; rather we found rainfall to be a driver of surface elevation variability at Ukerebagh Island. The influence of rainfall may be mediated through groundwater availability and elevated water levels in the estuary. Rogers and Saintilan (2009) demonstrated expansion of the soil volume in coastal wetlands at Homebush Bay, Australia when groundwater was elevated and conversely shrinkage of the soil volume when groundwater was depleted. Similarly, Whelan et al. (2005) demonstrated a correlation between surface elevation change and groundwater pressure at a mangrove forest along Shark River, Florida. In this case, the majority of the expansion and contraction was attributed to changes in soil volume at depths of 4–6 m. Elevated water levels in the estuary during wetter periods, as illustrated in Fig. 6, may be explained by enhanced groundwater contributions and overland flows to the estuary during periods of higher rainfall. Rainfall may also act to reduce salt marsh soil salinities, thereby limiting desiccation of propagules as they establish. Desiccation of propagules is postulated as a mechanism limiting expansion of *Avicennia marina* into salt marsh (Clarke and Allaway, 1993; Saintilan, 2003).

We reiterate the caution provided by Kim et al. (2010) regarding extrapolation of observed vegetation distribution dynamics to other spatial or temporal scales. Capturing the cause of observed vegetation distribution dynamics requires an integrated approach that accounts for coastal processes operating at a range of spatial and temporal scales. Here we have integrated geomorphic changes occurring over the past decade with remotely sensed ecological changes occurring over the past eight decades. Detection of processes driving the observed vegetation distribution dynamics may be improved by increasing the temporal scale of geomorphic analysis at Ukerebagh Island using radiometric techniques that capture sediment accumulation over longer time periods, such as ^{210}Pb dating techniques.

4.3. Implications for the response of coastal wetlands to climate change

While the rate of elevation increase lags rates of water-level rise in the estuary, this may not translate to systemic wetland collapse in the future, but may relate to a temporal lag between rising but fluctuating sea level and the mangrove elevation response (French, 1993; Allen, 2000; Fagherazzi et al., 2012). In the context of fluctuating rising sea levels, the wetland surface may continue to build elevation through accretion and below-ground processes; though a balance between elevation increase and water level increase may not be achieved until after relatively stable sea levels or steadily rising sea levels return (Allen, 2000). Adjustment is highly dependent upon the supply of autochthonous or allochthonous sediment that meets volume requirements for adjustment. Greater sediment supply, accretion and associated increases in elevation gain may accelerate adjustment to rising sea levels. The absence of wetland submergence at Ukerebagh Island, demonstrated for the past 12 years using SETs, and a relatively stable lower wetland boundary since 1985 (Saintilan, 1998) supports the claim that the system is not succumbing to systemic collapse; rather, at current rates of sea-level rise we have observed a geomorphic response which is accompanied by a more sensitive ecological response of the vegetation.

However, observations of wetland collapse elsewhere imply that under some conditions (Cahoon et al., 2003; Day et al., 2011) wetland resilience is diminished. Attention is being directed towards identifying these thresholds of resilience. Low tidal ranges and limited mineral sediment input may constrain the resilience of wetlands (Reed, 1995; Kirwan and Guntenspergen, 2010; Kirwan et al., 2010). These effects may be offset by vegetation growth, which can build elevation and limit submergence (Cahoon et al., 2006; McKee et al., 2007; McKee, 2011). Fagherazzi et al. (2012) propose that maintenance of wetland elevations suitable for vegetation survival is essential, rapid loss of elevation occurs following vegetation loss which subsequently precludes vegetation establishment. As vegetation is particularly sensitive to smaller perturbations, these events may contribute to the crossing of resilience thresholds in an ecosystem approaching collapse or where the lag between wetland elevation responses to sea-level rise is large.

Perhaps wetland shorelines in SE Australia with adjacent mangrove and salt marsh are more resilient to loss than salt marsh dominated wetland shorelines by virtue of the presence of mangroves at lower elevations. The resilience of mangrove to perturbations and their capacity to adapt to fluctuating water levels is receiving increasing research attention (Alongi, 2008; Duarte et al., 2013). Mangroves, and to a lesser extent salt marsh, attenuate wave action, surface complexity baffles flows and promotes sediment accumulation, and complex root structures bind soils and minimise erosion (Alongi, 2008; Gedan et al., 2011). In addition, the height and density of *Avicennia marina* pneumatophores reportedly varies proportionally in response to microtopography (Dahdouh-Guebas et al., 2007) and we have observed mangrove pneumatophores with lengths exceeding 0.7 m where inundation frequency and duration has promoted pneumatophore extension. In combination, mangrove root morphology builds resilience to erosion and inundation associated with water level increases. Here we demonstrate that mangroves have been increasing, and while more precise representations of mangrove and salt marsh dynamics can be achieved using high resolution digital elevation models (see for example Oliver et al., 2012; Rogers et al., 2013), extrapolation of the observed trend of mangrove incursion into salt marsh under moderate increases in water level highlights the fate of salt marsh under future sea-level rise. Salt marshes that are confined at their upper boundaries by topographic, built or tidal obstructions (e.g. steep catchments, infrastructure, levees and floodgates), or by shrinking accommodation space, as is the case at Ukerebagh Island, will continue to diminish in extent as seas rise this century; attention should be directed towards enhancing salt marsh resilience.

5. Conclusions

To maintain coastal wetland extent under conditions of increasing inundation depths, coastal wetlands must increase elevation at rates that maintain their elevation range within the tidal prism. This can be achieved by building soil elevation through autochthonous or allochthonous sediment inputs; by belowground-processes that increase the soil volume, such as below-ground primary production; or by migrating to elevations where their position within the tidal prism is realised. Observed

rates of elevation increase within mangrove and salt marsh at Ukerebagh Island lagged behind rates of water level increase within the estuary, and provides strong evidence for the expansion of mangrove into salt marsh since the 1940's. In this study we demonstrate that mangrove elevation trends at Ukerebagh Island are largely controlled by position within the tidal prism, which was defined by inundation depth, time and distance from the primary channel delivering tidal flows. Other external climatic variables, such as rainfall, acted as drivers of mangrove elevation variability. Sea-level rise may explain longer-term trends in wetland geomorphic change, particularly at multi-decadal and century timescales; however, the influence of climatic variables on wetland elevation variability will confound analyses of the elevation response of wetlands over shorter periods that do not adequately capture climatic perturbations. Due to the influence of climatic perturbations on elevation change, we propose that drivers of elevation trends and variability may vary between climatic settings and require further consideration at a global scale. This will aid the development of models for projecting the impact of climate change on coastal wetland distribution.

Acknowledgements

Air photograph interpretation and SET measurements reported in this paper were supported by the Tweed River Entrance Sand Bypassing Project, an initiative of the NSW Land and Property Information Service. The authors also thank the editor and two anonymous reviewers for their comments.

References

Akumu, C., Pathirana, S., Baban, S., Bucher, D., 2011. Examining the potential impacts of sea level rise on coastal wetlands in north-eastern NSW, Australia. J. Coast. Conserv. 15, 15–22.
Allan, R.J., Beck, K., Mitchell, W.M., 1990. Sea level and rainfall correlations in Australia: tropical links. J. Clim. 3, 838–846.
Allen, J.R.L., 2000. Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. Quat. Sci. Rev. 19, 1155–1231.
Alongi, D.M., 2008. Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. Estuar. Coast. Shelf Sci. 76, 1–13.
BOM, 2013. SOI (Southern Oscillation Index) Archives: 1876 to Present. Australian Government; Bureau of Meteorology.
Cahoon, D.R., Hensel, P., Rybczyk, J., McKee, K.L., Proffitt, C.E., Perez, B.C., 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. J. Ecol. 91, 1093–1105.
Cahoon, D.R., Hensel, P.F., Spencer, T., Reed, D.J., McKee, K.L., Saintilan, N., 2006. Coastal wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In: Verhoeven, J.T.A., Beltman, B., Bobbink, R., Whigham, D.F. (Eds.), Wetlands and Natural Resource Management. Springer, Berlin Heidelberg, pp. 271–292.
Cahoon, D.R., Lynch, J.C., Hensel, P., Boumans, R., Perez, B.C., Segura, B., Day Jr., J.W., 2002a. High-precision measurements of wetland sediment elevation: I. Recent improvements to the Sedimentation-Erosion Table. J. Sediment. Res. 72, 730–733.
Cahoon, D.R., Lynch, J.C., Perez, B.C., Segura, B., Holland, R.D., Stelly, C., Stephenson, G., Hensel, P., 2002b. High-precision measurements of wetland sediment elevation: II. The rod surface elevation table. J. Sediment. Res. 72, 734–739.
Cahoon, D.R., Reed, D.J., Day, J.W., 1995. Estimating shallow subsidence in microtidal salt marshes of the southeastern United States: Kaye and Barghoorn revisited. Mar. Geol. 128, 1–9.
Cahoon, D.R., Turner, R.E., 1989. Accretion and canal impacts in a rapidly subsiding wetland II. Feldspar marker horizon technique. Estuaries 12, 260–268.
Cavanaugh, K.C., Kellner, J.R., Forde, A.J., Gruner, D.S., Parker, J.D., Rodriguez, W., Feller, I.C., 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proc. Nat. Acad. Sci. 111 (2), 723–727.
Church, J.A., Clark, P.U., Cazenave, A., Gregory, J.M., Jevrejeva, S., Levermann, A., Merrifield, M.A., Milne, G.A., Nerem, R.S., Nunn, P.D., Payne, A.J., Pfeffer, W.T., Stammer, D., Unnikrishnan, A.S., 2013. Sea level change. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
Clarke, P.J., Allaway, W.G., 1993. The regeneration niche of the grey mangrove (*Avicennia marina*): effects of salinity, light and sediment factors on establishment, growth and survival in the field. Oecologia 93, 548–556.
Costanzo, S., O'Donohue, M., Dennison, W., 2003. Assessing the seasonal influence of sewage and agricultural nutrient inputs in a subtropical river estuary. Estuaries 26, 857–865.
Dahdouh-Guebas, F., Kairo, J.G., De Bondy, R., Koedam, N., 2007. Pneumatophore height and density in relation to micro-topography in the grey mangrove *Avicennia marina*. Belg. J. Bot. 2, 213–221.
Day, J., Britsch, L., Hawes, S., Shaffer, G., Reed, D., Cahoon, D., 2000. Pattern and process of land loss in the Mississippi Delta: a spatial and temporal analysis of wetland habitat change. Estuaries Coasts 23, 425–438.
Day, J., Christian, R., Boesch, D., Yáñez-Arancibia, A., Morris, J., Twilley, R., Naylor, L., Schaffner, L., Stevenson, C., 2008. Consequences of climate change on the eco-geomorphology of coastal wetlands. Estuaries Coasts 31, 477–491.
Day, J.W., Boesch, D.F., Clairain, E.J., Kemp, G.P., Laska, S.B., Mitsch, W.J., Orth, K., Mashriqui, H., Reed, D.J., Shabman, L., Simenstad, C.A., Streever, B.J., Twilley, R.R., Watson, C.C., Wells, J.T., Whigham, D.F., 2007. Restoration of the Mississippi Delta: lessons from hurricanes Katrina and Rita. Science 315, 1679–1684.
Day, J.W., Kemp, G.P., Reed, D.J., Cahoon, D.R., Boumans, R.M., Suhayda, J.M., Gambrell, R., 2011. Vegetation death and rapid loss of surface elevation in two contrasting Mississippi delta salt marshes: the role of sedimentation, autocompaction and sea-level rise. Ecol. Eng. 37, 229–240.
Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., Marba, N., 2013. The role of coastal plant communities for climate change mitigation and adaptation. Nat. Clim. Change 3, 961–968.
Eslami-Andargoli, L., Dale, P., Sipe, N., Chaseling, J., 2009. Mangrove expansion and rainfall patterns in Moreton Bay, southeast queensland, Australia. Estuar. Coast. Shelf Sci. 85, 292–298.
Eslami-Andargoli, L., Dale, P.E.R., Sipe, N., Chaseling, J., 2010. Local and landscape effects on spatial patterns of mangrove forest during wetter and drier periods: Moreton Bay, Southeast Queensland, Australia. Estuar. Coast. Shelf Sci. 89, 53–61.
Fagherazzi, S., Kirwan, M.L., Mudd, S.M., Guntenspergen, G.R., Temmerman, S., D'Alpaos, A., van de Koppel, J., Rybczyk, J.M., Reyes, E., Craft, C., Clough, J., 2012. Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. Rev. Geophys. 50. RG1002.
French, J.R., 1993. Numerical simulation of vertical marsh growth and adjustment to accelerated sea-level rise, North Norfolk, U.K. Earth Surf. Process. Landf. 18, 63–81.
Gedan, K., Kirwan, M., Wolanski, E., Barbier, E., Silliman, B., 2011. The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. Clim. Change 106, 7–29.
Gilman, E., Ellison, J., Coleman, R., 2007. Assessment of mangrove response to projected relative sea-level rise and recent historical reconstruction of shoreline position. Environ. Monit. Assess. 124, 105–130.
Hashimoto, T.R., Saintilan, N., Haberle, S.G., 2006. Mid-Holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond River estuary, New South Wales, Australia. Geogr. Res. 44, 63–76.
Kearney, M.S., Stevenson, J.C., 1991. Island land loss and marsh vertical accretion rate: evidence for historical sea-level changes in Chesapeake Bay. J. Coast. Res. 7, 403–415.
Kim, D., Bartholdy, J., Jung, S., Cairns, D.M., 2011. Salt marshes as potential indicators of global climate change. Geogr. Compass 5, 219–236.
Kim, D., Cairns, D., Bartholdy, J., 2010. Environmental controls on multiscale spatial patterns of salt marsh vegetation. Phys. Geogr. 31, 58–78.
Kirwan, M.L., Guntenspergen, G.R., 2010. Influence of tidal range on the stability of coastal marshland. J. Geophys. Res. 115. F02009.
Kirwan, M.L., Guntenspergen, G.R., D'Alpaos, A., Morris, J.T., Mudd, S.M., Temmerman, S., 2010. Limits on the adaptability of coastal marshes to rising sea level. Geophys. Res. Lett. 37. L23401.
Kirwan, M.L., Murray, A.B., 2007. A coupled geomorphic and ecological model of tidal marsh evolution. Proc. Natl. Acad. Sci. 104, 6118–6122.
Kirwan, M.L., Murray, A.B., Boyd, W.S., 2008. Temporary vegetation disturbance as an explanation for permanent loss of tidal wetlands. Geophys. Res. Lett. 35. L05403.
Krauss, K.W., McKee, K.L., Lovelock, C.E., Cahoon, D.R., Saintilan, N., Reef, R., Chen, L., 2014. How mangrove forests adjust to rising sea level. New. Phytol. 202, 19–34.
McKee, K., Rogers, K., Saintilan, N., 2012. Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In: Middleton, B.A. (Ed.), Global Change and the Function and Distribution of Wetlands. Springer, Netherlands, pp. 63–96.
McKee, K.L., 2011. Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. Estuar. Coast. Shelf Sci. 91, 475–483.
McKee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Glob. Ecol. Biogeogr. 16, 545–556.
McLoughlin, L., 1988. Mangroves and grass swamps: changes in the shoreline vegetation of the Middle Lane Cove River, Sydney, 1780's–1880's. Wetl. Aust. 7, 13–24.

Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea-levels. Ecology 83, 2869–2877.
Nerem, R.S., Chambers, D.P., Leuliette, E.W., Mitchum, G.T., Giese, B.S., 1999. Variations in global mean sea level associated with the 1997–1998 ENSO event: implications for measuring long term sea level change. Geophys. Res. Lett. 26, 3005–3008.
Oliver, T., Rogers, K., Chafer, C., Woodroffe, C., 2012. Measuring, mapping and modelling: an integrated approach to the management of mangrove and salt marsh in the Minnamurra River estuary, southeast Australia. Wetl. Ecol. Manag. 20, 353–371.
Pethick, J.S., 1981. Long-term accretion rates on tidal salt marshes. J. Sediment. Res. 51, 571–577.
Reed, D.J., 1995. The response of coastal marshes to sea-level rise: survival or submergence? Earth Surf. Process. Landf. 20, 39–48.
Reed, D.J., 2002. Sea-level rise and coastal marsh sustainability: geological and ecological factors in the Mississippi delta plain. Geomorphology 48, 233–243.
Rogers, K., Saintilan, N., 2009. Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. J. Coast. Res. 24, 63–69.
Rogers, K., Saintilan, N., Copeland, C., 2012. Modelling wetland surface elevation and its application to forecasting the effects of sea-level rise on estuarine wetlands. Ecol. Model. 244, 148–157.
Rogers, K., Saintilan, N., Copeland, C., 2013. Managed retreat of Saline coastal wetlands: challenges and opportunities identified from the Hunter river estuary, Australia. Estuaries Coasts, 1–12.
Rogers, K., Saintilan, N., Heijnis, H., 2005. Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence and sea level rise. Estuaries 28, 551–559.
Rogers, K., Wilton, K.M., Saintilan, N., 2006. Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. Estuar. Coast. Shelf Sci. 66, 559–569.
Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of south-east Australian estuaries. Estuar. Coast. Shelf Sci. 53, 351–384.
Saintilan, N., 1998. Photogrammetric survey of the Tweed River wetlands. Wetl. Aust. 17, 74–82.
Saintilan, N., 2003. The influence of nutrient enrichment upon mangrove seedling establishment and growth int he Hawkesbury River estuary, New South Wales, Australia. Wetl. Aust. 21, 29–35.
Saintilan, N., Hashimoto, T.R., 1999. Mangrove-salt marsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia. Hydrobiologia 413, 95–102.
Saintilan, N., Rogers, K., Mazumder, D., Woodroffe, C., 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuar. Coast. Shelf Sci. 128, 84–92.
Saintilan, N., Williams, R.J., 1999. Mangrove Transgression into salt marsh environments in south-east Australia. Glob. Ecol. Biogeogr. 8, 117–124.
Saintilan, N., Williams, R.J., 2000. The decline of saltmarshes in Southeast Australia: results of recent surveys. Wetl. Aust. 18, 49–54.
Saintilan, N., Wilson, N.C., Rogers, K., Rajkaran, A., Krauss, K.W., 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob. Change Biol. 20, 147–157.
Saintilan, N., Wilton, K., 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetl. Ecol. Manag. 9, 409–420.
Simpson, L.T., Feller, I.C., Chapman, S.K., 2013. Effects of competition and nutrient enrichment on *Avicennia germinans* in the salt marsh-mangrove ecotone. Aquat. Bot. 104, 55–59.
Stevens, P.W., Fox, S.L., Montague, C.L., 2006. The interplay between mangroves and salt marshes at the transition between temperate and subtropical climate in Florida. Wetl. Ecol. Manag. 14.
Traill, L.W., Perhans, K., Lovelock, C.E., Prohaska, A., McFallan, S., Rhodes, J.R., Wilson, K.A., 2011. Managing for change: wetland transitions under sea-level rise and outcomes for threatened species. Divers. Distrib. 17, 1225–1233.
Webb, E.L., Friess, D.A., Krauss, K.W., Cahoon, D.R., Guntenspergen, G.R., Phelps, J., 2013. A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. Nat. Clim. Change 3, 458–465.
Whelan, K., Smith, T., Cahoon, D., Lynch, J., Anderson, G., 2005. Groundwater control of mangrove surface elevation: shrink and swell varies with soil depth. Estuaries Coasts 28, 833–843.
Williamson, G., Boggs, G., Bowman, D., 2011. Late 20th century mangrove encroachment in the coastal Australian monsoon tropics parallels the regional increase in woody biomass. Reg. Environ. Change 11, 19–27.
Wolanski, E., Chappell, J., 1996. The response of tropical Australian estuaries to a sea level rise. J. Mar. Syst. 7, 267–279.
Woodroffe, C.D., 1990. The impact of sea-level rise on mangrove shorelines. Prog. Phys. Geogr. 14, 483–520.
Woodroffe, C.D., Murray-Wallace, C.V., 2012. Sea-level rise and coastal change: the past as a guide to the future. Quat. Sci. Rev. 54, 4–11.
Zhang, X., Church, J.A., 2012. Sea level trends, interannual and decadal variability in the Pacific Ocean. Geophys. Res. Lett. 39, L21701.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 15 March 2022
doi: 10.3389/fmars.2022.807588

Coastal Wetland Surface Elevation Change Is Dynamically Related to Accommodation Space and Influenced by Sedimentation and Sea-Level Rise Over Decadal Timescales

Kerrylee Rogers[1], Atun Zawadzki[2], Laura A. Mogensen[1] and Neil Saintilan[3]*

[1] School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW, Australia, [2] Australian Nuclear Science and Technology Organisation, Lucas Heights, NSW, Australia, [3] School of Natural Sciences, Macquarie University, North Ryde, NSW, Australia

The fate of mangroves and saltmarshes under conditions of accelerating sea-level rise is dependent upon sedimentation and surface elevation gain that is sufficient to maintain substrate positions within a shifting tidal frame. This study focuses on coastal wetlands fringing Westernport Bay, a large tidal embayment of southeastern Australia where mangroves occupy lower tidal positions than saltmarshes. Estimates of vertical accretion, surface elevation change, and autocompaction derived from a 20-year record of observations were integrated with estimates of sedimentation at the decadal to century time-scale derived from ^{210}Pb chronology to model the relationship between surface elevation gain and accommodation space at timescales relevant to management and decision-making. This model was validated against records of shoreline changes extracted from time-series aerial photography. Sedimentation and surface elevation gain vary spatially on the basis of available accommodation space and sediment supply, which are influenced by hydrodynamic conditions within the bay. Since sea-level rise increases available accommodation space, these relationships provided the means to project the outcome of accelerating sea-level rise on equilibrium accommodation space of mangroves and saltmarshes. Sea-level rise will generally deepen substrate positions within the tidal frame, creating conditions favorable for mangrove forests. Where sediment supply is high, maintenance (and some progradation) of mangrove shorelines may occur under projected low rates of sea-level rise; these conditions are limited to shorelines near sedimentary basins and where there is considerable lateral accommodation space. The same fate is not likely under a high sea-level rise scenario where shoreline retreat is projected in all settings. Given the limited accommodation space within saltmarshes at Westernport Bay, sedimentation will not be sufficient to maintain tidal positions and landward retreat will be critical for maintenance of saltmarsh biodiversity. This will require planning decisions to facilitate tidal incursions and conserve retreat pathways.

Keywords: mangrove, saltmarsh, ^{210}Pb geochronology, sediment supply, autocompaction, equilibrium elevation

OPEN ACCESS

Edited by:
Zhan Hu,
Sun Yat-sen University, China

Reviewed by:
Ya Ping Wang,
Nanjing University, China
Barend van Maanen,
University of Exeter, United Kingdom

****Correspondence:***
Kerrylee Rogers
kerrylee@uow.edu.au

Specialty section:
This article was submitted to Coastal Ocean Processes, a section of the journal Frontiers in Marine Science

Received: *02 November 2021*
Accepted: *11 February 2022*
Published: *15 March 2022*

Citation:
Rogers K, Zawadzki A, Mogensen LA and Saintilan N (2022) Coastal Wetland Surface Elevation Change Is Dynamically Related to Accommodation Space and Influenced by Sedimentation and Sea-Level Rise Over Decadal Timescales. Front. Mar. Sci. 9:807588. doi: 10.3389/fmars.2022.807588

INTRODUCTION

Saline coastal wetlands dominated by mangrove and saltmarsh occupy the intertidal zone and their lateral distribution is generally delimited by the landward extent of tidal inundation. Accumulation of mineral and organic material within substrates is facilitated by the low energy conditions that promote sediment deposition and the growth of halophytic vegetation; this material provides an important vertical subsidy when coastlines are exposed to relative sea-level rise (RSLR) (Woodroffe et al., 2016). Observational data indicates that coastal wetlands may be able to increase surface elevations under low to moderate rates of RSLR (Kirwan et al., 2016). However, there remains ongoing debate about the ability of coastal wetlands to adjust to the high rates of RSLR that are anticipated as eustatic SLR accelerates toward the end of the 21st century (Oppenheimer et al., 2019). Large spatial-scale analyses of paleoecological data indicate that mangroves can adapt to rates of RSLR of less than 7 mm year^{-1} (Saintilan et al., 2020). Similarly, saltmarshes in the United Kingdom have been found to adapt when rates of RSLR does not exceed 7 mm year^{-1} (Horton et al., 2018). Process based modeling indicates higher tolerance thresholds for saltmarshes, sometimes in excess of 10 mm year^{-1} when suspended sediment concentrations are high (Kirwan et al., 2016). These analyses of tolerance thresholds typically rely upon meta-data analyses of reported rates of vertical adjustment to improve confidence in estimates and, in doing so, treat site-scale measurements as data points that contribute to understanding of coastal wetland resilience at larger spatial scales. Local-scale data remains crucial for improving confidence in global- and regional-scale analyses. However, global-scale models are insuÿcient at the landscape scale where management and decision making require both accuracy and precision. Local-scale information is therefore a crucial data need that will improve both large-scale analyses and models, and local-scale management and decision-making.

At the landscape scale, there is general consensus that sedimentation of tidally-borne material is related to tidal inundation frequency and duration, with positions lower in the tidal frame accumulating sediment at a higher rate than locations higher in the tidal frame (Allen, 2000; Woodroffe et al., 2016). This spatial variation in sedimentation has a significant control on the long-term evolution of coastal wetlands. Under stable sea-level conditions, sedimentation is delimited by maximum tidal extents and is proportional to the depth below maximum tide level whilst surface elevations asymptote toward the height of maximum tide level (Rogers, 2021). RSLR alters the elevation of tidal planes over time; however, as sedimentation is proportional to tidal inundation (Rogers et al., 2005a) and position in the tidal frame, an incremental increase in sea level may result in a proportional increase in elevation adjustment, providing mineral sediment supply is not limited and organic matter addition to substrates is suÿcient. This negative feedback, first described by Pethick (1981), leads to self-organization of surface elevations with the outcome being the development of broad floodplains at elevations that asymptote toward a depth below maximum tide level where surface elevation gain matches the rate of RSLR.

Based on these negative feedbacks, mathematical simulations indicate that the depth of this asymptote below maximum tide level is dependent upon the proportion of substrate volume adjustment to the degree of RSLR (Fagherazzi et al., 2012). Where the proportion of elevation adjustment to RSLR is high, achieved through the accumulation of mineral and organic material within substrates, coastal wetland surfaces will asymptote at a higher elevation in the tidal frame. Where sediment supply and/or organic matter addition becomes increasingly limited, surface elevations asymptote at lower elevations in the tidal frame. When rates of mineral and organic matter addition to substrates are very low, substrates may asymptote at elevations too low to support vegetation, negative feedbacks breakdown, and the system can shift toward a chaotic state where erosional processes may dominate. Hence, rates of surface elevation adjustment with respect to RSLR is critical information needed to gauge whether wetland substrates will maintain their position within the tidal frame, shift toward a lower elevation in the tidal frame, or undergo existential breakdown.

The timescale over which data should be collected to establish relationships between sedimentation and RSLR has been debated. Breithaupt et al. (2018) propose that short-term measurements at inter-annual increments, particularly those derived from observations of surface elevation change using techniques such as surface elevation tables and marker horizons (SET-MH), may indicate rates of surface elevation change that are highly influenced by perturbations operating over the observational period. This has been confirmed with trajectories of surface elevation change being related to droughts (Rogers et al., 2005b, 2006), cyclones and hurricanes (Whelan et al., 2009; Osland et al., 2020; Yeates et al., 2020), groundwater availability (Rogers et al., 2005a; Whelan et al., 2005), and nutrient availability (Anisfeld and Hill, 2012; Reef et al., 2017). Irrespectively, analyses over shorter timescales provide useful information about processes influencing surface elevations, and, when collected over suÿcient time, may provide reliable trajectories of surface elevation change and indicate processes influencing these trajectories (Rogers and Saintilan, 2021).

Radiometric techniques that focus on processes operating over longer interdecadal timescales tend to produce time averaged indications of sedimentation and the influence of short-term perturbations on trajectories is moderated (Nolte et al., 2013). A range of techniques can be used which are dependent upon the capacity to detect isotopes that undergo decay over time. Accordingly, different techniques can be selected to characterize sedimentation over a range of timescales. Measurements of unsupported ^{210}Pb, which has a half-life of 22.3 years, has been effectively used to ascribe chronology over the past 100–150 years for coastal wetland sediments (Swales et al., 2015; Ruiz-Fernández et al., 2016; Arias-Ortiz et al., 2018; Rogers et al., 2019; Marx et al., 2020; FitzGerald et al., 2021). This timescale is particularly useful for developing relationships between sedimentation and RSLR as it corresponds to (i) the most intensive period of industrialization when global sea levels have been increasing; and (ii) the timescale at which projections of the response of coastal wetlands are most relevant for planning and decision making (Woodroffe and Murray-Wallace, 2012).

Recent advances in models for ascribing a ^{210}Pb chronology now accommodate a range of ^{210}Pb supply conditions and composition of sediments (i.e., the degree of mineral and organic material) (FitzGerald et al., 2021; Iurian et al., 2021). As these factors vary over time, the length of time that sedimentation is averaged is diminished, and variation in sedimentation can be determined over shorter-time periods. This provides the opportunity to characterize changes in sedimentation under varying conditions of RSLR.

This study focuses on establishing relationships between rates of sedimentation, surface elevation gain and SLR relevant to decadal timescales, and specifically addresses two knowledge gaps. First, it provides comprehensive empirical data of coastal wetland sedimentation and elevation adjustment in the southern hemisphere, a region for which there is relatively little data at decadal timescales and represents a significant knowledge gap that limits the development of robust regional and global-scale models. Second, it addresses timescale bias by developing relationships between rates of sedimentation and SLR that are relevant at the annual to decadal scale useful for management and decision making. Relationships were validated against both short-term data derived from SET-MH techniques and against geomorphological information of shoreline change at the decadal timescale. Our specific hypothesis was that rates of sedimentation were related to the three-dimensional space available for mineral and organic matter accumulation. Commonly known as accommodation space (Jervey, 1988; Rogers et al., 2019; Rogers, 2021), this space is delimited by the existing surface elevation, the maximum tide level, and hydrodynamic conditions suitable for deposition, and is influenced by SLR. We expected the substrates lower in the tidal frame would have higher rates of sedimentation, the substrates higher in the tidal frame would have lower rates of sedimentation, and that rates of adjustment would change over time on the basis of tidal position. Additionally, we assessed the resilience of coastal wetlands by standardizing rates of sedimentation and surface elevation change relative to accommodation space and comparing surface elevation change to current and projected rates of RSLR. These analyses considered the elevation that substrates would asymptote toward under different SLR scenarios and projected sedimentation rates and surface elevation change at the upper and lower limits of mangrove and saltmarsh vegetation, and the approximate elevation of the transition between mangrove and saltmarsh vegetation. This study focuses on Westernport Bay, Australia; a large tidal embayment that supports mangroves at tidal positions approximately between mean tide level (MTL) and mean high water springs (MHWS), and saltmarsh at positions higher in the tidal frame. We integrate reliable estimates of vertical accretion, surface elevation change and autocompaction derived from a 20-year record of observations (Rogers and Saintilan, 2021), with estimates of sedimentation at the decadal to century scale derived from ^{210}Pb-dating techniques applied to cores extracted from mangrove and saltmarsh zones at each study site. To reconstruct surface elevation, rates of sedimentation were adjusted for autocompaction using a site-specific model developed by Rogers and Saintilan (2021). This manuscript compliments Rogers and Saintilan (2021), which assesses processes influencing surface elevation change over a 20-year timescale from a network of 24 SET-MH. It is anticipated that this study will provide knowledge relevant to management of coastal wetlands at Westernport Bay, and will inform global scale models of the behavior of coastal wetlands to SLR and their resilience.

MATERIALS AND METHODS

Study Site and Design

Westernport Bay (38°21′S, 145°13′E) is a large coastal embayment of ∼680 km^2 that drains a catchment area of 3,433 km^2 located east of Melbourne Victoria, Australia (**Figure 1**). The region is prone to drought associated with negative phases of the El Niño Southern Oscillation, and the influence of drought on rainfall has been associated with changes in surface elevations of coastal wetlands around Westernport Bay (Rogers et al., 2005b). The embayment has two entrances to Bass Strait; the constriction of the eastern entrance near San Remo (38°31′S, 145°22′E) causes tides to propagate relatively freely through the western entrance, clockwise around French Island until they converge with anticlockwise tidal movement (Harris et al., 1979). The tidal regime is semi diurnal with a tidal range of up to 3.1 m and significant tidal amplification along the upper Northern Arm of Westernport Bay, near the study sites at French Island and Koweerup (Water Technology, 2014b). Despite its size, the embayment is relatively shallow and tides are reported to comprise approximately 30% of the total volume at high tide (Lee, 2011). Westernport Bay includes extensive intertidal flats (∼270 km^2) that support mangrove and saltmarsh communities along its low energy intertidal shorelines, estimated to cover approximately 12.3 and 10.9 km^2, respectively (Boon, 2011). These wetlands comprise a lower elevation mangrove zone that supports the cold tolerant mangrove, *Avicennia marina*, which is near its most latitudinal limit at this location. The upper intertidal zone also supports dense thickets of saltmarsh shrubs of the genus *Tecticornia* and a landward zone of herbs, grasses and sedges that are regarded to be highly diverse (Boon, 2011).

This study focuses on four locations where surface elevation table (SET) monitoring stations were established in October 2000 to monitor mangrove and saltmarsh vegetation dynamics and rates of vertical accretion and surface elevation change. These study sites included the northern shoreline of French Island, near abandoned saltworks at Palmer Point (henceforth termed French Island), the northern shoreline of the bay near Tooradin airport which adjoins Kooweerup Swamp (henceforth termed Kooweerup), the eastern shoreline of Quail Island near Warneet (henceforth termed Quail Island), and the upper reaches of Rhyll Inlet on Philip Island (henceforth termed Rhyll).

The original study of Rogers et al. (2005b) commenced in 2000 and provided quantitative information on the dynamics of mangrove and saltmarsh vegetation and changes in rates of vertical accretion and surface elevation within mangrove and saltmarsh of Westernport Bay, with consideration given to varying degrees of catchment development. Rogers et al. (2005b) established a network of version IV SET-MH throughout Westernport Bay. The SET serves as a stable benchmark against

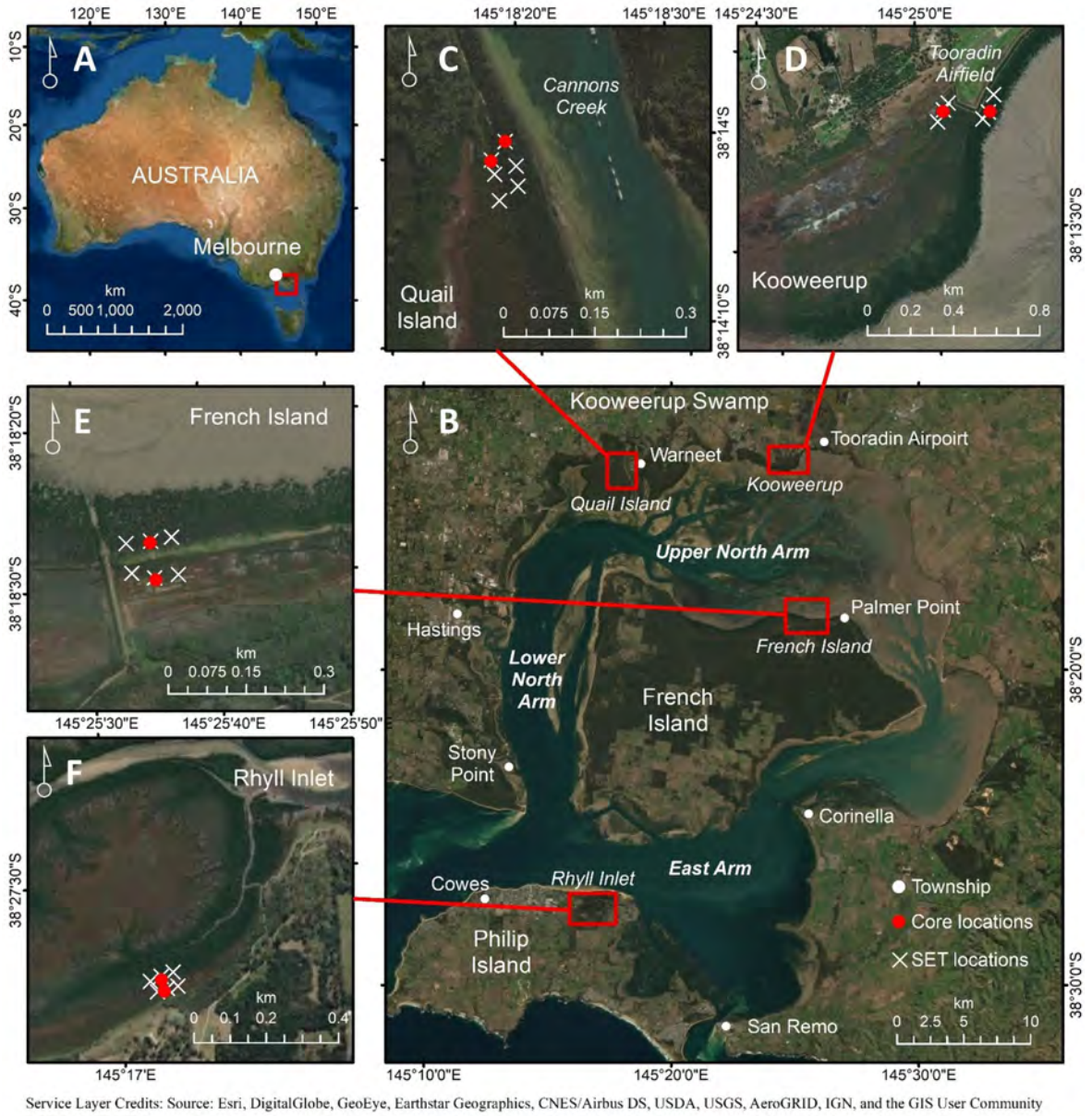


FIGURE 1 | (A) Location of Westernport Bay, Australia, and the **(B)** focal study sites where cores were extracted from the mangrove and saltmarsh at **(C)** Quail Island, **(D)** Kooweerup, **(E)** French Island, and **(F)** Rhyll.

which relative changes in surface elevation can be determined. Relative SET measurements can be converted to absolute measurements of surface elevation change by geolocating SET benchmarks using a real time kinematic global positioning system (RTK-GPS). The version IV SET has a reported 95% confidence limit of ±1.4 mm (Cahoon et al., 2002). Marker horizons of feldspar have been co-located with each SET and extraction of mini-cores from each MH at the time of SET measurements allows quantification of surface processes of vertical accretion. By deduction, the difference between the degree of surface elevation change and vertical accretion provides an indication of autocompaction processes operating in the substrate that alter the volume. This network comprised 24 SET-MH stations in a nested design whereby six SETs were co-located at French Island, Kooweerup, Quail Island, and Rhyll. At each location, SETs were positioned in groups of three within structurally similar vegetation: three located in the mangrove zone where the tidal position was lower; and three in the saltmarsh zone where the tidal position was higher. Rogers et al. (2005b) also determined sedimentation rates using ^{210}Pb-dating of sediments and undertook mapping from aerial photographs to determine changes in the distribution of mangrove and saltmarsh over the length of the aerial photographic records for each site. These study sites remain the focus of this research.

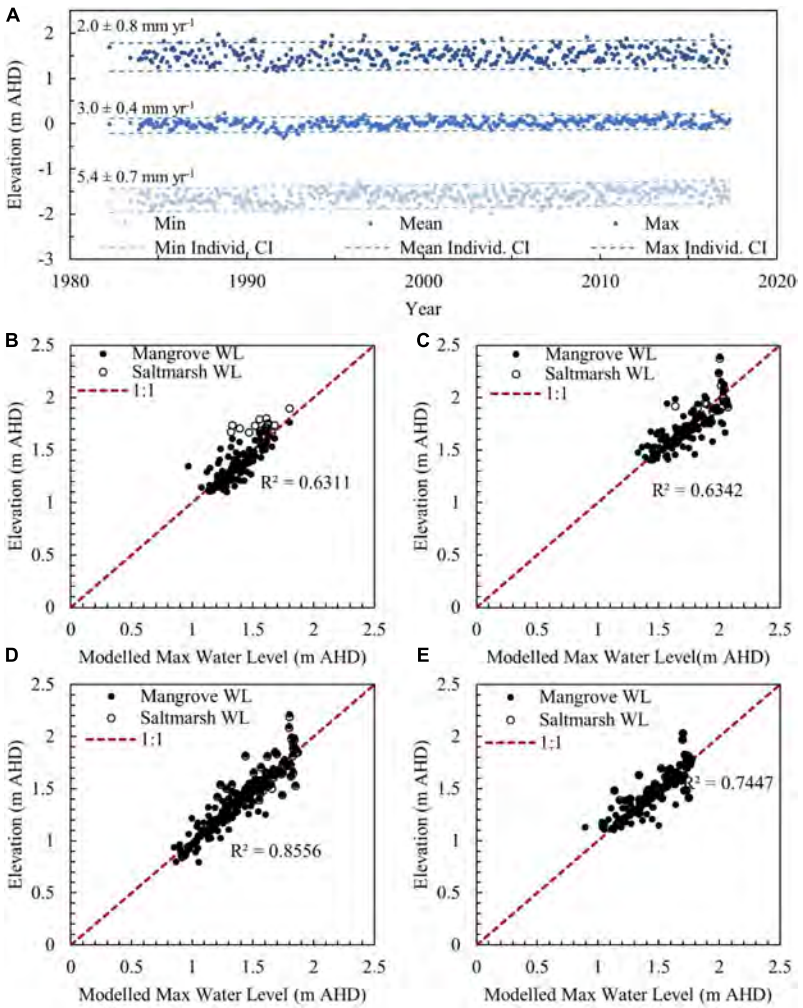


FIGURE 2 | (A) Minimum, mean, and maximum monthly water levels at the Stony Point tide gauge, with 5% and 95% confidence interval for each variable defined by the dashed lines. Relationship between observed daily maximum water levels in the mangrove and saltmarsh zones and modeled maximum water levels at **(B)** French Island, **(C)** Kooweerup, **(D)** Quail Island, and **(E)** Rhyll.

Since the commencement of the original study, access to spatial information, such as LiDAR point clouds and RTK-GPS technology, and access to low-cost sensors and data loggers has increased. Additional time-series mapping has been undertaken by Whitt et al. (2020) and an update of SET monitoring results is provided by Rogers and Saintilan (2021).

Tides and Accommodation Space

Water-level data from the tide gauge at Stony Point has been collected since 1981 and can be accessed as processed datasets indicating minimum, mean, and maximum monthly water levels (Bureau of Meteorology, 2021). This data was accessed for the full record length and analyzed to characterize RSLR over time. Water-level data underwent preliminary processing to remove any months where data gaps were greater than 10% of the gauging frequency each month. Linear regressions were used to identify the rate of change in minimum, mean, and maximum monthly water levels.

Water-level data from tide gauges can also be used to indicate the vertical position within the tidal frame that mangroves and saltmarshes occupy, and the space available for tidally-borne sedimentation, known as accommodation space. However, they may not be a precise indicator of tidal behavior at locations distal to tide gauges as tides can become amplified or attenuated as they propagate along estuaries and embayments (Kumbier et al., 2021). Tidal analyses have confirmed that tides do amplify along the northern arm of Westernport Bay (Water Technology, 2014a), due to the one quarter wavelength resonance of the lunar semidiurnal tide within Westernport Bay. Accordingly, the upper boundary of accommodation space at study sites along the Northern Arm, namely at French Island, Kooweerup and Quail Island, will likely be higher than indicated by tide gauge data alone.

To establish how much tidal amplification occurs at each study site, daily maximum water-level data from the Stony Point tide gauge was calibrated against water-level data collected

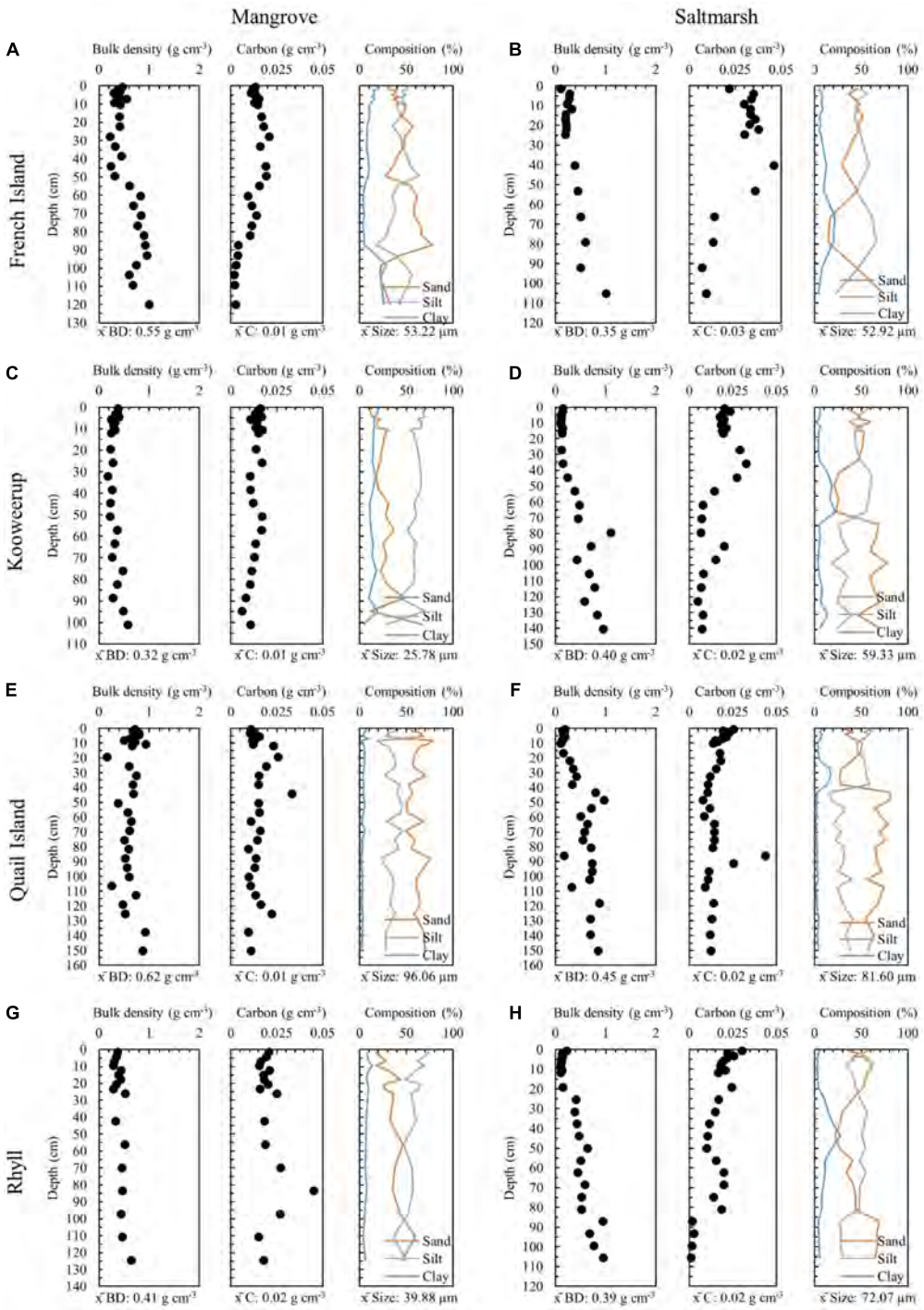


FIGURE 3 | Bulk density, carbon content, and grain size fraction down cores extracted from the mangrove and saltmarsh zones at **(A,B)** French Island, **(C,D)** Kooweerup, **(E,F)** Quail Island, and **(G,H)** Rhyll.

using Hobo water-level loggers that were placed within the mangrove and saltmarsh at each study site and co-located with SETs. The position of Hobo water-level loggers was determined using an RTK-GPS, and all values were calibrated against the Australian height datum (AHD). Hobo water-level loggers collected data at 15-min intervals from May 2015 to January 2016 at French Island, and April 2016 to November 2016 at Kooweerup, Quail Island, and Rhyll. These periods of data collection exceeded 6 months, included considerable variation in tidal height and included the high water spring

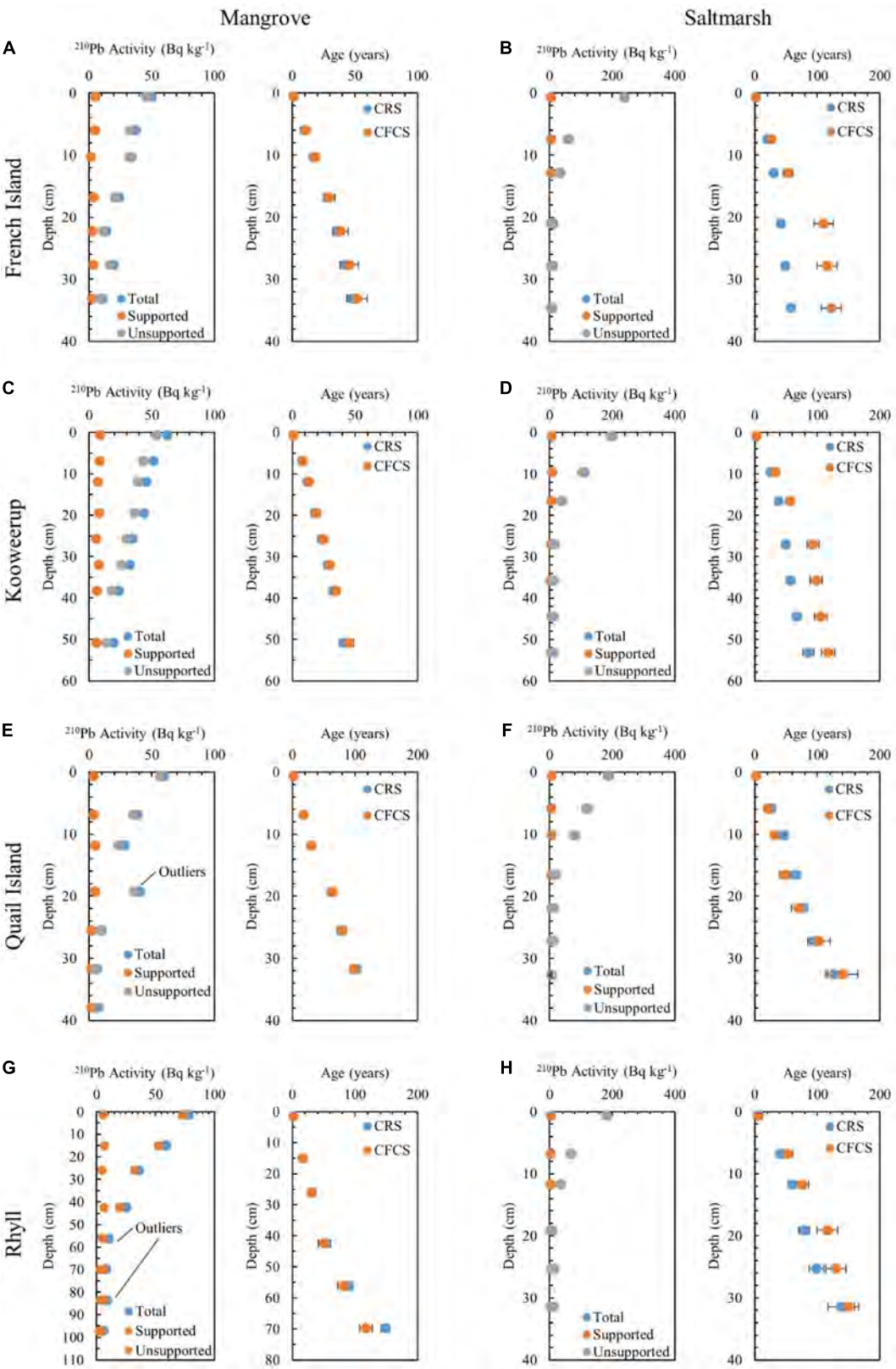


FIGURE 4 | ^{210}Pb activity and geochronological age of sediments at time of deposition down cores extracted from the mangrove and saltmarsh zones at **(A,B)** French Island, **(C,D)** Kooweerup, **(E,F)** Quail Island, and **(G,H)** Rhyll.

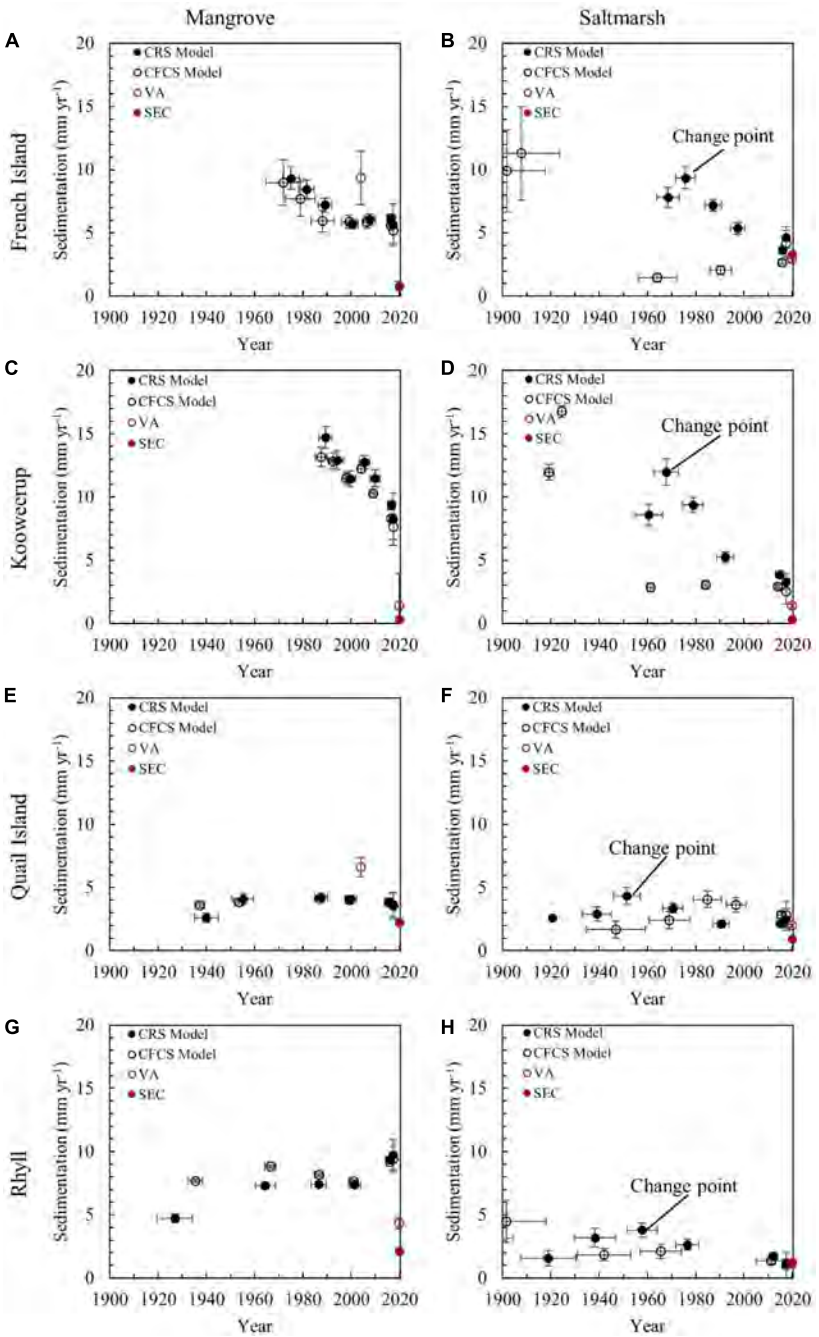


FIGURE 5 | Reconstructed sedimentation rates over time from the mangrove and saltmarsh zones at **(A,B)** French Island, **(C,D)** Kooweerup, **(E,F)** Quail Island, and **(G,H)** Rhyll. Sedimentation rates were validated against vertical accretion (VA) and surface elevation change (SEC) determined at the adjacent SET-MH monitoring station.

tides that occur approximately every 6 months. Modeled maximum daily tides at each study site were determined by calibrating daily maximum tides from the Stony Point tide gauge against observed water-level data collected using Hobo water level loggers by adding a tidal amplification factor to tide gauge data. The eÿc acy of calibration was determined using a matched pairs *t*-test and the deviation of observed values from the modeled values was determined using the coeÿcient of determination (r^2).

The upper boundary of accommodation space at each study site was subsequently modeled at any time step on the basis of the trend in the maximum monthly water-level data plus the tidal amplification factor determined for each study site. The lower boundary of the vegetated intertidal zone was presumed

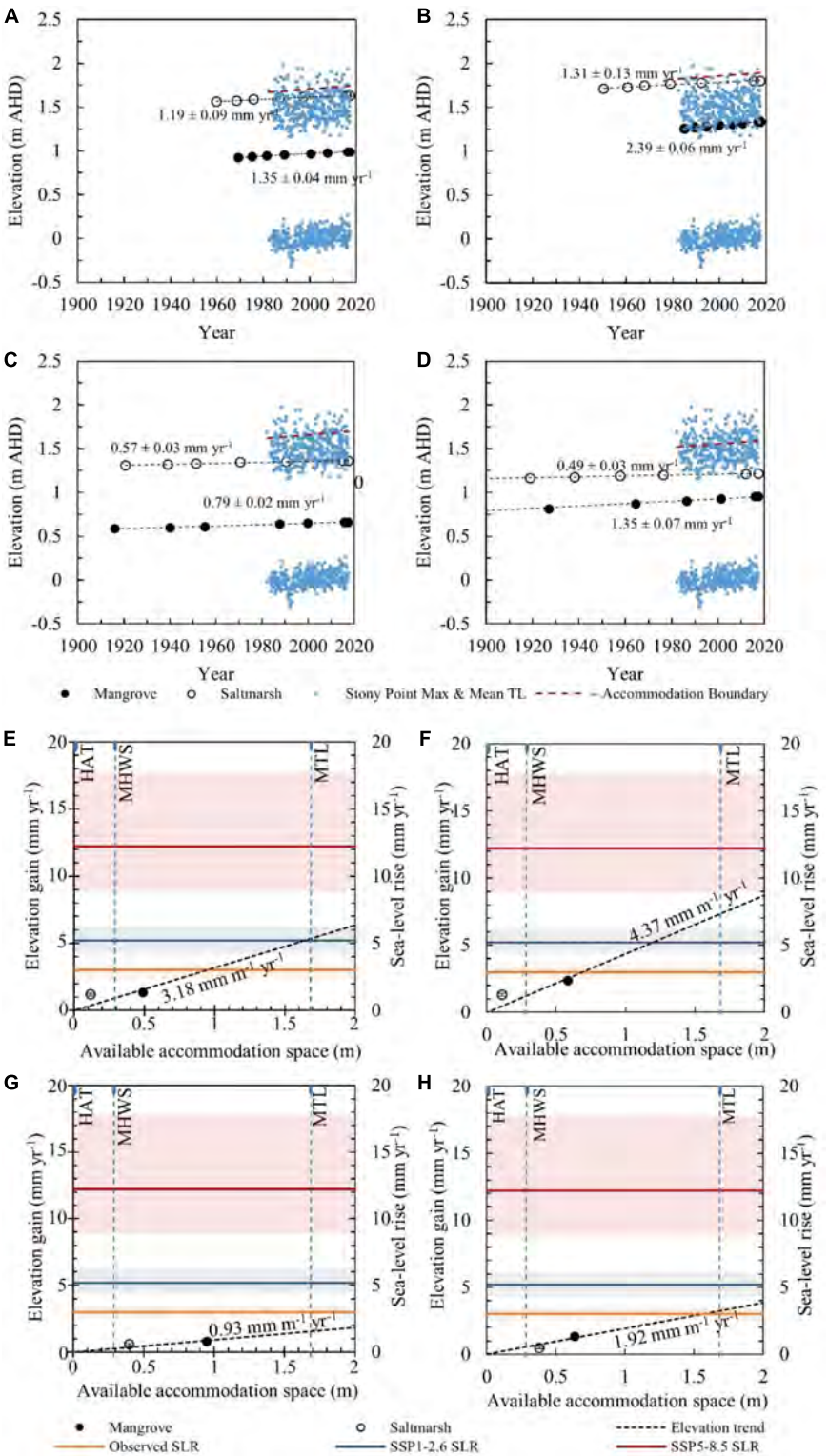


FIGURE 6 | Stony Point water levels, modeled upper boundary of accommodation space (based on amplification factor in **Supplementary Figure 2**) and reconstructed surface elevations (based on autocompaction relationship in **Supplementary Figure 1**) within the mangrove and saltmarsh zones at **(A)** French Island, **(B)** Kooweerup, **(C)** Quail Island, and **(D)** Rhyll; and relationship between surface elevation gain and available accommodation space at **(E)** French Island, **(F)** Kooweerup, **(G)** Quail Island, and **(H)** Rhyll. Observed rates and projected rates of SLR have been included for comparison of accommodation space dependent sedimentation rates in panels **(E–H)**.

TABLE 1 | Standardized rates of surface elevation gain (mm per meter of available accommodation space per year), derived from linear regression analyses in **Figure 6**; projected equilibrium available accommodation space where rates of surface elevation gain equal observed rates of sea-level rise (SLR) (3.0 mm year^{-1}), derived from intersection of linear regression and observed SLR in **Figure 6**; contemporary elevation and estimated available accommodation space at mean tide level (MTL) and mean high water springs (MHWS); projected rate of surface elevation gain, derived from intersection of linear regression and vertical dashed lines in **Figure 6** indicating MTL and MHWS; projected elevation deficit/surplus, derived from the difference between rates of surface elevation gain and observed rate of SLR; projected change in tidal position, based on evidence of a surface elevation deficit or surplus; and projected shoreline change at MTL and MHWS at each study site.

	French Island		**Kooweerup**		**Quail Island**		**Rhyll**	
Standardized surface elevation gain (mm m^{-1} year^{-1})	3.2		4.4		0.9		1.9	
Equilibrium accommodation space (m) at SLR 3 mm year^{-1}	0.9		0.7		3.2		1.6	
	MTL	**MHWS**	**MTL**	**MHWS**	**MTL**	**MHWS**	**MTL**	**MHWS**
Contemporary Elevation (m AHD)	0.1	1.5	0.1	1.6	0.1	1.4	0.1	1.3
Accommodation space (m)	1.7	0.3	1.8	0.3	1.6	0.3	1.5	0.3
Surface elevation gain (mm year^{-1})	5.4	0.9	8.0	1.3	1.5	0.3	3.0	0.6
Surface elevation deficit/surplus	2.4	−2.1	5.0	−1.7	−1.5	−2.7	0.0	−2.4
Tidal position change	↑	↓	↑	↓	↓	↓	Stable	↓
Projected shoreline change	– Progradation – Seaward mangrove expansion – Mangrove encroachment of saltmarsh		– Progradation – Seaward mangrove expansion – Mangrove encroachment of saltmarsh		– Shoreline retreat – Mangrove encroachment of saltmarsh		– No shoreline change – Mangrove encroachment of saltmarsh	

to be the elevation of mean sea level, as indicated on the Stony Point tide gauge.

Sediment Characterization

Sediment cores, eight in total, of approximately 1.5 m length were collected in 2017 adjacent to mangrove and saltmarsh SET monitoring stations at each study site. Cores were extracted in aluminium tubes of 75 mm diameter. The degree of sediment compaction that occurred during core collection was determined and cores were capped to ensure they remained continuous and intact for transport. Cores were placed in cold storage at 4°C until sample preparation was undertaken. The position of each core at the time of extraction was determined using an RTK-GPS with measurements made with respect to the AHD. Cores were split longitudinally and half of the core was subsampled at intervals of 2 cm in the upper strata of 10 cm, every 5 cm to depths of 1 m, and every 10 cm below 1 m for further analysis. These sample depths were adjusted for compaction and the remaining core was placed in storage. Samples were subsequently prepared for analysis of ^{210}Pb activity. Grain size of each sample was determined (μm) using a Malvern Mastersizer 2000 laser diffractometer and the proportion of each fraction determined. To determine dry bulk density (g cm^{-3}), samples were oven dried to constant weight at 60°C. Dry sample weight was determined and bulk density (BD) was estimated as the ratio of dry sample mass to wet sample volume. Dry bulk density was subsequently used to model sedimentation rates and quantify ^{210}Pb activity.

Lead-210 Activity and Chronology

Lead-210 is a naturally occurring radionuclide with a half-life of 22.3 years. Analysis of unsupported ^{210}Pb derived from the atmosphere facilitates the determination of sediment age at time of deposition. As sediments accumulate, ^{210}Pb decays according to its half-life, thus the rate of decline in unsupported ^{210}Pb with sediment depth allows the determination of sediment chronology and mass accumulation rates. Grain size can affect the adsorption of ^{210}Pb onto the sediment materials. Finer sediments with larger surface area adsorb ^{210}Pb more effectively than coarser grain size sediments with smaller surface area. To facilitate the detection of low level ^{210}Pb activities, samples from various core depths were sieved to concentrate the <63 μm fraction. Sieved samples were then provided to the Australian Nuclear Science and Technology Organisation (ANSTO) for ^{210}Pb dating by alpha particle spectrometry. Preliminary analysis was undertaken on five samples per core to determine whether unsupported ^{210}Pb activity decreased with core depth. Subsequent sample analyses were used to develop a more reliable chronology. Sample age was determined using both the constant rate of supply (CRS) (Appleby and Oldfield, 1978) and constant flux-constant rate of supply (CFCS) (Krishnaswamy et al., 1971) models. However, the CRS model has exhibited superior performance when dating sediment matrices comprised of significant organic matter in the sediment composite (Iurian et al., 2021). Accordingly, it was anticipated that the CRS model, which accounts for irregularities in unsupported ^{210}Pb activity would provide a more reliable chronology.

Independent validation of chronology is recommended to ensure high confidence in results (Smith, 2001). Measurements of ^{137}Cs peak activity is commonly used for validation; however, the relatively short-half-life of ^{137}Cs and lower activity within sediments of the southern hemisphere may limit validation using this approach (Arias-Ortiz et al., 2018). Analyses of ^{137}Cs activity did not yield results suitable for validation, hence an alternative

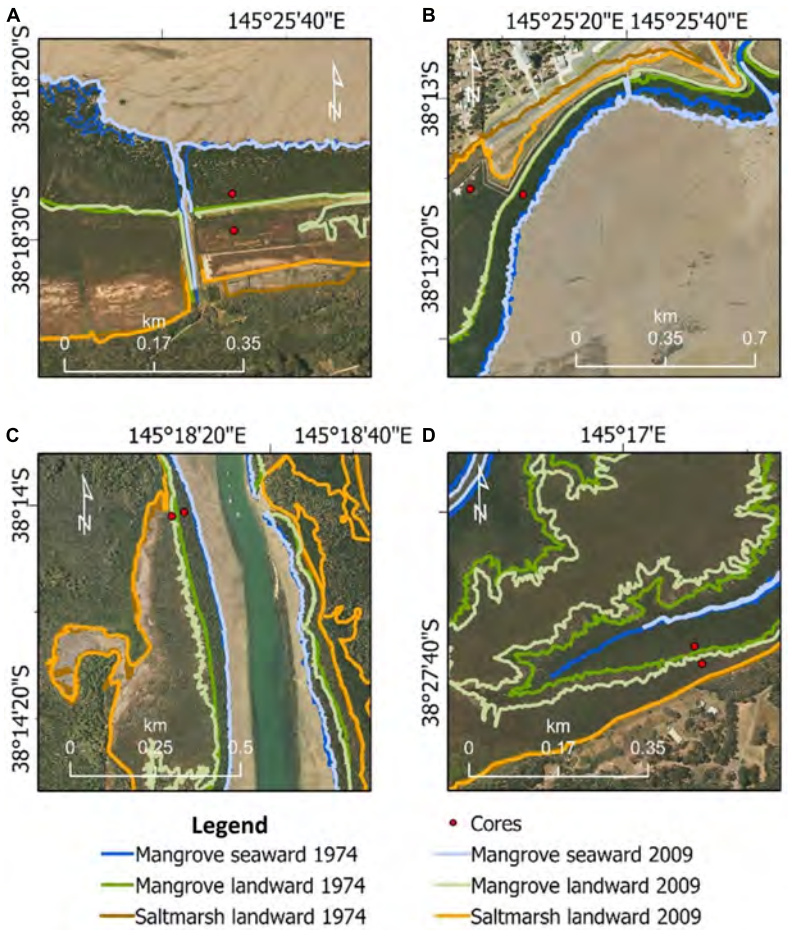


FIGURE 7 | Mangrove seaward and landward limits and saltmarsh landward limits digitized from 1973/74 and 2009 images at **(A)** French Island, **(B)** Kooweerup, **(C)** Quail Island, and **(D)** Rhyll. Notable shoreline progradation and mangrove expansion into saltmarsh is indicated. See **Supplementary Figures 3–6** for time-series maps.

TABLE 2 | Projected equilibrium accommodation space (or depth below the upper boundary of accommodation space) where rates of surface elevation gain equal projected sea-level rise (SLR) based on median values of a low and high SLR scenario, projected surface elevation deficit/surplus, and tidal position change at mean tide level (MTL) and mean high water springs (MHWS).

	French Island				Kooweerup				Quail Island				Rhyll			
SLR scenario	Low		High		Low		High		Low		High		Low		High	
Equilibrium accommodation space (m)	1.6		3.8		1.2		2.8		5.6		13.1		2.7		6.4	
	MTL	**MHWS**	**MTL**	**MHWS**	**MTL**	**MHWS**	**MTL**	**MHWS**	**MTL**	**MHWS**	**MTL**	**MHWS**	**MTL**	**MHWS**	**MTL**	**MHWS**
Surface elevation deficit/surplus (mm year^{-1})	0.2	−4.3	−6.8	−11.3	2.8	−3.9	−4.2	−10.9	−3.7	−4.9	−10.7	−11.9	−2.2	−4.6	−9.2	−11.6
Tidal position change	↑	↓	↓	↓	↑	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓

Median value of low SLR scenario from SSP1-2.6 at ~2,100, estimated at 5.2 mm year^{-1}. Median value of high SLR scenario from SSP5-8.5 at ~2,100, estimated at 12.2 mm year^{-1}.

approach was undertaken. Measurements of $^{239+240}$Pu activity, or bomb-pulse analyses, can also be undertaken, but can be costly and were not undertaken in this study as the results were validated using existing data from SET-MH analyses (Sanders et al., 2016; Marx et al., 2020). Initially, validation was undertaken by comparison with recent measurements of vertical accretion derived from SET-MH stations and reported in Rogers and Saintilan (2021). Validation of expected changes to shorelines

TABLE 3 | Sedimentation rates derived from ^{210}Pb geochronology for similar ecosystems in Australia and New Zealand, and reported global averages and common values.

Location	Dominant species/ community	Mean sedimentation rate (Range) (mm year^{-1})	Mean bulk density (Range) (g cm^{-3})	Sources
French Island, Westernport Bay	*A. marina*	6.9[a] (5.7–9.3)	0.38 (0.22–0.46)	This study
	Saltmarsh	6.3[a] (3.6–9.3)	0.30 (0.10–0.50)	
	Saltmarsh	1.4[b]		Rogers et al. (2005b)
Kooweerup, Westernport Bay	*A. marina*	11.6[a] (8.3–14.7)	0.26 (0.18–0.38)	This study
	Saltmarsh	7.1[a] (3.3–12.0)	0.18 (0.11–0.38)	
	Saltmarsh	1.63[b]		Rogers et al. (2005b)
Quail Island, Westernport Bay	*A. marina*	3.8[a] (2.6–4.2)	0.67 (0.0.60–0.72)	This study
	Saltmarsh	2.8[a] (2.1–4.3)	0.24 (0.11–0.42)	
	Saltmarsh	1.4[b]		Rogers et al. (2005b)
Rhyll, Westernport Bay	*A. marina*	7.7[a] (4.7–9.8)	0.42 (0.33–0.52)	This study
	Saltmarsh	2.3[a] (1.2–3.8)	0.23 (0.10–0.41)	
	Saltmarsh	2.5[b]		Rogers et al. (2005b)
Corinda Creek, Westernport Bay	Saltmarsh	(2.7–2.9)[a]		Lewis et al. (2019)
Terranora, Tweed River	*A. marina*	5.5[a] (2.1–8.3)		Marx et al. (2020)
Southern Moreton Bay, Brisbane	*A. marina*	4.2–6.7[a]	NA	Sanders et al. (2016)
Firth of Thames, New Zealand	*A. marina:*		NA	Swales et al. (2015)
	Upper	(7–12)[a]		
	Intermediate	(33–100)[a]		
	Basal	(10–22)[a]		
Global Mean	Mangrove[b]	2.8 mm/y	NA	Breithaupt et al. (2012)
Common Values	Mangrove[b]	7.7 (1.0–36)	0.45	Arias-Ortiz et al. (2018)
	Saltmarsh[b]	6.2 (0.7–42)	0.43	

[a]*Denotes values derived from constant rate of supply (CRS) model,* [b]*denotes values derived from constant initial concentration (CIC) model.*

was also undertaken using time-series aerial photograph analysis, as described below.

Sedimentation, Surface Elevation Gain, and Accommodation Space

As the CRS model accounts for variation in volume and mass of sediment accumulated over time, it provided the opportunity to assess changes in sedimentation rates over time on the basis of the age and depth of each sediment sample, as per Rogers et al. (2019). Change point detection was applied using JMP statistical software when a change in sedimentation trajectories was evident; peaks in sedimentation were interpreted in the context of available accommodation space.

Reconstructing surface elevations requires information about the elevation of the contemporary substrate surface, compaction associated with core extraction, and post-depositional autocompaction. The elevation of the contemporary substrate surface was determined at the time of core extraction using an RTK-GPS, and compaction associated was core extraction was quantified. To account for post-depositional autocompaction, we adapted the relationship established by Rogers and Saintilan (2021) between autocompaction and vertical accretion at Westernport Bay (see **Supplementary Data 1**, **Supplementary Figure 1**, and **Supplementary Table 2**). Autocompaction was modeled to be linearly related to sedimentation (r^2 = 0.82), with approximately 80% of deposited sediment within a year undergoing post-depositional autocompaction, resulting in 20% of annual sedimentation volume contributing to surface elevation gain. This relationship was applied to sedimentation rates at each time step to determine the rate of autocompaction. The rate of surface elevation change was established from the difference between the rates of sedimentation derived from ^{210}Pb analyses and autocompaction. The rate of surface elevation change was time-adjusted to determine the total surface elevation change between each time step, and absolute surface elevations were reconstructed using total surface elevation change between each time step. Mean rates of surface elevation change were determined by applying linear regression analysis to reconstructed surface elevations.

Standardized Rates of Surface Elevation Change

The upper boundary of accommodation space at the time of core extraction was determined by applying the tidal amplification factor to the modeled trend in maximum monthly water levels at each study site. Available accommodation space was defined as the vertical space between the upper boundary of accommodation space and the surface elevation at the time of core extraction. Mean rates of surface elevation gain within mangrove and saltmarsh cores at each study site were

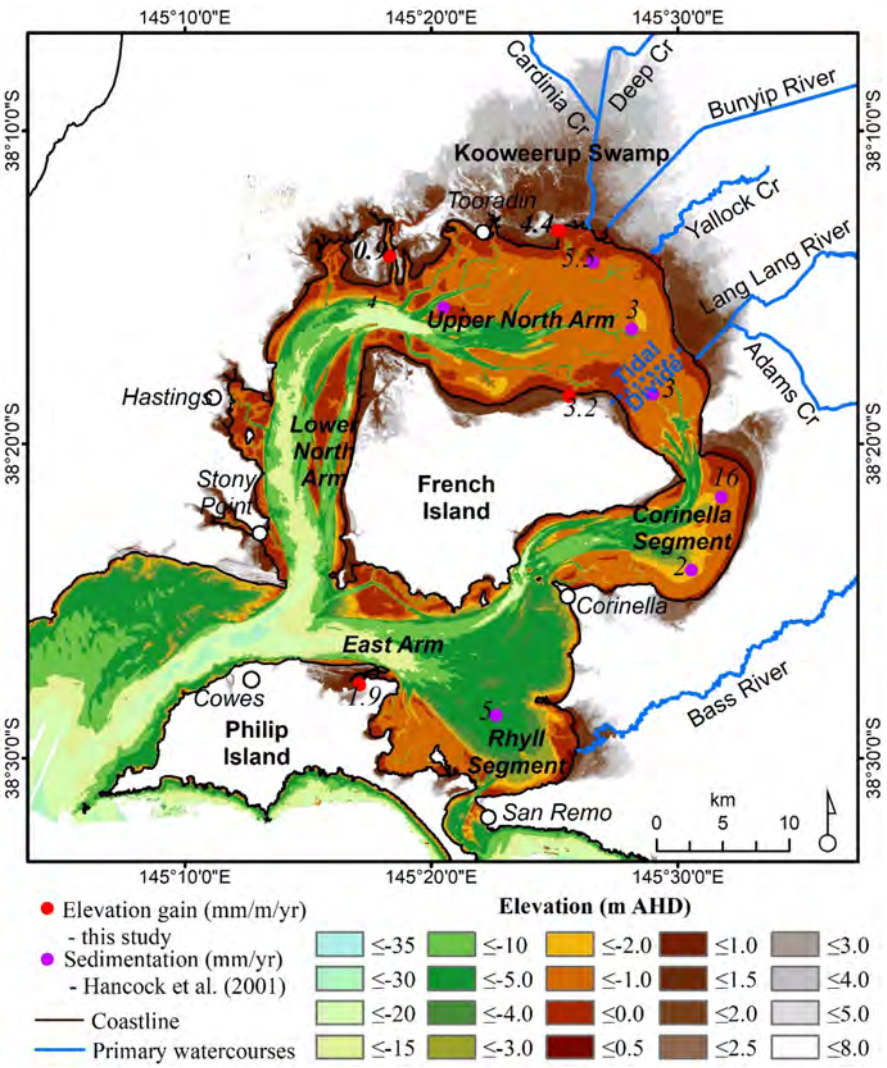


FIGURE 8 | Elevation and bathymetry of Westernport Bay, water circulation, and sedimentary basins in the Upper North Arm, Corinella Segment, and Rhyll Segment. Sedimentation rates detected in this study and within the sedimentary basins by Hancock et al. (2001) also indicated.

subsequently plotted against available accommodation space. As tidally-borne sedimentation is presumed to be negligible at the upper boundary of accommodation space, surface elevation change was also presumed to be negligible. Whether substrate elevations adjusted across the intertidal zone according to a linear or peak model relationship has received consideration globally and at this location (Kirwan and Megonigal, 2013; Mogensen and Rogers, 2018; Rogers and Saintilan, 2021). Quantifying sedimentation at multiple positions across the intertidal zone using lead-210 activity was not feasible due to the resources required to undertake this across the expanse of Westernport Bay. This limited the capacity to determine the behavior of substrate elevations at each study location and it was subsequently assumed that substrate elevations behaved linearly. On this assumption, linear regression analyses that passed through the origin were applied at each study site. A standardized rate of surface elevation gain per meter of available accommodation space was also determined at each study site. These standardized rates were used to determine whether a change in tidal position and shoreline change had occurred over the observational record when sea level was rising in the order of 3 mm year^{-1}. Under these conditions of SLR, it was expected that surface elevations would asymptote toward a depth below the upper boundary of accommodation space where rates of surface elevation gain correspond to rates of SLR, termed equilibrium accommodation space. At depths below the upper boundary of accommodation space where rates of surface elevation gain exceed rates of SLR, infilling will continue, tidal position should increase and shoreline progradation would occur over extended periods of time. Mangrove and saltmarsh distribution is expected to change accordingly, with seaward expansion of mangroves occurring where rates of surface elevation gain exceeds rates of SLR.

Where rates of surface elevation gain do not exceed rates of SLR at any tidal position, even when there is ample available accommodation space, tidal position will decrease and shoreline retreat will eventually occur. Mangrove expansion into the saltmarsh would also occur where surface elevation gain was less than SLR. Standardized rates of surface elevation gain were specifically used to estimate rates of surface elevation gain at MTL and MHWS. These elevations were selected as they approximate the lower boundary of mangrove vegetation and the lower boundary of saltmarsh vegetation. Changes in tidal position were subsequently projected as the difference between the observed rate of surface elevation gain and SLR: a deficit between surface elevation gain and SLR indicates retreat, whilst a surplus indicates progradation.

Time-Series Shoreline Analyses

Comparison of changes in shoreline position from aerial photography provides the capacity to confirm projections of changing tidal position and shoreline change. Observed patterns of vegetation change were delineated at each study site by mapping mangrove and saltmarsh distribution changes from historic and contemporary aerial photography that approximated the period of tide-gauge data collection (i.e., 1981–2017). The best available contemporary imagery was pre-processed orthophotography from 2009 provided by the Victorian Government. The best available historical color aerial photographs were captured at a resolution of 1:15,000 in 1973/4 near the commencement of tide-gauge data collection (**Supplementary Table 2**). These were scanned at 600 dpi and georectified against the contemporary orthophotography using a projective transformation. Each georectified image was merged into a single mosaic for each study site. This imagery was visually digitized to delineate the lower mangrove boundary (presumed to be near MTL), the boundary between mangrove and saltmarsh vegetation (presumed to be near MHWS), and the landward boundary of intertidal vegetation [presumed to be near highest astronomical tide (HAT)]. Lateral changes in the position of MTL and MHWS were subsequently measured within the vicinity of core extraction sites to establish the direction and extent of vegetation distribution changes. Changes in vegetation distribution that corresponded to projected vegetation changes served to validate standardized rates of surface elevation gain.

Implications of Projected Sea-Level Rise on Equilibrium Accommodation Space and Coastal Wetland Distribution

Following validation of standardized rates of surface elevation gain against observed changes in vegetation distribution, the resilience of each study site was projected under two different SLR scenarios that represent end-members of future scenarios: (i) the projected median rate of SLR for a low SLR scenario at ∼2100 (i.e., SSP1-2.6 = 5.2 mm year^{-1} (4.4–6.2 likely range); and (ii) the projected median rate of SLR for a high SLR scenario at ∼2100 (i.e., SSP5-8.5 = 12.2 mm year^{-1} (8.8–17.7 likely range) (Fox-Kemper et al., 2021). The equilibrium accommodation space was specifically quantified as the accommodation space where the rates of surface elevation gain and SLR corresponded under each SLR scenario. This was also assessed by estimating changes in tidal position on the basis of the difference between surface elevation gain at MTL and MHWS and projected rates of SLR; a deficit was presumed to indicate shoreline retreat, whilst a surplus was presumed to indicate progradation.

RESULTS

Tides and Accommodation Space

Minimum, mean, and maximum monthly tide levels increased at rates of 5.4 ± 0.7, 3.0 ± 0.4, and 2.0 ± 0.8 mm year^{-1}, respectively (**Figure 2A**) over the period 1981–2017. The observed rise in MTL was later used to consider the resilience of each study site to observed rates of SLR.

Observed daily maximum tide level within the mangrove and saltmarsh at each study site calibrated well against maximum water levels at Stony Point when amplification factors were applied (**Supplementary Figure 2**). Optimal amplification factors were estimated to be 0.2 m at French Island, 0.35 m at Kooweerup, 0.15 m at Quail Island, and 0.05 m at Rhyll. These amplification factors are reasonably consistent with hydrodynamic modeling of tidal amplification around Westernport Bay (Water Technology, 2014b). No significant difference between observed and modeled water levels (**Figures 2B–E**); however, greater deviation occurred at French Island (p = 0.7144, r^2 = 0.6311) and Kooweerup (p = 0.1408, r^2 = 0.6342) than Quail Island (p = 0.7796, r^2 = 0.8556) and Rhyll (p = 0.4278, r^2 = 0.7447). The deviation at French Island is most prominent in the saltmarsh and likely relates to pooling of tides within abandoned ponds previously used for salt production. The upper boundary of accommodation space was subsequently modeled at each study site based on the linear trajectory of daily maximum tide level plus the tidal amplification factor for the relevant site.

Sediment Characterization

Sediment analyses established that sediments comprised of both mineral and organic matter fractions, and confirmed that bulk density varied down core and was synchronous with variation in carbon content (**Figure 3**). Organic matter fractions were typically highest in the surface strata; however, peaks in carbon were also evident in other strata. Bulk density ranged between 0.32–0.62 g cm^{-3} with a mean of 0.44 ± 0.10 g cm^{-3}, whilst carbon ranged between 0.1–0.3 g cm^{-3} with a mean value of 0.02 ± 0.01 g cm^{-3}. Sediments were largely comprised of sand and silt fractions with mean grain sizes ranging between 26 and 96 μm. Mean grain size was higher in the saltmarsh than mangrove zones at Kooweerup and Rhyll, and was consistently high in both zones at Quail Island and French Island. The predominance of sand in some cores confirmed the need to concentrate the mineral fraction of sediments to <63 μm prior to undertaking ^{210}Pb analyses. In addition, sediment variably comprising of mineral and organic fractions supported assumptions that the CRS model, which determines

sedimentation rates on the basis of the sediment composite, would improve the accuracy of sedimentation rates.

Lead-210 Activity and Chronology

Lead-210 activity and modeled sediment ages using the CRS and CFCS models confirmed decay of unsupported ^{210}Pb activities against depth, as indicated in **Figure 4**. Outliers were excluded from age calculations and the three identified outliers were limited to mangrove sediments at Quail Island and Rhyll.

Sedimentation, Surface Elevation Gain, and Accommodation Space

For all cores, except the mangrove cores at Kooweerup and Rhyll, incremental rates of sedimentation derived from ^{210}Pb chronologies corresponded to rates of vertical accretion derived from nearby MH over the same time period (**Figure 5**). For mangrove cores at both Kooweerup and Rhyll, rates of sedimentation derived from ^{210}Pb chronologies were approximately twice the amount detected using the MH technique; these differences may arise from known limitations associated with determining accretion using MH, which are prone to bioturbation, erosion, and dispersal. General agreement between sedimentation rates derived from ^{210}Pb chronologies and MH data provided confidence in both estimates of vertical accretion derived from MH and sedimentation using ^{210}Pb chronologies.

Sedimentation rates ranged between a maximum of 15 ± 0.88 mm year^{-1} in the mangrove zone at Kooweerup to a minimum of 1.2 ± 0.34 mm year^{-1} in the saltmarsh zone at Rhyll. Sedimentation rates were typically higher in mangrove cores than saltmarsh cores at each study site but exhibited differences between sites. Deceleration of sedimentation was evident over the past 40–60 years in the mangrove and saltmarsh at French Island and Kooweerup, and the saltmarsh at Quail Island and Rhyll (**Figures 5A–D,F,H**). In all saltmarsh cores, deceleration followed an initial period of acceleration in sedimentation. Change point detection confirmed this same pattern in sedimentation occurring within all saltmarsh cores. The inflection between phases of acceleration and deceleration in saltmarsh cores occurred in the mid-20th century between 1951 (Quail Island) and 1975 (French Island). Contrasting other cores, acceleration in sedimentation was evident over the past 100 years in the mangrove at Rhyll (**Figure 5G**), and sedimentation rates remained relatively stable in the mangrove at Quail Island (**Figure 5E**). Given the considerable temporal variability in sedimentation, mean rates have not been reported as they provide little indication of realistic sedimentation over time.

Reconstruction of surface elevations with respect to accommodation space at each study site provides additional context to the conditions under which patterns of acceleration and deceleration occurred (**Figures 6A–D**). Deceleration was associated with surface elevations increasing and accommodation space becoming increasingly limited; that is surface elevations were higher in the tidal frame when sedimentation rates decelerated. Surface elevations, particularly in the mangrove and saltmarsh at French Island and Kooweerup (**Figures 6A,B**), were approaching the maximum elevation of inundation, and sedimentation was likely facilitated by high rates of sediment supply at these locations combined with lower hydrodynamic energy, as indicated in various models (Harris et al., 1979; Water Technology, 2014a). As accommodation space becomes increasingly limited in the saltmarsh, negative feedbacks between sedimentation and inundation, evident by consistent patterns of initial acceleration and subsequent deceleration, may indicate transition toward a dynamic equilibrium of surface elevations with respect to available accommodation space. In contrast, the mangrove at Rhyll has undergone relatively rapid accumulation of sediment as considerable accommodation space remains available and substrates continue to transition to higher intertidal positions (**Figure 6D**).

Standardized Rates of Surface Elevation Gain

Rates of surface elevation gain per unit of available accommodation space were highest at Kooweerup (4.37 mm m^{-1} year^{-1}), followed by French Island (3.18 mm m^{-1} year^{-1}), Rhyll (1.92 mm m^{-1} year^{-1}), and Quail Island (0.93 mm m^{-1} year^{-1}) (**Figures 6E–H**). These rates of surface elevation gain influenced the position at which elevation gain matched SLR; as such, this occurred at a higher position in the tidal frame where there was less available accommodation space at Kooweerup (**Figure 6F**), whilst there was no location within the vegetated intertidal zone at Quail Island (**Figure 6G**) where rates of surface elevation gain matched observed or projected SLR scenarios.

Based on current rates of SLR of 3.0 mm year^{-1}, it was estimated that equilibrium occurred where there was 0.7 m of available accommodation space at Kooweerup, 0.9 m at French Island and 1.6 m at Rhyll (**Table 1**). The depth below the upper boundary at which equilibrium occurred at Quail Island was 3.2 m. It is noted this is below MTL and not within the vegetated intertidal zone. The equilibrium available accommodation space, or depths below the upper boundary where the rate of surface elevation gain matched the rate of SLR, transitioned to lower elevations as the rate of SLR increased. Standardized rates of surface elevation gain were used to estimate rates of surface elevation gain at MTL and subsequently compared to observed rates of SLR to indicate whether shoreline building processes were significant; if so, it was expected that shoreline progradation would be evident within aerial photography.

Time-Series Shoreline Analyses

Changes to shoreline position, inferred from time-series analysis of vegetation distribution changes, validated projected changes to shoreline position. More specifically, at Kooweerup and French Island, as rates of surface elevation gain at MTL (**Table 1**) exceeded observed rates of SLR, shoreline progradation was projected, and this corresponded to observations of seaward mangrove expansion between 1973/74 and 2009. Progradation of the seaward mangrove boundary was in the order of ∼20 m quantified immediately seaward of the mangrove core at Kooweerup, and up to 80 m immediately east of the mangrove

core (**Figure 7B**). Similarly, at French Island shoreline retreat was not evident within the immediate proximity of cores and progradation of up to 20 m was evident by seaward expansion of the mangrove canopy (**Figure 7A**). Infilling of the tidal creek immediately adjacent to the mangrove core at Rhyll may indicate progressive infilling between 1973 and 2009 or may be related to increasing mangrove crown sizes. Infilling would be associated with higher rates of surface elevation gain than was projected using standardized rates of surface elevation gain. As the elevation of MTL coincides with the position of equilibrium accommodation space, stability was projected, and this corresponds to the stability of many of the shorelines at the margins of the inlet (**Figure 7D**).

The change in position of the seaward limit of mangrove vegetation at Quail Island, within the vicinity of the mangrove core, was less than 4 m (**Figure 7C**). This very modest increase likely relates to the increasing crown size as trees matured along the shoreline. Mature crown sizes along the shoreline were evident in 2009 imagery, and there was an absence of juvenile mangroves seaward of the mature trees. Low rates of sedimentation and surface elevation gain at Quail Island indicated that retreat may be expected, but it is probable that this could be delayed given the maturity and resilience of mangrove trees along this shoreline.

As the equilibrium elevation at all locations was projected to be below MHWS, landward encroachment of mangrove into saltmarsh was projected and this was confirmed at all study sites. Whilst the degree of lateral encroachment is dependent upon the slope of the saltmarsh, it remains informative that the degree of lateral encroachment is lower where standardized rates of surface elevation gain were higher (i.e., <5 m lateral encroachment at French Island, 5 m at Kooweerup) and more pronounced where rates were lower (i.e., 12 m at both Quail Island and Rhyll).

Implications of Projected Sea-Level Rise on Equilibrium Accommodation Space and Coastal Wetland Distribution

Under a low projected SLR scenario, shoreline progradation may continue at Kooweerup and French Island; however, despite high rates of sediment supply and deposition, shoreline resilience will not be maintained under a high SLR scenario (**Table 2**). At Rhyll and Quail Island, shoreline retreat is anticipated under all projected SLR scenarios. As the rate of surface elevation gain at MHWS is less than median projected rates of SLR at all study sites, mangrove encroachment of saltmarsh is likely, and saltmarsh will become increasingly restricted to elevations beyond their contemporary distribution.

DISCUSSION

Sedimentation, Surface Elevation Gain, and Accommodation Space

Sedimentation rates ranged from 1.2 to 15 mm $year^{-1}$ and at each study site sedimentation rates were typically higher where there was more accommodation space (i.e., in the mangrove zone) than where accommodation space was becoming exhausted (i.e., in the saltmarsh). Acceleration in sedimentation rates at each core location occurred when more vertical accommodation space was available whilst deceleration occurred when surface elevations were high in the tidal frame and accommodation space was becoming limited. High sedimentation rates and acceleration in sedimentation was dependent upon rates of sediment supply and favorable conditions for deposition, with mean deposition rates found to be highest at Kooweerup, followed by French Island, Rhyll, and Quail Island (**Table 3**). By accounting for autocompaction of sediments, standardized rates of surface elevation gain were established; critically, these rates were different between study sites, indicating significant variation in hydrodynamic energy, sediment supply, sedimentation, and surface elevation gain across Westernport Bay.

A range of factors may influence the spatial variation in the observed relationship with sedimentation. Sediment supplied to Westernport Bay largely arises from hillslope, gully, and riverbank erosion occurring in the sub-catchments located on the northeastern shorelines of Westernport Bay (Bunyip River, Cardinia Creek, Lang Lang River, Yallock Creek, and Bass River) and is reportedly in the order of 156 kt $year^{-1}$ (Hughes et al., 2003). Of this supply, approximately 96 kt $year^{-1}$ is estimated to be exported from catchments to Westernport Bay for deposition. Suspended sediment and bedload yields have been modeled using the Revised Universal Soil Loss Equation (RUSLE). Sediment yield was reported to be greatest from Lang Lang River (0.47 t ha^{-1} $year^{-1}$), Bass River (0.30 t ha^{-1} $year^{-1}$) and Bunyip River (0.25 t ha^{-1} $year^{-1}$), and least for Yallock Creek (0.21 t ha^{-1} $year^{-1}$) and Cardinia Creek (0.15 t ha^{-1} $year^{-1}$). Bedload export is reported to be greatest from Bunyip River (0.18 t ha^{-1} $year^{-1}$), Lang Lang River (0.14 t ha^{-1} $year^{-1}$) and Bass River (0.08 t ha^{-1} $year^{-1}$), and least for Yallock Creek (0.07 t ha^{-1} $year^{-1}$) and Cardinia Creek (0.05 t ha^{-1} $year^{-1}$) (Hughes et al., 2003). The Bunyip River, has the largest sub-catchment area (890 km^2) and contributed the greatest bedload yield; however, suspended sediment yield was greatest from the Lang Lang River which has a markedly smaller sub-catchment area (423 km^2). These differences may arise from the varying degrees of hillslope, bank, and gully erosion in each of the sub-catchments. Despite high bedload and suspended sediment supply from these tributaries, it is not suÿcient to offset the prolonged erosion of peats and shoreline retreat occurring where these tributaries enter Westernport Bay. Fetch-based waves generated by prevailing westerly winds ensure that the northwestern shoreline remains a source of sediment and contributes to subaerial sedimentation. Accordingly, active cliff erosion occurs due to direct exposure to wave action during high tides and storms (Water Technology, 2014b).

Analyses of subaerial sediment redistribution within Westernport Bay confirm movement of sand and mud along the Upper North Arm toward depositional basins within the vicinity of the French Island and Kooweerup study sites (Harris et al., 1979), where deposition is reported to be approximately 55 mm $year^{-1}$ (Hancock et al., 2001). Sediment supply to Rhyll is limited by the prevailing transport of sediment away from Rhyll and along the Eastern Arm to the depositional

basin east of Rhyll Inlet, where deposition is reported to be 50 mm year^{-1}. Bathymetry along the Upper North Arm indicates that lateral accommodation space suitable for shoreline progradation is broad and low gradient mudflats dominate seaward of the latter sites (**Figure 8**). Indeed, recent imagery confirms active colonization of mudflats at Kooweerup and French Island and provides additional evidence of progradation (**Figure 7**). Sediment supply to the Quail Island study site is dependent upon the limited supply of sediment from catchments entering the western side of the bay or supply from Cannons Creek. Prior hydrodynamic modeling (Lee, 2011; Water Technology, 2014a,b) indicates conditions that promote sediment transport occur along Cannons Creek, the channel immediately adjacent to the Quail Island study site, whilst low energy hydrodynamic conditions prevail at Kooweerup and French Island. Given these restrictions on sediment supply to the eastern shoreline of Quail Island and high hydrodynamic energy, it is not surprising that observed sedimentation rates were low at this location. However, analyses of shoreline change at Quail Island indicate that progradation has been occurring in the reaches of the Upper Arm where lateral accommodation space remains available and sediment supply is not restricted by higher hydrodynamic energy. Conversely, high sedimentation rates at the remaining sites were facilitated by favorable hydrodynamic conditions and higher rates of sediment supply.

Rates of sedimentation reported in this study are reasonably high and, in most cases, well-beyond the average rates reported for mangroves (Breithaupt et al., 2012), but within the range observed elsewhere (Arias-Ortiz et al., 2018) (**Table 3**). The pattern of acceleration in sedimentation, followed by deceleration is consistent with analyses at Firth of Thames, New Zealand (Swales et al., 2015), where excess sediment facilitated rapid infilling of accommodation space and active mangrove colonization and progradation. Given the established relationship between accommodation space, sediment supply and sedimentation rates, we suggest that comparison of sedimentation rates from one site with another site is meaningless without also controlling for available accommodation space. Whilst comparisons within an ecosystem type (i.e., comparing saltmarsh rates from one location to another) partly recognizes the influence of accommodation space on sedimentation, it may not be suÿcient when ecosystems occupy a large proportion of vertical accommodation space. In particular, mangrove forests dominated by *A. marina* occupy a larger vertical range of available accommodation space than saltmarsh and should exhibit greater variation in sedimentation rates. This was confirmed in this study by higher peaks in sedimentation within mangrove cores than saltmarsh cores.

Despite relatively high rates of sedimentation, particularly at Kooweerup and French Island, we demonstrate that this is likely to have translated to relatively modest rates of surface elevation gain. By converting sedimentation rates into rates of surface elevation gain by adjusting for autocompaction (following Rogers and Saintilan, 2021), we were able to reconstruct surface elevations through time. Comparisons with shoreline change in aerial photography provided some confidence that reconstructions of surface elevation were valid. Validation of ^{210}Pb chronology is typically undertaken against chronologies derived from alternative radiometric approach, such as using ^{137}Cs concentrations; however, given the relatively short half-life and decreasing availability of ^{137}Cs, particularly in the southern hemisphere where concentrations were initially low, efforts have now been directed toward validation using other approaches. ^{14}C bomb-pulse analyses have been successfully applied to validate ^{210}Pb chronology at other locations in southeastern Australia (Sanders et al., 2016; Marx et al., 2020). Given reductions in ^{137}Cs activity, the validation approach undertaken in this study using SET-MH data and shoreline analyses from aerial photography represent reliable alternative validation approaches. This validation provides suÿcient confidence to consider the combined implications of SLR and sediment supply for shoreline resilience.

Implications for Resilience of Coastal Wetlands to Sea-Level Rise

The mid- to late-Holocene sea-level history for this region is one of considerable stability with evidence indicating sea level was near present levels or up to 2 m higher since about 7 ka (Sloss et al., 2007; Lewis et al., 2013; Dougherty et al., 2019). Under these conditions of relatively stable sea levels for a sustained period, surface elevations would increase toward maximum water levels, or may exceed maximum water levels if sea level fell over the previous millennia. Substrates beyond the vertical range of accommodation space would continue to increase elevation with terrigenous sediment being supplied overland and/or facilitated by organic production within substrates, as theorized by Allen (2000). Vertical accommodation space would become increasingly limited and sedimentation would occur laterally, resulting in shoreline progradation. The broad low-lying swamps and fringing marshes of Westernport Bay at elevations less than 8 m, particularly near Kooweerup Swamp, suggest this mode of shoreline evolution (**Figure 8**).

Recent observed SLR has created new vertical accommodation space, and this study has confirmed that sedimentation was related to accommodation space over the past century. At all locations, sedimentation rates in the saltmarsh, where accommodation space was limited, closely corresponded to observed rates of SLR at the nearest tide gauge for the period 1981–2017, indicating that substrates asymptote toward elevations below maximum tide level that support saltmarsh. Mangrove cores exhibited sedimentation rates, in some cases, well beyond observed rates of SLR, implying ongoing infill of accommodation space and progradation, although this is likely to be at a slower rate than occurred under stable sea-level conditions. Shoreline analyses of the lower and upper limits of intertidal vegetation and the mangrove-saltmarsh transition confirmed sediment supply and ensuing sedimentation were relatively high at Kooweerup, French Island, and Rhyll. However, this pattern of accommodation space infill only remains possible should anticipated rates of SLR by 2100 remain low.

Numerous studies indicate that substrate elevation changes peak at positions across the intertidal zone where both the

addition of organic material from vegetation and sediments are high (Morris et al., 2002; Temmerman et al., 2003; Kirwan and Megonigal, 2013); and there is evidence from Westernport Bay that peak models may provide an improved representation of the relationship between rates of surface elevation gain and accommodation space (Rogers and Saintilan, 2021). The ability to quantify the behavior of surface elevation gain across the intertidal zone at each study site was limited due to the resource intensive nature of determining sedimentation rates and rates of surface elevation gain using ^{210}Pb-dating and SET-MH techniques, and analyses were limited to measurements from a single tidal position in the mangrove and saltmarsh at each study site. Accordingly, simple linear regression analyses were applied in this study. The implications of applying a linear model, rather than a peak model is likely to be an over-estimation of the resilience of substrates at higher elevations, that is in the saltmarsh, and potentially an under-estimation of the resilience of lower elevations, that is in the mangrove zone. However, validation of the model against aerial photography provides some confidence that the difference between using linear or peak models may be marginal.

Established linear relationships between sedimentation, surface elevation gain, and accommodation space indicate only positions lower in the tidal frame that are dominated by mangroves (i.e., above MTL and below MHWS) can maintain rates of sedimentation that match or exceed anticipated rates of SLR under a low SLR scenario providing sedimentation remains proportional to accommodation space. Under a high SLR scenario, mangrove shorelines are projected to retreat at all study sites. The outcome of either SLR scenario will be increasing dominance of mangrove as they retreat across substrates that currently support saltmarsh, leading to declines in saltmarsh vegetation extent. The expansion of mangrove into saltmarsh has already been documented along tidal creeks of Westernport Bay (Rogers et al., 2005b; Whitt et al., 2020) and more broadly where mangrove and saltmarsh co-occur in southeastern Australia (Saintilan and Williams, 1999). Should this change in vegetation distribution continue, as our linear relationships between sedimentation, surface elevation gain, and accommodation space imply, the intertidal vegetated platform will develop at an asymptote elevation where rates of surface elevation gain match rates of increase in accommodation space created by SLR. This will result in surface elevations transitioning to elevations that are considerably deeper than current monthly maximum water levels, as proposed by other models (Fagherazzi et al., 2012). Transition of substrates to this asymptote elevation will create conditions suitable for mangrove dominance and considerable landward incursion of tides will eventuate. Decoupling of accretion from inundation has been simulated to occur as a result of mangrove vegetation modulating tidal currents (Xie et al., 2020), and an increase in the dominance of mangrove may hasten this process and further reduce the resilience of higher elevation saltmarshes. As sediment supply and hydrodynamic conditions are variable across Westernport Bay, it is expected that equilibrium elevations will vary with higher asymptote surface elevations developing where sediment budgets are high. Modifications within catchments that alter hydrodynamic conditions and sediment supply will modify relationships between surface elevation gain and accommodation space, and any reductions in sediment deposition will hasten a transition to lower equilibrium elevations.

CONCLUSION

Sedimentation rates reported in this study are beyond threshold rates derived from paleoecological studies of vertical mangrove growth (Saintilan et al., 2020) and vertical adjustment of United Kingdom saltmarshes (Horton et al., 2018); however, it is not anticipated that an equivalent degree of surface elevation gain will occur due to processes of autocompaction. It remains feasible that established mature mangroves can sustain vertical substrate growth providing mineral and organic matter addition is suÿcient. Irrespective of the capacity for mangrove vertical growth at rates matching or exceeding SLR, saltmarsh substrates higher in the tidal frame will not be able to sustain the same rates of surface elevation gain due to lower rates of sedimentation. The resilience of saltmarsh will therefore be dependent upon landward space for saltmarsh retreat. There remains considerable low-elevation land at Kooweerup Swamp for saltmarsh retreat (**Figure 8**); though, decisions regarding the management of drains, floodgates, and bund walls are required to ensure tidal inundation occurs. Should engineering works (e.g., ring drains, bund walls, flood gates, buildings, elevated roadways, and culverts) and land-use decisions prevent landward tidal incursion, coastal squeeze of saltmarsh will occur (Rogers et al., 2016). In these circumstances, conservation reserves at French Island and Quail Island will become crucial sanctuaries for the highly diverse saltmarsh communities of Westernport Bay. Mangrove forests will have considerable space to encroach upon existing saltmarsh when SLR accelerates; however, planning decisions and management actions to establish setbacks and protect saltmarsh retreat pathways will be necessary to improve conservation outcomes for saltmarsh.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

KR, AZ, and NS undertook data collection and analysis. LM led the timer-series mapping. KR led the writing. All authors contributed to the article and approved the submitted version.

FUNDING

The Victorian Government provided financial support to establish this research in 2000 and subsequent funding in 2017 to maintain research continuity and deliver knowledge that assist with management of coastal wetlands of Westernport

Bay. KR received an Australian Research Council Future Fellowship (FT130100532) that provided financial support for measurements and sediment analyses from 2014 to 2018.

ACKNOWLEDGMENTS

We acknowledge the custodians of the Western Port area, the Bunurong (Boonerwrung) people of the Kulin Nation. We recognize the contribution of field and laboratory assistants in undertaking this work; over 20 years of analysis there are too many to mention but we remember every field trip fondly. Special thanks is given to Lawrance Ferns who has supported this research and the Victorian Government who has provided financial support with the initial establishment and recent measurements.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.807588/full#supplementary-material

REFERENCES

Allen, J. R. L. (2000). Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. *Q. Sci. Rev.* 19, 1155–1231. doi: 10.1016/S0277-3791(99)00034-7

Anisfeld, S. C., and Hill, T. D. (2012). Fertilization effects on elevation change and belowground carbon balance in a Long Island Sound tidal marsh. *Estu. Coasts* 35, 201–211. doi: 10.1007/s12237-011-9440-4

Appleby, P., and Oldfield, F. (1978). The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210Pb to the sediment. *Catena* 5, 1–8. doi: 10.1016/S0341-8162(78)80002-2

Arias-Ortiz, A., Masqué, P., Garcia-Orellana, J., Serrano, O., Mazarrasa, I., Marbà, N., et al. (2018). Reviews and syntheses: ^{210}Pb-derived sediment and carbon accumulation rates in vegetated coastal ecosystems–setting the record straight. *Biogeosciences* 15, 6791–6818. doi: 10.5194/bg-15-6791-2018

Boon, P. (2011). "Saltmarshes," in *Understanding the Western Port Environent: A summary of current knowledge and priorities for future research*, ed. S. G. O. Victoria (Melbourne: State Government of Victoria, Port Phillips and Westernport CMA, and Melbourne Water).

Breithaupt, J. L., Smoak, J. M., Byrne, R. H., Waters, M. N., Moyer, R. P., and Sanders, C. J. (2018). Avoiding timescale bias in assessments of coastal wetland vertical change. *Limnol. Oceanogr.* 63, S477–S495. doi: 10.1002/lno.10783

Breithaupt, J. L., Smoak, J. M., Smith, T. J. III, Sanders, C. J., and Hoare, A. (2012). Organic carbon burial rates in mangrove sediments: strengthening the global budget. *Glob. Cycles* 2012:26. doi: 10.1029/2012GB004375

Bureau of Meteorology. (2021). *Monthly sea levels for Stony Point* [Online]. Australian Government. Available: http://www.bom.gov.au/ntc/IDO71054/IDO71054SLD.shtml [Accessed 1 september 2021]

Cahoon, D. R., Lynch, J. C., Hensel, P., Boumans, R., Perez, B. C., Segura, B., et al. (2002). High-precision measurements of wetland sediment elevation: I. Recent improvements to the Sedimentation-Erosion Table. *J. Sediment. Res.* 72, 730–733. doi: 10.1306/020702720730

Dougherty, A. J., Thomas, Z. A., Fogwill, C., Hogg, A., Palmer, J., Rainsley, E., et al. (2019). Redating the earliest evidence of the mid-Holocene relative sea-level highstand in Australia and implications for global sea-level rise. *PLoS One* 14:e0218430. doi: 10.1371/journal.pone.0218430

Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenspergen, G. R., Temmerman, S., D'Alpaos, A., et al. (2012). Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. *Rev. Geophys.* 50:RG1002. doi: 10.1029/2011RG000359

FitzGerald, D. M., Hein, C. J., Connell, J. E., Hughes, Z. J., Georgiou, I. Y., and Novak, A. B. (2021). Largest marsh in New England near a precipice. *Geomorphology* 379:107625. doi: 10.1016/j.geomorph.2021.107625

Fox-Kemper, B., Hewitt, H. T., Xiao, C., Aðalgeirsdóttir, G., Drijfhout, S. S., Edwards, T. L., et al. (2021). "Ocean, Cryosphere and Sea Level Change," in *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, eds V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, et al. (Cambridge, MA: Cambridge University Press).

Hancock, G. J., Olley, J. M., and Wallbrink, P. (2001). "Sediment transport and accumulation in Western Port: Report on Phase I of a study determining the sources of sediment to Western Port," in *Technical Report 47/01*, (Canberra: CSIRO).

Harris, J., Hinwood, J., Marsden, M., and Sternberg, R. (1979). Water movements, sediment transport and deposition, Western Port, Victoria. *Mar. Geol.* 30, 131–161. doi: 10.1016/0025-3227(79)90010-0

Horton, B. P., Shennan, I., Bradley, S. L., Cahill, N., Kirwan, M., Kopp, R. E., et al. (2018). Predicting marsh vulnerability to sea-level rise using Holocene relative sea-level data. *Na. Comm.* 9, 1–7. doi: 10.1038/s41467-018-05080-0

Hughes, A., Prosser, I., Wallbrink, P., and Stevenson, J. (2003). "Suspended sediment and bedload budgets for the Western Port Bay Basin," in *CSIRO Land Water Technical Report: Technical reprt 4/03*, (Canberra: CSIRO).

Iurian, A., Millward, G., Blake, W., and Hernández, J. A. (2021). Fine-tuning of ^{210}Pb-based methods for dating vegetated saltmarsh sediments. *Q. Geochronol.* 62:101153. doi: 10.1016/j.quageo.2021.101153

Jervey, M. (1988). Quantitative geological modeling of siliciclastic rock sequences and their seismic expression. *SEPM Special Publ.* 1988, 47–69. doi: 10.2110/pec.88.01.0047

Kirwan, M. L., and Megonigal, J. P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504, 53–60. doi: 10.1038/nature12856

Kirwan, M. L., Temmerman, S., Skeehan, E. E., Guntenspergen, G. R., and Fagherazzi, S. (2016). Overestimation of marsh vulnerability to sea level rise. *Nature Climate Change* 6, 253–260. doi: 10.1038/nclimate2909

Krishnaswamy, S., Lal, D., Martin, J. M., and Meybeck, M. (1971). Geochronology of lake sediments. *Earth Planet. Sci. Lett.* 11, 407–414. doi: 10.1016/0012-821X(71)90202-0

Kumbier, K., Hughes, M. G., Rogers, K., and Woodroffe, C. D. (2021). Inundation characteristics of mangrove and saltmarsh in micro-tidal estuaries. *Est. Coast. Shelf Sci.* 261:107553. doi: 10.1016/j.ecss.2021.107553

Lee, R. (2011). "Physical and chemical setting," in *Understanding the Western Port Environent: A summary of current knowledge and priorities for future research*, ed. S. G. O. Victoria (Melbourne: State Government of Victoria, Port Phillips and Westernport CMA, and Melbourne Water).

Lewis, C. J. E., Baldock, J. A., Hawke, B., Gadd, P. S., Zawadzki, A., Heijnis, H., et al. (2019). Impacts of land reclamation on tidal marsh 'blue carbon'stocks. *Sci. Total Env.* 672, 427–437. doi: 10.1016/j.scitotenv.2019.03.345

Lewis, S. E., Sloss, C. R., Murray-Wallace, C. V., Woodroffe, C. D., and Smithers, S. G. (2013). Post-glacial sea-level changes around the Australian margin: a review. *Q. Sci. Rev.* 74, 115–138. doi: 10.1016/j.quascirev.2012.09.006

Marx, S. K., Knight, J. M., Dwyer, P. G., Child, D. P., Hotchkis, M. A., and Zawadzki, A. (2020). Examining the response of an eastern Australian mangrove forest to changes in hydro-period over the last century. *Est. Coast. Shelf Sci.* 241:106813. doi: 10.1016/j.ecss.2020.106813

Mogensen, L. A., and Rogers, K. (2018). Validation and Comparison of a Model of the Effect of Sea-Level Rise on Coastal Wetlands. *Sci. Rep.* 8:1369. doi: 10.1038/s41598-018-19695-2

Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B., and Cahoon, D. R. (2002). Responses of coastal wetlands to rising sea-levels. *Ecology* 83, 2869–2877. doi: 10.1890/0012-9658(2002)083[2869:ROCWTR]2.0.CO;2

Nolte, S., Koppenaal, E. C., Esselink, P., Dijkema, K. S., Schuerch, M., Groot, A. V., et al. (2013). Measuring sedimentation in tidal marshes: a review on methods and their applicability in biogeomorphological studies. *J. Coast. Conserv.* 17, 301–325. doi: 10.1007/s11852-013-0238-3

Oppenheimer, M., Glavovic, B., Hinkel, J., van de Wal, R., Magnan, A. K., Abd-Elgawad, A., et al. (2019). "Chapter 4: Sea level rise and implications for low lying islands, coasts and communities," in *IPCC special report on the ocean and cryosphere in a changing climate*, (Intergovenmental Panel on Climate Change).

Osland, M. J., Feher, L. C., Anderson, G. H., Vervaeke, W. C., Krauss, K. W., Whelan, K. R., et al. (2020). A tropical cyclone-induced ecological regime shift: Mangrove forest conversion to mudflat in Everglades National Park (Florida. USA). *Wetlands* 40, 1445–1458. doi: 10.1007/s13157-020-01291-8

Pethick, J. S. (1981). Long-term accretion rates on tidal salt marshes. *J. Sed. Res.* 51, 571–577. doi: 10.1306/212F7CDE-2B24-11D7-8648000102C1865D

Reef, R., Spencer, T., Moller, I., Lovelock, C. E., Christie, E. K., McIvor, A. L., et al. (2017). The effects of elevated CO_2 and eutrophication on surface elevation gain in a European salt marsh. *Glob. Chang. Biol.* 23, 881–890. doi: 10.1111/gcb.13396

Rogers, K. (2021). Accommodation space as a framework for assessing the response of mangroves to relative sea-level rise. *Sing. J. Tro. Geogr.* 42, 163–183. doi: 10.1111/sjtg.12357

Rogers, K., Boon, P. I., Branigan, S., Duke, N. C., Field, C. D., Fitzsimons, J. A., et al. (2016). The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. *Mar. Pol.* 72, 139–155. doi: 10.1016/j.marpol.2016.06.025

Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., et al. (2019). Wetland carbon storage controlled by millennialscale variation in relative sea-level rise. *Nature* 567, 91–95. doi: 10.1038/s41586-019-0951-7

Rogers, K., and Saintilan, N. (2021). Processes Influencing Autocompaction Modulate Coastal Wetland Surface Elevation Adjustment With Sea-Level Rise. *Front. Mar. Sci.* 8:879. doi: 10.3389/fmars.2021.694039

Rogers, K., Saintilan, N., and Cahoon, D. (2005a). Surface Elevation Dynamics in a Regenerating Mangrove Forest at Homebush Bay, Australia. *Wetl. Ecol. Manage.* 13, 587–598. doi: 10.1007/s11273-004-0003-3

Rogers, K., Saintilan, N., and Heijnis, H. (2005b). Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence and sea level rise. *Estuaries* 28, 551–559. doi: 10.1007/BF02696066

Rogers, K., Wilton, K. M., and Saintilan, N. (2006). Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Est. Coast. Shelf Sci.* 66, 559–569. doi: 10.1016/j.ecss.2005.11.004

Ruiz-Fernández, A. C., Sanchez-Cabeza, J.-A., Serrato de la Pena, J. L., Perez-Bernal, L. H., Cearreta, A., Flores-Verdugo, F., et al. (2016). Accretion rates in coastal wetlands of the southeastern Gulf of California and their relationship with sea-level rise. *Holocene* 26, 1126–1137. doi: 10.1177/0959683616632882

Saintilan, N., Khan, N., Ashe, E., Kelleway, J., Rogers, K., Woodroffe, C. D., et al. (2020). Thresholds of mangrove survival under rapid sea level rise. *Science* 368, 1118–1121. doi: 10.1126/science.aba2656

Saintilan, N., and Williams, R. J. (1999). Mangrove Transgression into Saltmarsh Environments in South-East Australia. *Glob. Ecol. Biogeogr.* 8, 117–124. doi: 10.1046/j.1365-2699.1999.00133.x

Sanders, C. J., Santos, I. R., Maher, D. T., Breithaupt, J. L., Smoak, J. M., Ketterer, M., et al. (2016). Examining 239+ 240Pu, 210Pb and historical events to determine carbon, nitrogen and phosphorus burial in mangrove sediments of Moreton Bay, Australia. *J. Env. Radioact.* 151, 623–629. doi: 10.1016/j.jenvrad.2015.04.018

Sloss, C. R., Murray-Wallace, C. V., and Jones, B. G. (2007). Holocene sea-level change on the southeast coast of Australia: a review. *Holocene* 17, 999–1014. doi: 10.1177/0959683607082415

Smith, J. N. J. J. O. E. R. (2001). Why should we believe 210Pb sediment geochronologies? *J. Environ. Radioact.* 55, 121–123. doi: 10.1016/S0265-931X(00)00152-1

Swales, A., Bentley, S. J., and Lovelock, C. E. (2015). Mangrove-forest evolution in a sediment-rich estuarine system: opportunists or agents of geomorphic change? *Earth Surf. Proc. Landf.* 40, 1672–1687. doi: 10.1002/esp.3759

Temmerman, S., Govers, G., Wartel, S., and Meire, P. (2003). Spatial and temporal factors controlling short-term sedimentation in a salt and freshwater tidal marsh, Scheldt estuary, Belgium, SW Netherlands. *Earth Surf. Proc. Landf.* 28, 739–755. doi: 10.1002/esp.495

Water Technology (2014a). *Western Port Local Coastal Hazard Assessment: Report 04 (R04) – Inundation Hazards*. Melbourne: Melbourne Water.

Water Technology (2014b). *Western Port Local Coastal Hazard Assessment: Report 05 (R05) – Erosion Hazards*. Melbourne: Melbourne Water.

Whelan, K., Smith, T., Cahoon, D., Lynch, J., and Anderson, G. (2005). Groundwater control of mangrove surface elevation: Shrink and swell varies with soil depth. *Est. Coasts* 28, 833–843. doi: 10.1007/BF02696013

Whelan, K. R. T., Smith, T. J., Anderson, G. H., and Ouellette, M. L. (2009). Hurricane Wilma's Impact on Overall Soil Elevation and Zones Within the Soil Profile in a Mangrove Forest. *Wetlands* 29, 16–23. doi: 10.1672/08-125.1

Whitt, A. A., Coleman, R., Lovelock, C. E., Gillies, C., Ierodiaconou, D., Liyanapathirana, M., et al. (2020). March of the mangroves: drivers of encroachment into southern temperate saltmarsh. *Est. Coast. Shelf Sci.* 240:106776. doi: 10.1016/j.ecss.2020.106776

Woodroffe, C. D., and Murray-Wallace, C. V. (2012). Sea-level rise and coastal change: the past as a guide to the future. *Quat. Rev.* 54, 4–11. doi: 10.1016/j.quascirev.2012.05.009

Woodroffe, C. D., Rogers, K., McKee, K. L., Lovelock, C. E., Mendelssohn, I., and Saintilan, N. (2016). Mangrove sedimentation and response to relative sea-level rise. *Annu. Rev. Mar. Sci.* 8, 243–266. doi: 10.1146/annurev-marine-122414-034025

Xie, D., Schwarz, C., Brückner, M. Z., Kleinhans, M. G., Urrego, D. H., Zhou, Z., et al. (2020). Mangrove diversity loss under sea-level rise triggered by bio-morphodynamic feedbacks and anthropogenic pressures. *Env. Res. Lett.* 15:114033. doi: 10.1088/1748-9326/abc122

Yeates, A. G., Grace, J. B., Olker, J. H., Guntenspergen, G. R., Cahoon, D. R., Adamowicz, S., et al. (2020). Hurricane Sandy effects on coastal marsh elevation change. *Est. Coasts* 43, 1640–1657. doi: 10.1007/s12237-020-00758-5

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's Note: All claims expressed in this article are solely those of the authors and do not necessarily represent those of their aÿliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Copyright © 2022 Rogers, Zawadzki, Mogensen and Saintilan. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

Estuaries and Coasts
https://doi.org/10.1007/s12237-023-01267-x

SPECIAL ISSUE: WETLAND ELEVATION DYNAMICS

Vertical Accretion Trends in Australian Tidal Wetlands

Neil Saintilan[1] · Yujie Sun[1] · Catherine E. Lovelock[2] · Kerrylee Rogers[3] · Madeline Goddard[4] · Lindsay B. Hutley[4] · Jeffrey Kelleway[3] · Luke Mosley[5] · Sabine Dittmann[6] · Nicole Cormier[1] · Kirti K. Lal[3,7] · Alice Jones[8]

Received: 24 April 2023 / Revised: 13 August 2023 / Accepted: 19 August 2023
© The Author(s) 2023

Abstract

Australian tidal wetlands differ in important respects to better studied northern hemisphere systems, an artefact stable to falling sea levels over millennia. A network of Surface Elevation Table-Marker Horizon (SET-MH) monitoring stations has been established across the continent to assess accretionary and elevation responses to sea-level rise. This network currently consists of 289 SET-MH installations across all mainland Australian coastal states and territories. SET-MH installations are mostly in mangrove forests but also cover a range of tidal marsh and supratidal forest ecosystems. Mangroves were found to have higher rates of accretion and elevation gain than all the other categories of tidal wetland, a result attributable to their lower position within the tidal frame (promoting higher rates of accretion) higher biomass (with potentially higher rates of root growth), and lower rates of organic decomposition. While Australian tidal marshes in general show an increase in elevation over time, in 80% of locations, this was lower than the rate of sea-level rise. High rates of accretion did not translate into high rates of elevation gain, because the rate of subsidence in the shallow substrate increased with higher accretion rates ($r^2 = 0.87$). The Australian SET-MH network, already in many locations spanning two decades of measurement, provides an important benchmark against which to assess wetland responses to accelerating sea-level rise in the decades ahead.

Keywords Accretion · Elevation gain · Sea-level rise · Tidal marsh · Mangrove

Introduction

Tidal wetlands (mangroves, tidal marshes and supratidal forests) are important coastal zone habitats. These three communities differ in structural characteristics and zonation in relation to the tidal frame. In Australia, mangroves (typically Rhizophoraceae and Avicenniaceae) generally grow between mean sea level and mean high water spring tides (Saintilan et al. 2019). Tidal marshes (or saltmarshes) consist of low-growing herbs and grasses (common species include *Sporobolus virginicus*, *Sarcocornia quinqueflora*, *Samolus repens*, *Triglochin striata*, *Suaeda australis*), salt bushes (of the genera *Tecticornia*, *Atriplex*) and in more brackish to freshwater environments rushes (e.g. *Juncus*, *Phragmites*). Australian tidal marshes are more frequently found in upper intertidal environments, inundated by spring tides (Saintilan et al. 2019), and extending beyond highest astronomical tide where substrate conditions are favourable (i.e. freshwater supply and saline substrate). Tidal forests (predominantly of the genera *Casuarina* and/or *Melaleuca*) are tolerant of infrequent tidal inundation. They occur between mean high water spring tidal levels through to elevations at or above the highest astronomical tides (Kelleway et al. 2021).

Communicated by Meagan Eagle

✉ Neil Saintilan
neil.saintilan@mq.edu.au

[1] School of Natural Sciences, Macquarie University, Sydney, Australia

[2] School of Biological Sciences, University of Queensland, Brisbane, Australia

[3] School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, Australia

[4] Research Institute of the Environment and Livelihoods, Faculty of Science, Technology and Environment, Charles Darwin University, Darwin, Australia

[5] School of Agriculture, Food and Wine, University of Adelaide, Adelaide, Australia

[6] College of Science and Engineering, Flinders University, Adelaide, Australia

[7] Science, Economics and Insights Division, NSW Department of Planning and Environment, Lidcombe, Australia

[8] School of Biological Sciences and Environment Institute, University of Adelaide, Adelaide, Australia

Published online: 27 September 2023

Australian mangroves, tidal marshes and supratidal forests make important contributions to a range of ecosystem services (Kelleway et al. 2017; Hagger et al. 2022). The disproportionate contribution of these habitats to natural carbon sequestration has been demonstrated for all three habitats, and they are the subject of emerging opportunities for blue carbon emission reductions (Kelleway et al. 2020; Lovelock et al. 2022). The contribution of mangroves and tidal marshes to estuarine fisheries has also been demonstrated (Mazumder et al. 2006, 2011; Sheaves et al. 2015; Prahalad et al. 2019). They are important habitat for a number of endangered and vulnerable species of birds and mammals (Gonsalves et al. 2013; Kelleway et al. 2017; Sievers et al. 2019).

The continued provision of the ecosystem services from coastal wetland environments is threatened by climate change. Several climate drivers influence survival and competitive interactions in coastal wetlands, including temperature, elevated carbon dioxide concentrations, precipitation and sea-level rise (McKee et al. 2012). The proliferation of mangroves in higher latitudes, where they compete with tidal marshes, has been demonstrated on five continents and linked to all of these drivers (Saintilan et al. 2014). In southeast Australia, tidal marsh land cover has been converting to mangrove land cover in most estuaries where long-term habitat dynamics have been studied, and the proportion of decline is consistent with sea-level trends over the period of observation (Saintilan et al. 2014). Tidal forest transitions to tidal marsh have also been observed, and the contribution of tidal forest habitats to carbon sequestration in Australia has only recently been considered (Kelleway et al. 2021).

While vulnerable to sea-level rise by virtue of their position in relation to tidal inundation, tidal wetlands can build elevation relative in response to sea-level rise, ameliorating the impacts of increased water level (Schuerch et al. 2018). Indeed, the effect of sea-level rise and increased hydroperiod is to increase the rate of sedimentation, which is proportional to the depth and duration of inundation. Also, increased frequency of inundation can promote plant growth, which may be limited higher in the tidal frame by higher porewater salinities and/or and lower nutrient concentrations (Feller et al. 2003). Increased biomass production contributes to the building of root volume, an important component of wetland elevation gain (Morris et al. 2002, 2016; Rogers et al. 2005a, b; Ola et al. 2018). Also, the more anaerobic conditions created by increased inundation can lead to greater carbon preservation, enhancing the blue carbon efficacy of tidal wetlands (Rogers et al. 2019).

Increases in water level may be balanced by increases in the elevation of the marsh, a negative feedback which may lead to marsh equilibrium with sea-level rise. Under this model, marshes rise or fall in the tidal frame to an optimal position (Pethick 1981; Cahoon et al. 2019), Fig. 1). Modelling based on accretion responses in tidal marshes has suggested a robust response even to comparably high rates of sea-level rise given sufficient sediment supply and deposition, prompting the suggestion that the vulnerability of tidal marshes has been overestimated in previous studies (Kirwan et al. 2016; Moritsch et al. 2022). However, the extent and efficacy of negative feedbacks between sea-level rise and vertical accretion are still poorly understood. Recent syntheses from palaeo-stratigraphic observations of marsh responses to sea-level rise during the early Holocene, when rates of RSLR were higher than today, suggest that while coastal wetlands can track low rates of sea-level rise, this capacity is lost under rates exceeding 5–7 mm per year (Horton et al. 2018; Saintilan et al. 2020).

Contemporary observations of marsh responses to sea-level rise derived from accretion records (derived from radiometric and artificial markers) provide information on rates of sediment accumulation, but the extent to which this translates into elevation gain is critically important in determining marsh survival. Recently, deposited sediment is subject to autocompaction, and ongoing accretion contributes to the autocompaction of sediment below the surface (termed upper-level subsidence). Upper-level subsidence of accreting soil compromises the contribution of accretion to surface elevation gain and may be a key determinant of the resilience of wetlands under sea-level rise (Rogers and Saintilan 2021; Saintilan et al. 2022).

The Surface Elevation Table-Marker Horizon (SET-MH) technique measures the accretion and elevation of wetlands (Cahoon et al. 2000). A survey benchmark rod serves as a fixed benchmark against which relative changes in the elevation of the wetland surface are measured; these changes can be converted to absolute measurements when calibrated against a fixed datum, such as the Australian height datum. The rod is driven deep into the wetland substrate (up to 30 m), and measurements are periodically made using a detachable arm, from which pins are lowered to the wetland surface. As the wetland accretes and the elevation of the substrate surface increases, the pins appear higher against the level arm.

Two SET designs have been commonly deployed globally. The original SET consisted of an aluminium tube, manually driven into the wetland substrate to a maximum depth of 8 m; the depth was largely delimited by the length of aluminium tube of the depth to basement. An insert tube was concreted into the top of the SET pole, upon which the SET arm was attached (Fig. 2). A subsequent innovation of the SET utilised a solid stainless steel rod as the SET benchmark, allowing far greater depth of installation (Cahoon et al. 2002). This type of SET is termed the rod-SET, or rSET, and a lighter linear arm is used (Fig. 2). At the time of installation, feldspar marker horizons are often laid on the wetland surface, and sediment accretion can be

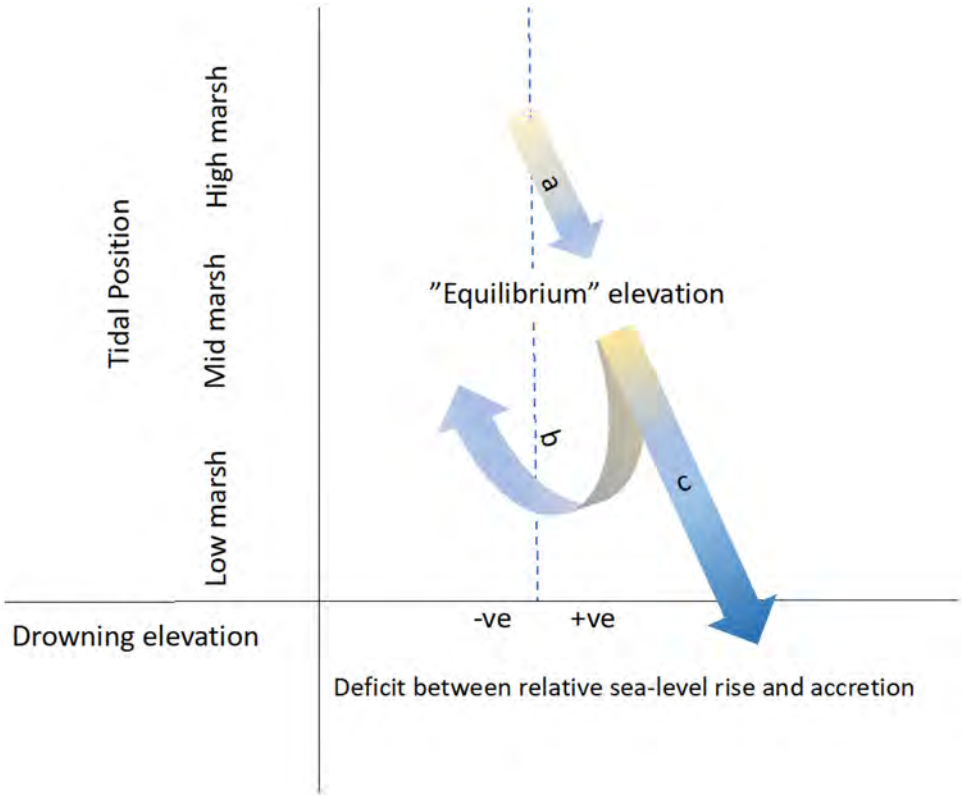


Fig. 1 Marsh equilibrium model for coastal wetlands experiencing sea-level rise. A deficit between marsh elevation gain and relative sea-level rise (RSLR) decreases the position of a marsh in the tidal frame (trajectory "a"), which enhances accretion, lowering the rate of relative sea-level rise and restoring the marsh to an optimal position in the tidal frame (trajectory "b"). However, if the position of the marsh becomes too low, or this feedback is too weak, anoxic conditions lead to marsh drowning (trajectory "c"), rapid elevation loss and conversion to open water

determined by measuring sediment accumulation above the horizon over time. The accretion of sediment above the feldspar layer is gauged by sampling shallow cores in the feldspar plots. These two measurements combined are known as the Surface Elevation Table-Marker Horizon technique or SET-MH. Upper-level subsidence is inferred as the difference between vertical accretion measured against the feldspar marker horizon and elevation gain as measured from the SET benchmark rod. This defines subsidence occurring between the surface and the base of the benchmark rod.

Fig. 2 Measuring the rod Surface Elevation Table (left) and the original Surface Elevation Table (right). (Credit: Catherine Lovelock; Neil Saintilan)

At Comerong Island, New South Wales, shallow rSETS (Cahoon et al. 2002) were also installed to measure the contribution of root zone processes to surface elevation trends.

SET-MH measurements are often compared to water level changes at nearby tide gauges (Fig. 3). If the rate of water level increase exceeds the rate of elevation gain over the same period (termed the period of observation or contemporaneous sea-level rise), then the location at which SET measurements are taken may be subject to an elevation deficit; other locations, particularly those lower in the tidal frame, may not exhibit an elevation deficit (Morris 2006). Locations within a wetland that exhibit an elevation deficit are transitioning to lower positions within the tidal frame, where they may equilibrate with sea-level rise or may continue their trajectory towards submergence (Fagherazzi et al. 2020). Over time, the fate of such wetlands will depend on the timing and strength of the negative feedbacks between water level rise and vertical accretion described previously. For this reason, long-term SET-MH measures are essential in order to capture feedback responses that may occur over decadal time periods. Syntheses of SET-MH observations usually reject observation periods of less than 3 years.

To date, approximately 1000 SET-MH stations have been installed in over 40 countries worldwide (https://www.usgs.gov/centers/eesc/science/surface-elevation-table). Extensive regional SET networks include Europe (UK, the European North Sea and Mediterranean coastlines), US Gulf of Mexico and East Coast regions, South Africa, Central America and the Caribbean, Asia (Singapore, Thailand, China, Vietnam, Indonesia), Oceania (New Zealand, Micronesia) and Australia. The technique has been described as the "global standard" for wetland monitoring against sea-level rise (Webb et al. 2013) and subject to important regional and global-scale synthesis reviews (Lovelock et al. 2015; Jankowski et al. 2017; Saintilan et al. 2022). While significant gaps in global coverage remain (Equatorial Africa, South America, Arctic coastline, Middle East), the network encompasses a range of bioclimatic zones, tidal ranges and rates of relative sea-level rise.

The Australian SET-MH network has grown over two decades to include at least 289 installations across 30 geographic locations. Habitats represented in the network include mangrove (temperate and subtropical forests of *Avicennia* and tropical mangroves dominated by *Rhizophora* and *Bruguiera*), saltmarshes (incorporating the saltbushes, brackish rushes and herbaceous saltmarsh) and more recently supratidal forests and some tidal restoration sites. The network covers five Australian states and territories, spanning geomorphic settings including macrotidal estuaries, drowned river valleys, microtidal barrier estuaries and coral islands, as well as restoration sites. Data from this network has hitherto never been collated or analysed.

The SET-MH technique has been extensively applied to inform estuary-scale models of sea-level rise in coastal

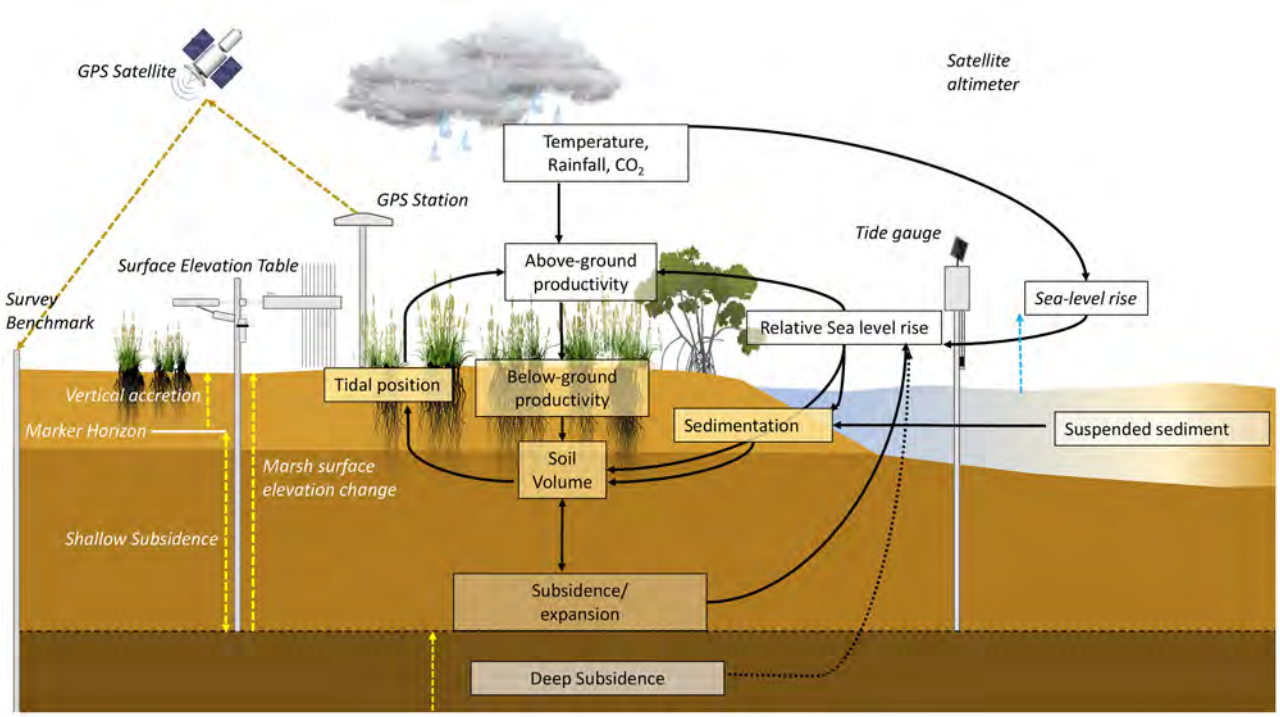


Fig. 3 Operation of the SET-MH benchmark station, illustrating factors contributing to soil volume change

Table 1 Data custodians within the Australian SET-MH network

Custodian	Sites (see Table 2 for coordinates)	Contact
Prof Kerrylee Rogers, University of Wollongong; Prof Neil Saintilan, Macquarie University	Tweed River, Tomago Wetland, Kooragang Island, Berowra Creek, Marramarra Creek, Homebush Bay, Minnamurra River, Currambene Creek, Cararma Inlet, Kooweerup, Quaill Island, Rhyll, French Island	kerrylee@uow.edu.au, neil.saintilan@mq.edu.au
Professor Kerrylee Rogers, University of Wollongong; Dr Kirti K. Lal, NSW Department of Planning and Environment	Comerong Island	kerrylee@uow.edu.au, kirti.lal@environment.nsw.gov.au
Prof Catherine Lovelock, University of Queensland	Tinchi, Nundah, Amity South, Adams, Halloran, Daintree River, Yandina, Maroochy, Giralia, Culham Inlet, Oyster Harbour, Leschenault, Peel-Harvey Inlet, Swan River	c.lovelock@uq.edu.au
Ms Madeline Goddard, Prof Lindsay Hutley, Charles Darwin University	Darwin Harbour	Lindsay.Hutley@cdu.edu.au
Dr Jeffrey Kelleway, University of Wollongong	Corner Inlet, Towra Point	jeffreyk@uow.edu.au
A/Prof Sarah Hamylton, University of Wollongong	Woody Island (Great Barrier Reef)	shamylto@uow.edu.au
A/Prof Luke Mosley, University of Adelaide	Dry Creek salt field	luke.mosley@adelaide.edu.au
Dr Alice Jones, University of Adelaide	Torrens Island, Mutton Cove, Cowleds Landing, Tumby Bay, Acraman Creek	alice.jones01@adelaide.edu.au

lowlands in New South Wales (Oliver et al. 2012; Traill et al. 2011; Rogers et al. 2012), Victoria (Rogers and Saintilan 2021; Rogers et al. 2022) and Queensland (Traill et al. 2011; Runting et al. 2017; Mazor et al. 2021). However, greater insight can be gained by the collation and synthesis of information from SETs covering a range of hydrological and geomorphic settings (Saintilan et al. 2022), as a means of identifying important biological and environmental controls. We purposed therefore to (i) compile the existing SET-MH dataset for Australia, including the location of SET-MH stations, data custodian, the length of record and existing data, while identifying gaps; (ii) compile ancillary environmental data relevant to the interpretation of SET-MH trends, including climate, geomorphic setting, tide range, dominant species and the rate of local sea-level rise for the period of SET-MH measurement; and (iii) conduct analyses of SET-derived tidal wetland elevation trends in relation to key climatic and environmental drivers, including the efficacy of restoration (Table 1).

Methods

Surface Elevation Tables were first installed in Australia in 2000–2001. With assistance from the US Geological Survey, SET-MH stations were installed in 2000–2001 in New South Wales (Tweed River, Hunter River, Hawkesbury River, Parramatta River, Minnamurra River, Jervis Bay) and in Victoria (Westernport Bay). SET-MH installation in Queensland commenced in 2007, initially in Moreton Bay, expanding to the Daintree River in 2014 and most recently at the most poleward extent of mangroves at Corner Inlet, Victoria (2019) and Woody Island, of the Low Isles within the Great Barrier Reef lagoon (2022). Installation of SET-MH stations in Darwin Harbour commenced in 2016 funded under the Darwin Harbour Integrated Marine Monitoring and Research Program (IMMRP). In Western Australia, SET-MH stations were installed in the Exmouth Gulf in 2011 and in the saltmarshes of the south of the state in 2021. In South Australia, SETs were installed in 2017 within a tidal restoration site in a decommissioned salt production pond (Dittmann et al. 2019), as well as two mangrove sites close to Adelaide, with further SET-MHs installed in the west of the state since 2020.

Data were compiled with the assistance of SET-MH data custodians as set out in Table 2. Variables provided by data custodians included sampling location, the date of the initial reading and the most recent observations and the dominant species found at the site. Data custodians also provided the rate of elevation gain (in millimetres per year) as the linear trend of the SET pin measurements for the duration of the (r)SET-MH record and sediment accretion (in millimetres per year) as the linear trend of the MH observations for the duration of the accretion record (in some but not all cases). For each (r)SET, relative pin height was calculated by subtracting baseline pin height from all subsequent readings. Relative pin heights were averaged for each measurement date hierarchically within each SET arm position and then across positions to integrate small-scale spatial variation in surface elevation across the measurement area. At the time of publication, the short length of record for tidal forest SETs precluded their incorporation into the analysis.

Table 2 Location and sampling times of Australian SET-MH stations. Site numbers correspond to those indicated in Fig.4

Site	Coordinates	#SETs	First sample date (DD-MM-YYYY)	Last sample date (DD-MM-YYYY)	# years measured
New South Wales					
1. Ukerebagh Island (Tweed River)	−28.19, 153.55	3 mangrove, 3 saltmarsh	30–11-2000	23–01-2018	17.16
2. Tomago (Hunter River)	−32.82, 151.77	9 saltmarsh (6 restoration, 3 control)	01–10-2014	02–02-2023	8.34
3. Kooragang Island (Hunter River)	−32.85, 151.72	3 mangrove, 9 mixed, 3 saltmarsh	29–01-2002	03–02-2016	14.02
4. Marramarra Creek (Hawkesbury River)	−33.52, 151.11	3 mangrove, 3 rush	02–04-2003	12–04-2010	7.05
5. Berowra Creek (Hawkesbury River)	−33.62, 151.12	3 mangrove, 3 rush	11–12-2002	02–09-2017	14.74
6. Homebush Bay (Sydney Harbour)	−33.84, 151.07	3 mangrove, 3 mixed, 3 saltmarsh	15–08-2000	11–09-2020	20.09
7. Towra Point (Botany Bay)	−34.02, 151.16	5 tidal forest, 2 rush, 2 saltmarsh, 3 mangrove	15–04-2022	08–11-22	0.57
8. Minnamurra River	−34.62, 150.84	3 mangrove, 3 saltmarsh	11–09-2001	15–03-2017	15.52
9. Comerong Island (Shoalhaven River)	−34.88°, 150.73°	Deep: 6 mangrove, 3 saltmarsh Shallow: 4 mangrove, 2 saltmarsh	01–10-2015	15–09-2022	6.96
10. Cararma Inlet (Jervis Bay)	−34.98, 150.78	3 mangrove, 3 saltmarsh	02–08-2001	04–03-2020	18.6
11. Currambene Creek (Jervis Bay)	−35.02, 150.66	3 mangrove 2 rush, 1 saltmarsh, 3 mixed	03–02-2001	03–03-2020	19.09
Victoria					
12. Kooweerup (Westernport Bay)	−38.22, 151.42	3 mangrove, 3 saltbush	18–10-2000	12–11-2019	19.08
13. Quaill Island (Westernport Bay)	−38.23, 145.31	3 mangrove, 3 saltbush	16–10-2000	14–11-2019	19.09
14. Rhyll (Westernport Bay)	−38.46, 145.28	3 mangrove, 3 saltmarsh	17–10-2000	13–11-2019	19.08
15. French Island (Westernport Bay)	−38.31, 145.43	3 mangrove, 3 saltbush restoration	15–10-2000	18–03-2022	21.4
16. Corner Inlet	−38.91, 146.30	6 tidal forest, 3 mangrove, 3 saltmarsh	14–03-2020	18–03-2022	1.01
Queensland					
17. Woody Island (Great Barrier Reef)	−16.38, 145.57	9 mangrove	n/a	n/a	n/a
18. Daintree River	−16.29, 145.40	18 mangrove	10–08-2014	03–09-2021	7.07
19. Yandina	−26.56, 153.04	6 mangrove, 3 tidal forest	03–07-2020	n/a	n/a
20. Maroochy	−26.61, 153.05	3 mangrove	25–08-2020	n/a	n/a
21. Tinchi	−27.29, 153.04	3 mangrove, 3 saltmarsh	16–03-2007	11–10-2018	11.58
22. Nundah	−27.29, 153.04	3 mangrove, 3 saltmarsh	19–03-2007	18–10-2018	11.59
23. Amity South	−27.43, 153.43	3 mangrove, 3 saltmarsh	22–03-2007	13–11-2018	11.65
24. Amity North	−27.43, 153.44	3 mangrove, 3 saltmarsh	22–03-2007	13–11-2018	11.65
25. Adams	−27.52, 153.43	3 mangrove, 3 saltmarsh	13–06-2007	08–11-2018	11.43
26. Halloran	−27.56, 153.29	3 mangrove, 3 saltmarsh	13–06-2007	14–11-2018	11.43
Northern Territory					
27. Darwin Harbour	−12.48, 130.91	39 mangrove	11–07-2016	24–12-2021	5.45
Western Australia					
28. Giralia	−22.49, 114.32	6 mangrove, 6 hypersaline flat	15–08-2011	15/06/2018	6.84
29. Culham Inlet	−33.92, 120.05	3 saltmarsh	15–04-2021	n/a	n/a
30. Oyster Harbour	−34.92, 117.97	3 saltmarsh	15–04-2021	n/a	n/a

Table 2 (continued)

Site	Coordinates	#SETs	First sample date (DD-MM-YYYY)	Last sample date (DD-MM-YYYY)	# years measured
31. Leshanault	−33.21, 115.68	6 saltmarsh	15–04-2021	n/a	n/a
32. Peel-Harvey Inlet	−32.75, 115.69	3 saltmarsh	15–04-2021	n/a	n/a
33. Swan River	−31.92, 115.95	3 saltmarsh	15–04-2021	n/a	n/a
South Australia					
34. Dry Creek salt field	−34.72, 138.51	2 saltmarsh restoration	10/10/2017	23/06/2022	4.70
34. Dry Creek salt field	−34.72, 138.51	2 saltmarsh restoration	21/10/2021	23/06/2022	0.67
35. Torrens Island	−34.78, 138.53	1 saltmarsh	18/06/2017	07/11/2022	5.39
36. Mutton Cove	−34.78, 138.51	2 mangrove	18/06/2017	07/11/2022	5.39
37. Cowleds Landing	−33.10, 137.52	1 saltbush	08/09/2020	09/12/2022	2.25
38. Tumby Bay	−34.40, 136.11	1 saltmarsh	10/09/2020	24/01/2023	2.37
39. Acraman	−32.44, 134.04	1 saltmarsh	27/10/2021	21/02/2023	1.32

Rainfall and temperature variables were sourced from the Bureau of Meteorology (http://www.bom.gov.au/climate/data/), and sea-level trends were calculated from the closest tide gauge in the Australian Baseline Sea Level Monitoring Network (http://www.bom.gov.au/oceanography/projects/abslmp/abslmp.shtml). A full list of variable names and their explanations is provided in Table 5 in the Appendix. Linear regression models were used to test relationships between accretion, elevation gain, shallow subsidence and water level. Paired t-tests were used to compare elevation trends between mangrove and tidal marsh SETs.

Sites were classified according to the geomorphic units using a typology that defines estuarine settings on the basis of dominance of river, wave and tide energy (Dalrymple et al. 1992) and using the Roy et al. (2001) model of estuary classification for southeast Australian estuaries: barrier estuarine (estuaries sheltered behind sand barriers along wave-dominated coastlines), river delta (sites associated with river systems where fluvial sedimentation is building active deltas), drowned river valley (sites of meso-macrotidal range in which tidal deposition and erosion are dominant processes), coral island (sites associated with coral reef barriers) and marine embayment (sites protected from oceanic waves by shoreline configuration but for which fluvial influence is minor). In three cases, SET-MH installations occurred in sites historically or actively subject to tidal marsh restoration. In two cases, these consisted of former commercial salt evaporation ponds subject to tidal restoration: French Island, Westernport, abandoned early in the twentieth century, and at Dry Creek, South Australia, where tidal restoration commenced in 2017. At the Tomago Wetland, New South Wales, tidal reinstatement occurred in 2015, with the intention of restoring coastal wetlands to an agricultural floodplain protected by flood control works. Many of the sites have also been modified by humans, with drainage, ditching and infill common at the margins of coastal wetlands, or wetlands were formally used for grazing purposes.

Results

Location and Site Characteristics

The Australian SET network currently consists of 289 documented benchmark installations distributed across 31 sites in all the mainland coastal states and territories (Table 1, Fig. 1). While SET installations are numerically clustered around the major SE Australian population centres of Adelaide, Melbourne, Sydney, Newcastle and Brisbane, the network has expanded in recent years to several locations in Western Australia and the Tropical north (Darwin Harbour, Daintree, and Woody Island in the Great Barrier Reef). The Australian SET network encompasses a range of geomorphic settings; it is dominated by sites in river deltas, marine embayments and drowned river valleys (Table 3, Fig. 4).

Table 3 The number of SET-MH stations falling within defined geomorphic settings and habitat types

	Low Saltmarsh/ salt flat	Rush	Saltbush	Mangrove	Tidal forest	Total
Barrier estuary	36	3	0	21	0	69
Drowned river valley	10	6	0	51	5	72
Marine embayment	9	9	12	30	6	70
River delta	27	0	0	48	3	78
Coral island	0	0	0	9	0	9
Total	86	18	12	159	14	289

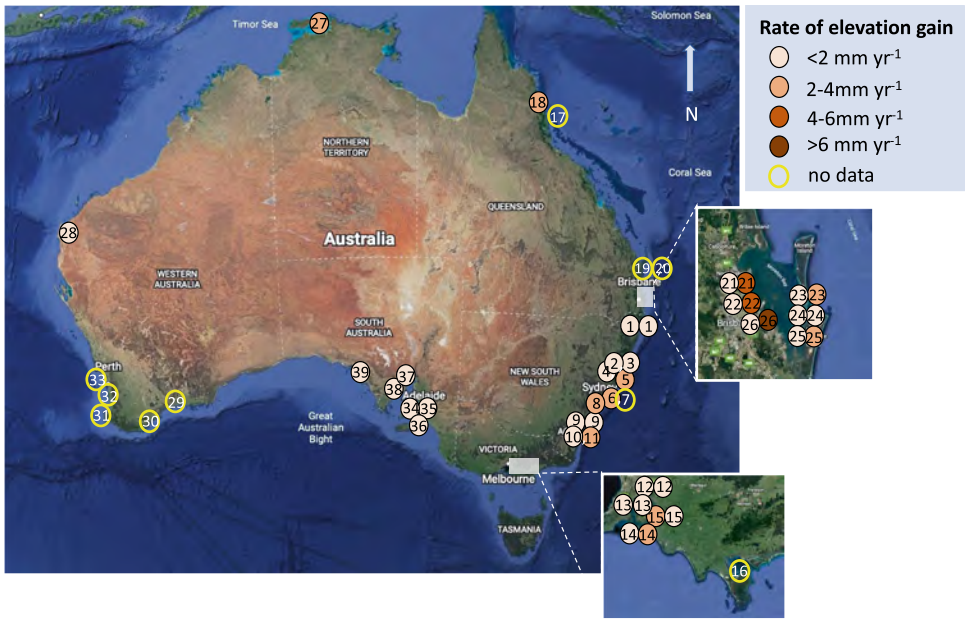


Fig. 4 Distribution of the Australian SET-MH network and rate of elevation gain. Locations are approximate (coordinates and site numbers shown in Table 2). Yellow circles show recently installed SET-MH stations (no data). Paired sites show tidal marsh on the left and mangrove on the right

Australian SET-MH stations are equally divided between mangrove (53%) and tidal marshes (43%), with supratidal forests (4%) being under-represented in the network (Fig. 4). Being the most recent habitat sampled, supratidal forest elevation trend and accretion data are not yet available.

Rates of Elevation Gain in Relation to Sea Level

The average rate of elevation gain for mangrove and tidal marsh sites is shown in Table 4 and Figs. 4 and 5. Table 4 does not include sites recently established for which return readings have not been undertaken or for which the duration of record is too brief to derive a reliable trend (all of the Western Australian Sites, Corner Inlet in Victoria, Towra Point in New South Wales and Woody Island on the Great Barrier Reef). Of the mangrove sites, 83% showed an increased in elevation averaged across the SETs, and 63% of tidal marsh sites showed an increasing elevation trend over the period of measurement (Table 4). Mangroves have a higher rate of accretion (3.77 ± 3.04 mm yr^{-1}) than tidal marshes (1.80 ± 1.04 mm yr^{-1}; $p < 0.001$) and higher elevation gain (2.34 ± 3.97 mm yr^{-1}) than tidal marshes (0.61 ± 1.43 mm yr^{-1}; $p < 0.001$), consistent with their lower position in the tidal frame (Fig. 5).

Of 44 locations (sites with specific vegetation habitat: Table 4), only three sites showed a significant loss of elevation over the period of measure: the two Tomago sites in New South Wales subject to tidal restoration (-5.64 ± 4.60 mm yr^{-1} in the zone subject to greatest tidal exposure and 2.91 ± 2.86 mm yr^{-1} in a zone subject to lesser tidal exposure) and the Dry Creek Salt Field site in South Australia (-3.72 ± 2.53 mm yr^{-1}), also subject to tidal restoration. All other sites showed a stable (> 1 mm yr^{-1} change: 45% of sites) or increasing elevation trend (48% of sites).

Three of the New South Wales saltmarsh sites were subject to mangrove encroachment during the 20-year period of observation, and all had very low rates of elevation gain. These were Currambene Creek (0.32 ± 0.47 mm yr^{-1}), the Minnamurra River (0.49 ± 0.57 mm yr^{-1}) and Ukerebagh Island on the Tweed River estuary (0.24 ± 0.61 mm yr^{-1}).

Nearly all sites in the Australian SET-MH network show a deficit in elevation gain compared to water level rises over the period of SET-MH measurement (Table 4). Only three showed a surplus of elevation gain over sea-level rise averaged across SETs: the two Giralia sites in Western Australia, an artefact of a declining relative sea-level trend over the period of measurement, and the Marramarra site in New South Wales, an artefact of a stable sea-level trend over the period of measurement. Of the 50 locations for which elevation trend data were available (Table 1), 80% show a deficit between elevation gain and water level increase. Of the mangrove locations, 72% showed an elevation deficit, a lower proportion than for tidal marshes (88%).

Drivers of Vertical Accretion and Elevation Gain

Elevation gain was weakly correlated with the rate of sediment accretion ($p = 0.028$, $r^2 = 0.04$). The relationship between the rate of accretion and sea-level rise was weak ($r^2 = 0.07$) but significant ($p = 0.005$; $n = 108$). Similarly, the relationship between elevation gain and sea-level rise was weak ($r^2 = 0.08$) but significant ($p = 0.0006$). The rate of subsidence was directly proportional to the rate of accretion ($r^2 = 0.76$), in a near 1:1 relationship (Fig. 6a). Because subsidence is reducing the contribution of accretion to net elevation gain

Table 4 Rate of accretion and elevation gain* for original and deep rSETs, averaged by habitat type, compared to water level trends over the period of measurement (derived from nearest tide gauges). The elevation surplus (positive) or deficit (negative) is the difference between the rate of elevation gain and the water level trend. *Several of the sites listed in Table 2 are too recent or have insufficient data to calculate an elevation trend. [a]Tidal reinstatement occurred at Tomago in 2015 and Dry Creek in 2017. No long-term water level trend data are provided for this site. [b]South Australian water level trend data based on historic data to 2017

Site	Accretion trend (mm yr^{-1})	Elevation trend (mm yr^{-1})	Water level trend (mm yr^{-1})	Surplus (+) Deficit (−) (mm yr^{-1})	Accretion trend (mm yr^{-1})	Elevation trend (mm yr^{-1})	Water level trend (mm yr^{-1})	Surplus (+) Deficit (−) (mm yr^{-1})
	Mangrove				Tidal marsh			
New South Wales								
Cararma Inlet	2.90 ± 0.65	2.18 ± 1.18	2.38	−0.20	0.89 ± 0.56	1.15 ± 0.21	2.38	−1.24
Curram-bene	0.30 ± 0.09	0.003 ± 0.26	2.38	−2.38	0.32 ± 0.05	−0.21 ± 0.47	2.38	−2.59
Homebush Bay	3.08 ± 0.31	2.92 ± 0.39	5.40	−2.48	2.48 ± 0.44	2.73 ± 0.49	5.40	−2.67
Minna-murra	ND	1.40 ± 0.30	4.45	−3.05	0.46 ± 0.35	0.49 ± 0.57	4.45	−3.957
Tweed River	2.05 ($n = 1$)	1.81 ± 0.83	4.9	−3.09	1.64 ± 0.77	0.236 ± 0.61	4.9	−4.664
Berowra Creek	2.01 ± 0.46	2.46 ± 2.10	3.42	−0.96	2.75 ± 0.46	1.27 ± 0.41	3.42	−2.15
Marramarra	6.17 ± 7.49	2.29 ± 0.38	0.01	2.286	0.75 ± 0.23	0.39 ± 1.40	0.01	0.34
Kooragang	2.48 ± 0.41	0.89 ± 1.33	3.11	−2.22	1.22 ± 0.25	1.71 ± 0.12	3.475	−1.77
Tomago high impact	n/a	n/a	n/a	n/a	6.09 ± 6.21	−5.64 ± 4.60	n/a[a]	n/a
Tomago low impact	n/a	n/a	n/a	n/a	1.09 ± 0.97	−2.91 ± 2.86	n/a[a]	n/a
Comerong Is. Southern	2.31 ± 0.26	0.39 ± 0.56	0.009	0.38	n/a	n/a	n/a	n/a
Comerong Is. Central	n/a	n/a	n/a	n/a	n/a	−0.42 ± 0.48	0.009	−0.43
Comerong Is. Northern	n/a	n/a	n/a	n/a	n/a	0.25 ± 0.41	0.009	0.24
Victoria								
Kooweerup	7.37 ± 1.50	1.06 ± 1.52	3.00	−1.94	1.43 ± 0.06	0.25 ± 0.47	2.03	−1.78
Quail Island	6.92 ± 1.40	0.41 ± 0.73	3.00	−2.59	2.04 ± 0.56	0.86 ± 1.34	2.03	−1.17
Rhyll	4.57 ± 2.07	2.29 ± 0.90	3.00	−0.71	1.40 ± 0.19	1.17 ± 0.12	2.03	−0.86
French Island	6.93 ± 5.16	0.94 ± 0.74	3.00	−2.06	3.21 ± 0.44	2.96 ± 0.65	2.03	0.93
Queensland								
Tinchi	n.d	5.23 ± 3.30	3.85	1.38	1.38	0.03 ± 0.04	3.85	−3.82
Nundah	n.d	5.90 ± 1.64	3.85	2.05	2.03	0.08 ± 0.14	3.85	−3.78
Amity South	n.d	0.41 ± 0.99	3.85	−3.44	2.87	0.15 ± 0.14	3.85	−3.70
Amity North	n.d	2.34 ± 0.97	3.85	−1.54	1.47	−0.01 ± 0.02	3.85	−3.86
Adams	n.d	2.42 ± 2.10	3.85	−1.43	3.10	0.42 ± 0.78	3.85	−3.44
Halloran	n.d	6.22 ± 1.91	3.85	2.37	1.11	−0.03 ± 0.02	3.85	−3.88
Daintree River	n.d	2.13 ± 6.25	8.40	−6.28	n/a	n/a	n/a	n/a
Northern Territory								
Darwin	n.d	2.92 ± 6.25	9.31	−6.39	n/a	n/a	n/a	n/a

Table 4 (continued)

Site	Accretion trend (mm yr^{-1})	Elevation trend (mm yr^{-1})	Water level trend (mm yr^{-1})	Surplus (+) Deficit (−) (mm yr^{-1})	Accretion trend (mm yr^{-1})	Elevation trend (mm yr^{-1})	Water level trend (mm yr^{-1})	Surplus (+) Deficit (−) (mm yr^{-1})
Western Australia								
Giralia	n.d	−0.23 ± 0.11 (fringe)	−4.76	3.61	n.d	−0.23 ± 0.58	−4.76	−4.99
Giralia	n.d	−0.02 ± 0.21 (scrub)	−4.76	4.74	n/a	n/a	n/a	n/a
South Australia								
Dry Creek salt flat	n/a	n/a	n/a	n/a	n.d	−3.72 ± 2.53	1.7	−5.42
Acraman[b]	n/a	n/a	n/a	n/a	n.d	1.86	2.36	−0.50
Tumby Bay[b]	n/a	n/a	n/a	n/a	n.d	−1.06	2.36	−3.42
Cowleds Landing[b]	n/a	n/a	n/a	n/a	n.d	−1.72	2.36	−4.08
Torrens Island[b]	n.d	0.011	2.36	−2.35	n/a	n/a	n/a	n/a
Mutton Cove[b]		0.69 ± 0.36	2.36	−1.67		n/a	n/a	n/a

in direct proportion to the rate of accretion, a deficit between elevation gain and relative sea-level increases under high rates of relative sea-level rise (Fig. 6b).

Discussion

The Australian SET-MH network has been established to explore the vertical adjustment of tidal wetlands to

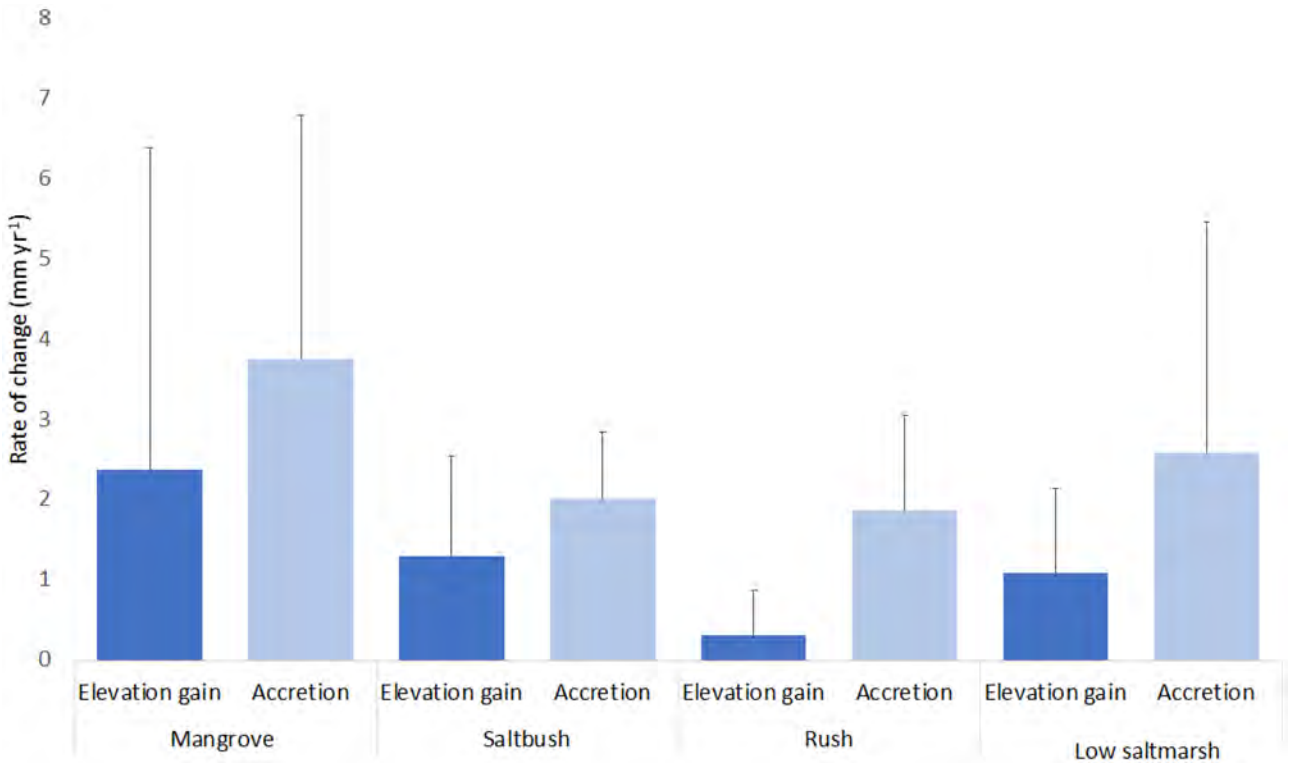


Fig. 5 Comparison of the rate of accretion (from the MH horizon) and elevation gain (against the SET benchmark) in mangrove compared to the three structural categories of tidal marsh

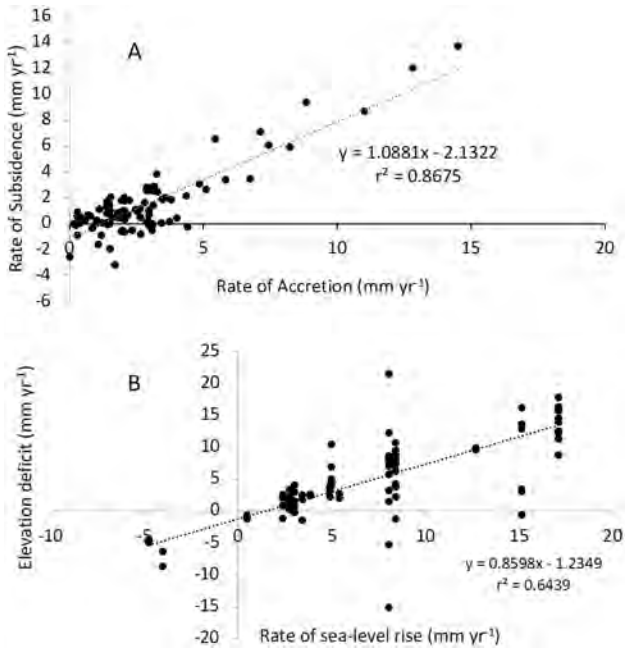


Fig. 6 Relationship between the rate of sediment accretion above the feldspar marker horizon and the rate of upper-level subsidence (**A**) in Australian tidal wetlands (mangrove and tidal marsh combined: $n=108$). Relationship between relative sea-level rise (RSLR) and the deficit between RSLR and elevation gain (**B**) in Australian tidal wetlands ($n=183$)

sea-level rise and the processes influencing this adjustment. The collation and synthesis of the Australian SET-MH data have provided the opportunity to understand accretionary and elevation responses across a range of biogeomorphic settings. Results from the Australian SET-MH network are largely consistent with other regional and global-scale syntheses. At over 80% of sites, the rate of surface elevation gain lagged behind local sea-level rise, a proportion similar to SET-MH observations from 51 sites in Florida, USA (Feher et al. 2022). The relationship between accretion and upper-level subsidence, previously noted in Westernport (Rogers and Saintilan 2021) and in global tidal marsh analyses (Saintilan et al. 2022), extended across the Australian network and was particularly strong ($r^2=0.87$). The result helps explain why Australian tidal marshes are showing a near ubiquitous deficit in relation to RSLR, and why the size of this deficit increases consistently with RSLR ($r^2=0.66$). Surface accretion is correlated with subsidence of upper layers of sediment, which, in addition to the increased water burden, introduces negative feedback into the RSLR accretion response. The result underscores the importance of considering elevation gain rather than surficial sediment accretion in assessing the vulnerability of tidal wetlands to sea-level rise, in both monitoring and modelling exercises.

The lower rate of elevation gain in tidal marshes is partly partly an artefactt of their higher position in the tidal frame. Detailed consideration of the response of the Westernport SETs has shown elevation gain to be closely related to sediment supply and increased accommodation afforded by sea-level rise (Rogers et al. 2022). The deficit that emerges between elevation gain and sea-level rise may be temporary, with higher rates of elevation gain restored lower in the tidal frame. Mangroves exhibit higher rates of accretion and elevation gain, and further work is required to determine the relative contributions of autochthonous organic contributions, allochthonous sediment inputs and decomposition rates in driving these higher rates of elevation gain. Mangrove encroachment into saltmarsh may facilitate this adjustment if their more efficient elevation gain is partly intrinsic. However, in some of the instances where mangrove encroachment into tidal marsh SET plots has been observed, the initial response has been a decline in the rate of elevation gain (e.g. Rogers et al 2013). This may be a short-term response associated with saltmarsh dieback.

Two sites in the network (Dry Creek, South Australia, and Tomago Wetland in New South Wales) were measured immediately following tidal restoration. Tidal reinstatement in wetlands previously isolated from tidal exchange is a restoration mechanism successfully applied to degraded floodplains in Australia (Streever 1998; Glamore et al. 2021; Bell-James and Lovelock 2019) and has emerged as a promising opportunity for "blue carbon" emissions abatement (Hagger et al. 2022; Kelleway et al. 2020). Early results from both Tomago and Dry Creek suggest an initial response of the surface may be elevation loss, and this was quite rapid compared to elevation trajectories in natural wetlands and, in the case of Tomago, despite a low position within the tidal frame. Possible mechanisms for elevation loss in these settings may include subsidence following dieback of prior vegetation (Cahoon 2006), desiccation and erosion of the exposed surface and loading of the upper sediments from reintroduction of tidal inundation. The French Island saltmarsh site was a salt work abandoned in the early nineteenth century, and strong elevation gain at this site suggests that long-term elevation gains may be possible, and the Mutton Cove site in South Australia is a tidal reinstatement site showing elevation gains. Differences in elevation responses between these settings may relate to the time since tidal restoration but may also be influenced by available sediment, being relatively high at French Island and limited at Dry Creek.

Further work is required to better understand the response of Australian tidal wetlands to sea-level rise. The Australian SET-MH network is heavily clustered to sites easily accessible to major population centres. This has helped maintain an appropriate frequency of measures but has restricted sampling of some important wetland types. Until recently, arid zone wetlands were poorly represented, but new SET-MH installations in Western Australia and South Australia (Eyre Peninsula) will help to redress this issue. The macrotidal wetlands of northern Australia,

the region of the greatest extent of tidal wetland in Australia, are represented by Darwin Harbour alone. Installations elsewhere in northern Australia would help interpret tidal wetland responses to climate change in this highly dynamic environment. Within the existing network, accurate survey of the elevation of SET-MH installations in relation to fixed tidal datum would help interpret the implications of elevation deficits in relation to "elevation capital", the elevation of the wetland above lower survival limits.

Finally, application of the Australian SET-MH data will help the research and management community develop better models of coastal lowland responses to sea-level rise. The US National Oceanographic and Atmospheric Administration (NOAA) has recently released a sea-level rise visualisation tool that includes a marsh accretion model based on SET-MH data (https://coast.noaa.gov/slr/#). The marsh migration module showcases the potential application of dynamic elevation models in coastal planning. Differences between rates of elevation gain between coastal wetland community types are implicated in vegetation transitions between, for example, mangrove and saltmarsh in SE Australia (Rogers et al. 2005a, b, 2006). These data provide the potential to model both vegetation transition and components of soil carbon stock change under a range of climate change and planning scenarios.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions This work was undertaken for the Marine and Coastal Hub, a collaborative partnership supported through funding from the Australian Government's National Environmental Science Program (NESP). Funding and support in SA from the Eyre Peninsula Landscape Board, the SA Department for Environment and Water, the SA Coast Protection Board and the Goyder Institute for Water Research. Thanks to the Acraman Creek Conservation Park Co-management Board and the Barngarla Determination Aboriginal Corporation for permission to install and monitor SETs on country.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

Appendix

Table 5 Identifiers and variables compiled

Site.SET.identifier	Individual SET-MH descriptor
Lead	Lead scientists responsible for readings and site data custodians
Site.label	Site identifier
Latitude	Latitude of individual SET in decimal degrees
Longitude	Longitude of individual SET in decimal degrees
Start	Date of first reading
End	Date of most recent reading
Years	Time between start and end in years
elevation.rate	Rate of elevation gain (linear trend) from the SET record (mm yr^{-1})
RSLR.period.of.measure	RSLR for each site for the period of SET measurement (i.e. between Start and End). Linear trend (mm yr^{-1})
elevDeficit	Elevation deficit, defined as RSLR period of measure minus elevation rate (mm yr^{-1})
accretion	Rate of accretion above the feldspar horizon, linear trend (mm yr^{-1})
Subsidence	Rate of accretion—elevation rate (mm yr^{-1})
tidal.range	Difference between MHW and MLW (m)
tidalCat	Classification of tidal range as micro, meso or macrotidal
maxTemp	Average daily maximum temperature of the warmest month of the year in degrees Celsius (sourced from the Bureau of Meteorology, nearest weather station)
rainfall	Average annual rainfall (mm) (sourced from the Bureau of Meteorology, nearest weather station)
Geomorphic setting	Classification of geomorphic setting as: river deltaic, tide dominant, barrier lagoon, barrier estuary, marine embayment, drowned river valley
Dominant.vegetation	Dominant genus or species in the vicinity of the SET station
shortGrassesHerbs	Dominated by short grasses and herbs (*Sporobolus*, *Distichlis*, *Salicornia*, *Sarcocornia*, *Poa*, *Glaux*, *Borrichia*, *Puccinellia*, *Paspalum*, *Elymus*, *Impatiens*), binary
brackishRushes	Dominated by brackish rushes (*Juncus*, *Baumea*)
saltbushes	Dominated by saltbushes or shrubs (*Atriplex*, *Tecticornia*)
mangrove	Dominated by mangrove (*Avicennia*, *Rhizophora*, *Bruguiera*, *Ceriops*)

References

Bell-James, J., and C.E. Lovelock. 2019. Legal barriers and enablers for reintroducing tides: An Australian case study in reconverting ponded pasture for climate change mitigation. *Land Use Policy* 88: 104192.

Cahoon, D.R., P.E. Marin, B.K. Black, and J.C. Lynch. 2000. A method for measuring vertical accretion, elevation, and compaction of soft, shallow-water sediments. *Journal of Sedimentary Research* 70 (5): 1250–1253.

Cahoon, D.R., J.C. Lynch, B.C. Perez, B. Segura, R.D. Holland, C. Stelly, and G. Stephenson. 2002. Philippe Hensel; High-precision measurements of wetland sediment elevation: II. The rod surface elevation table. *Journal of Sedimentary Research* 72(5): 734–739. https://doi.org/10.1306/020702720734

Cahoon, D.R. 2006. A review of major storm impacts on coastal wetland elevations. *Estuaries and Coasts* 29: 889–898.

Cahoon, D.R., J.C. Lynch, C.T. Roman, J.P. Schmit, and D.E. Skidds. 2019. Evaluating the relationship among wetland vertical development, elevation capital, sea-level rise, and tidal marsh sustainability. *Estuaries and Coasts* 42: 1–15.

Dalrymple, R.W., B.A. Zaitlin, and R. Boyd. 1992. Estuarine facies models; conceptual basis and stratigraphic implications. *Journal of Sedimentary Research* 62: 1130–1146.

Dittmann, S., L. Mosley, K. Beaumont, B. Clarke, E. Bestland, H. Guan, H. Sandhu, M. Clanahan, R. Baring, J. Quinn, and R. Seaman. 2019. From salt to C; carbon sequestration through ecological restoration at the dry creek salt field. *Goyder Institute for Water Research Technical Report Series* 19(28): 1–102.

Fagherazzi, S., Mariotti, G., Leonardi, N., Canestrelli, A., Nardin, W., & Kearney, W. S. 2020. Salt marsh dynamics in a period of accelerated sea level rise. *Journal of Geophysical Research: Earth Surface*, 125(8), e2019JF005200.

Feher, L.C., M.J Osland, K.L. McKee, K.R. Whelan, C. Coronado-Molina, F.H. Sklar, and L. Allain. 2022. Soil elevation change in mangrove forests and marshes of the Greater Everglades: A regional synthesis of surface elevation table-marker horizon (SET-MH) data. *Estuaries and Coasts* 1–30.

Feller, I.C., K.L. Mckee, D.F. Whigham, and O'neill, J. P. 2003. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 62: 145–175.

Glamore, W., D. Rayner, J. Ruprecht, M. Sadat-Noori, and D. Khojasteh. 2021. Eco-hydrology as a driver for tidal restoration: Observations from a Ramsar wetland in eastern Australia. *PLoS ONE* 16 (8): e0254701.

Gonsalves, L., B. Law, C. Webb, and V. Monamy. 2013. Foraging ranges of insectivorous bats shift relative to changes in mosquito abundance. *PLoS ONE* 8: e64081.

Hagger, V., N.J. Waltham, and C. E. Lovelock. 2022. Opportunities for coastal wetland restoration for blue carbon with co-benefits for biodiversity, coastal fisheries, and water quality. *Ecosystem Services* 55: 101423. https://doi.org/10.1016/j.ecoser.2022.101423

Horton, B.P., I. Shennan, S.L. Bradley, N. Cahill, M. Kirwan, R.E. Kopp, and T.A. Shaw. 2018. Predicting marsh vulnerability to sea-level rise using Holocene relative sea-level data. *Nature Communications* 9: 1–7.

Jankowski, K.L., T.E. Törnqvist, and A.M. Fernandes. 2017. Vulnerability of Louisiana's coastal wetlands to present-day rates of relative sea-level rise. *Nature Communications* 8: 1–7.

Kelleway, J.J., M.F. Adame, C. Gorham, J. Bratchell, O. Serrano, P.S. Lavery, C.J. Owers, K. Rogers, Z. Nagel-Tynan, and N. Saintilan. 2021. Carbon storage in the coastal swamp oak forest wetlands of Australia. *Wetland Carbon and Environmental Management* 339–353.

Kelleway, J.J., K. Cavanaugh, K. Rogers, I.C. Feller, E. Ens, C. Doughty, and N. Saintilan. 2017. Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Global Change Biology* 23: 3967–3983.

Kelleway, J.J., O. Serrano, J.A. Baldock, R. Burgess, T. Cannard, P.S. Lavery, C.E. Lovelock, P.I. Macreadie, P. Masqué, and M. Newnham. 2020. A national approach to greenhouse gas abatement through blue carbon management. *Global Environmental Change* 63: 102083.

Kirwan, M.L., S. Temmerman, E.E. Skeehan, G.R. Guntenspergen, and S. Fagherazzi. 2016. Overestimation of marsh vulnerability to sea level rise. *Nature Climate Change* 6: 253–260.

Lovelock, C.E., M.F. Adame, J. Bradley, S. Dittmann, V. Hagger, S.M. Hickey, L.B Hutley, A. Jones, J.J. Kelleway, and P.S. Lavery. 2022. An Australian blue carbon method to estimate climate change mitigation benefits of coastal wetland restoration. *Restoration Ecology* e13739.

Lovelock, C.E., D.R. Cahoon, D.A. Friess, G.R. Guntenspergen, K.W. Krauss, R. Reef, K. Rogers, M.L. Saunders, F. Sidik, and A. Swales. 2015. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* 526: 559–563.

Mazor, T., R.K. Runting, M.I. Saunders, D. Huang, D.A. Friess, N.T. Nguyen, R.J. Lowe, J.P. Gilmour, P.A. Todd, and C.E. Lovelock. 2021. Future-proofing conservation priorities for sea level rise in coastal urban ecosystems. *Biological Conservation* 260: 109190.

Mazumder, D., N. Saintilan, and R.J. Williams. 2006. Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. *Marine and Freshwater Research* 57: 193–199.

Mazumder, D., N. Saintilan, R.J. Williams, and R. Szymczak. 2011. Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: Evidence from multiple stable isotope analyses. *Marine and Freshwater Research* 62: 11–19.

McKee, K., K. Rogers, and N. Saintilan. 2012. Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. *Global change and the function and distribution of wetlands* 63–96.

Moritsch, M.M., K.B. Byrd, M. Davis, A. Good, J.Z. Drexler, J.T. Morris, and J.M. Rybczyk. (2022). Can coastal habitats rise to the challenge? Resilience of estuarine habitats, carbon accumulation, and economic value to sea-level rise in a Puget Sound estuary. *Estuaries and Coasts 45*(8): 2293–2309.

Morris, J.T. 2006. Competition among marsh macrophytes by means of geomorphological displacement in the intertidal zone. *Estuarine, Coastal and Shelf Science* 69: 395–402.

Morris, J.T., D.C. Barber, J.C. Callaway, R. Chambers, S.C. Hagen, C.S. Hopkinson, B.J. Johnson, P. Megonigal, S.C. Neubauer, and T. Troxler. 2016. Contributions of organic and inorganic matter to sediment volume and accretion in tidal wetlands at steady state. *Earth' s Future* 4: 110–121.

Morris, J.T., P. Sundareshwar, C.T. Nietch, B. Kjerfve, and D.R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83: 2869–2877.

Ola, A., S. Schmidt, and C.E. Lovelock. 2018. The effect of heterogeneous soil bulk density on root growth of field-grown mangrove species. *Plant and Soil* 432: 91–105.

Oliver, T.S., K. Rogers, C.J. Chafer, and C.D. Woodroffe. 2012. Measuring, mapping and modelling: An integrated approach to the management of mangrove and saltmarsh in the Minnamurra River estuary, southeast Australia. *Wetlands Ecology and Management* 20: 353–371.

Pethick, J.S. 1981. Long-term accretion rates on tidal salt marshes. *Journal of Sedimentary Research* 51 (2): 571–577.

Prahalad, V., V. Harrison-Day, P. McQuillan, and C. Creighton. 2019. Expanding fish productivity in Tasmanian saltmarsh wetlands through tidal reconnection and habitat repair. *Marine and Freshwater Research* 70 (1): 140–151.

Rogers, K., N. Saintilan, and D. Cahoon. 2005a. Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetlands Ecology and Management* 13: 587–598.

Rogers, K., N. Saintilan, and H. Heijnis. 2005b. Mangrove encroachment of salt marsh in Western Port Bay, Victoria: The role of sedimentation, subsidence, and sea level rise. *Estuaries* 28: 551–559.

Rogers, K., K.M. Wilton, and N. Saintilan. 2006. Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science* 66 (3–4): 559–569.

Rogers, K., N. Saintilan, and C. Copeland. 2012. Modelling wetland surface elevation dynamics and its application to forecasting the effects of sea-level rise on estuarine wetlands. *Ecological Modelling* 244: 148–157.

Rogers, K., N. Saintilan, A.J. Howe, and J.F. Rodríguez. 2013. Sedimentation, elevation and marsh evolution in a southeastern Australian estuary during changing climatic conditions. *Estuarine, Coastal and Shelf Science* 133: 172–181.

Rogers, K., J.J. Kelleway, N. Saintilan, J.P. Megonigal, J.B. Adams, J.R. Holmquist, M. Lu, L. Schile-Beers, A. Zawadzki, and D. Mazumder. 2019. Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature* 567: 91–95.

Rogers, K., and N. Saintilan. 2021. Processes influencing autocompaction modulate coastal wetland surface elevation adjustment with sea-level rise. *Frontiers in Marine Science* 879.

Rogers, K., A. Zawadzki, L.A. Mogensen, and N. Saintilan. 2022. Coastal wetland surface elevation change is dynamically related to accommodation space and influenced by sedimentation and sea-level rise over decadal timescales. *Frontiers in Marine Science* 9: 807588.

Roy, P. S., R.J. Williams, A.R. Jones, I. Yassini, P.J. Gibbs, B. Coates, and S. Nichol. (2001). Structure and function of south-east Australian estuaries. *Estuarine, coastal and shelf science 53*(3): 351–384.

Runting, R.K., C.E. Lovelock, H.L. Beyer, and J.R. Rhodes. 2017. Costs and opportunities for preserving coastal wetlands under sea level rise. *Conservation Letters* 10 (1): 49–57.

Saintilan, N., N. Khan, E. Ashe, J. Kelleway, K. Rogers, C.D. Woodroffe, and B. Horton. 2020. Thresholds of mangrove survival under rapid sea level rise. *Science* 368: 1118–1121.

Saintilan, N., K.E. Kovalenko, G. Guntenspergen, K. Rogers, J.C. Lynch, D.R. Cahoon, C.E. Lovelock, et al. 2022. Constraints on the adjustment of tidal marshes to accelerating sea level rise. *Science* 377: 523–527.

Saintilan, N., K. Rogers, J. Kelleway, E. Ens, and D. Sloane. 2019. Climate change impacts on the coastal wetlands of Australia. *Wetlands* 39: 1145–1154.

Saintilan, N., N.C. Wilson, K. Rogers, A. Rajkaran, and K.W. Krauss. 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology* 20: 147–157.

Schuerch, M., T. Spencer, S. Temmerman, M.L. Kirwan, C. Wolff, D. Lincke, and S. Brown. 2018. Future response of global coastal wetlands to sea-level rise. *Nature 561*(7722): 231–234.

Sheaves, M., R. Baker, I. Nagelkerken, and R.M. Connolly. 2015. True value of estuarine and coastal nurseries for fish: Incorporating complexity and dynamics. *Estuaries and Coasts* 38: 401–414.

Sievers, M., C.J. Brown, V.J. Tulloch, R.M. Pearson, J.A. Haig, M.P. Turschwell, and R.M. Connolly. 2019. The role of vegetated coastal wetlands for marine megafauna conservation. *Trends in Ecology & Evolution* 34 (9): 807–817.

Streever, W.J. 1998. Kooragang Wetland Rehabilitation Project: Opportunities and constraints in an urban wetland rehabilitation project. *Urban Ecosystems* 2: 205–218.

Traill, L.W., K. Perhans, C.E. Lovelock, A. Prohaska, S. Mcfallan, J.R. Rhodes, and K.A. Wilson. 2011. Managing for change: Wetland transitions under sea-level rise and outcomes for threatened species. *Diversity and Distributions* 17: 1225–1233.

Webb, E.L., D.A. Friess, K.W. Krauss, D.R. Cahoon, G.R. Guntenspergen, and J. Phelps. 2013. A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. *Nature Climate Change* 3: 458–465.

LETTER

doi:10.1038/nature15538

The vulnerability of Indo–Pacific mangrove forests to sea–level rise

Catherine E. Lovelock[1,2], Donald R. Cahoon[3], Daniel A. Friess[4], Glenn R. Guntenspergen[3], Ken W. Krauss[5], Ruth Reef[1,2,6], Kerrylee Rogers[7], Megan L. Saunders[2], Frida Sidik[8], Andrew Swales[1,9], Neil Saintilan[10], Le Xuan Thuyen[11] & Tran Triet[11,12]

Sea-level rise can threaten the long-term sustainability of coastal communities and valuable ecosystems such as coral reefs, salt marshes and mangroves[1,2]. Mangrove forests have the capacity to keep pace with sea-level rise and to avoid inundation through vertical accretion of sediments, which allows them to maintain wetland soil elevations suitable for plant growth[3]. The Indo-Pacific region holds most of the world's mangrove forests[4], but sediment delivery in this region is declining, owing to anthropogenic activities such as damming of rivers[5]. This decline is of particular concern because the Indo-Pacific region is expected to have variable, but high, rates of future sea-level rise[6,7]. Here we analyse recent trends in mangrove surface elevation changes across the Indo-Pacific region using data from a network of surface elevation table instruments[8–10]. We find that sediment availability can enable mangrove forests to maintain rates of soil-surface elevation gain that match or exceed that of sea-level rise, but for 69 per cent of our study sites the current rate of sea-level rise exceeded the soil surface elevation gain. We also present a model based on our field data, which suggests that mangrove forests at sites with low tidal range and low sediment supply could be submerged as early as 2070.

Intertidal mangrove forests occur on tropical and subtropical shorelines, and provide a wide range of ecosystem services, including the support of fisheries, coastal protection and carbon sequestration, which are collectively and conservatively estimated to be worth US$194,000 per hectare per year (refs 11, 12). Although mangrove tree species are able to tolerate inundation by tides, they can die and their former habitat can convert to open water or tidal flats when sea-level rise (SLR) causes the frequency and duration of inundation to exceed species-specific physiological thresholds[13], resulting in shoreline retreat[14]. In low-sediment-supply systems such as Caribbean atolls, the capacity of the soil surface to keep pace with SLR is strongly dependent on the accumulation of organic matter derived from roots that decompose slowly in anaerobic soils[15]. But sediment accretion on the soil surface in the Indo-Pacific region can also play a crucial role in surface elevation gains[16].

Changes in the elevation of the soil surface over time can be measured using the surface elevation table–marker horizon (SET–MH) methodology[8,9], which has been widely used and recommended for monitoring intertidal surface-elevation trajectories in coastal wetlands[10]. Here we use an extensive network of SET–MH stations (Fig. 1) with records of 1–16.6 years in length to investigate the role of sediments in maintaining surface elevation gain in these Indo-Pacific mangrove forests and to identify their vulnerability to future SLR. Recent trends in mangrove surface elevation change across 27 sites in the Indo-Pacific (Supplementary Table 1) were analysed with respect to environmental factors, including suspended-matter concentration and the regional rate of SLR obtained from tide gauges. Future vulnerability to SLR was modelled on the basis of the results of this analysis using a surface elevation change model and likely future SLR scenarios.

Throughout the Indo-Pacific region, we found that mangrove soil-surface elevation gains are strongly dependent on rates of accretion of sediment on the soil surface (Fig. 2a) as well as subsurface organic matter accumulation, which has been observed in sites in the Caribbean[15]. One site in southeast Java, Indonesia, has particularly high rates of surface accretion, owing to a mud-volcano eruption[17], but even with this site removed from the analysis, surface elevation gain remains significantly correlated with sediment accretion ($R^2 = 0.259$, $P < 0.001$, F test). As expected from theoretical models[18], we found that the concentration of total suspended matter (TSM) in the water column, derived from remotely sensed MERIS (medium resolution imaging spectrometer) imagery, was proportional to surface accretion (Fig. 2b) and to surface elevation gains (Fig. 2c), although the relationship between surface elevation and TSM was more variable than that observed between surface elevation and locally measured rates of surface accretion. These relationships link the supply of sediments to the maintenance of soil elevation relative to sea level in mangrove forests at regional scales within the Indo-Pacific region. Other factors (such as rate of SLR, geomorphology, habitat and dominant species) explained a smaller proportion of the variation in the surface elevation gains (Extended Data Table 1). On the basis of our network of SET–MH sites, we conclude that sediment supply is important to surface elevation gains and therefore to preventing mangrove-forest loss in the future.

We found that 69% of surface elevation records in the Indo-Pacific data set (90 out of a total of 153 SET–MH stations) had rates of surface elevation gain that were less than the long-term rate of SLR for the region (Extended Data Fig. 1b). The remaining 31% of the records are from sites in Australia, New Zealand, Vietnam and Indonesia. Many of the sites that had rates of surface elevation gain less than SLR also exhibited shallow subsidence (Extended Data Fig. 1a). Shallow subsidence can be caused by a range of factors that increase compaction of the near-surface sediments and that are responsive to local environmental factors, including forest degradation[19]. But whether subsidence and the 'elevation deficit' relative to local rates of SLR indicate vulnerability of these mangrove forests to loss with increasing rates of SLR is unknown. If the topography allows the mangrove forest to migrate landward, with no anthropogenic barriers (such as infrastructure or flood-defence barriers), then mangroves may delay submergence by 'back-stepping' into adjacent habitats[20]. However, barriers to landward expansion of mangrove forests occur throughout the Indo-Pacific region, particularly in sites that have intensive aquaculture, urban development and low-lying agricultural land. We have therefore assumed that broad-scale landward retreat of human settlements in

[1]School of Biological Sciences, The University of Queensland, Brisbane 4072, Australia. [2]Global Change Institute, The University of Queensland, Brisbane 4072, Australia. [3]Patuxent Wildlife Research Center, United States Geological Survey, Maryland 20708, USA. [4]Department of Geography, National University of Singapore, 1 Arts Link, Singapore 117570, Singapore. [5]National Wetlands Research Center, United States Geological Survey, Louisiana 70506, USA. [6]Cambridge Coastal Research Unit, Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK. [7]School of Earth and Environmental Science, University of Wollongong, Wollongong 2522, Australia. [8]The Institute for Marine Research and Observation, Ministry of Marine Affairs and Fisheries, Bali 82251, Indonesia. [9]National Institute of Water and Atmospheric Research, Hamilton 3251, New Zealand. [10]Department of Environmental Sciences, Macquarie University, Sydney 2109, Australia. [11]University of Science, Vietnam National University, Ho Chi Minh City, Vietnam. [12]International Crane Foundation, Wisconsin 53913, USA.

©2015 Macmillan Publishers Limited. All rights reserved

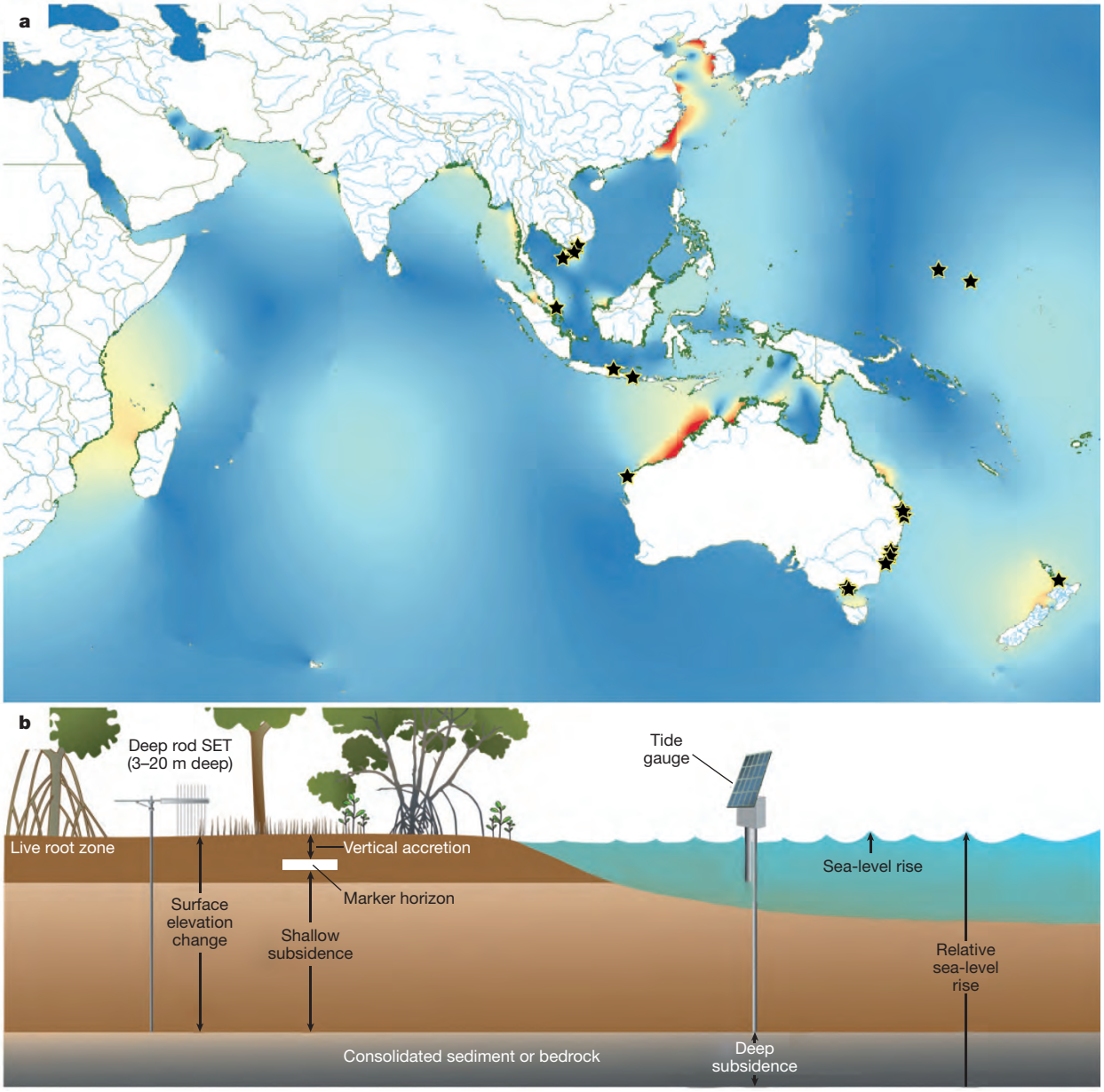


Figure 1 | Map of the Indo-Pacific region study sites and a schematic of the SET–MH. a, Study sites are indicated by stars; mangrove forests are shown in dark green. The colour of the coastal ocean represents variation in tidal range (Aviso + FES2012 tide model), where blue is microtidal (0–2 m), yellow is mesotidal (2–4 m) and red is macrotidal (>4 m). **b**, The SET–MH installation monitors changes in soil-surface elevation, surface accretion above a marker horizon and shallow subsidence (by difference[8,9]); see Methods for details.

the region is unlikely as a result of political uncertainty and because in many nations coastal inhabitants are 'trapped' by a lack of capital and available inland sites that would support migration[21].

To examine the future vulnerability of Indo-Pacific mangroves to SLR, we developed a model of mangrove habitat suitability based on position in the tidal frame. Mangrove forests persist in the portion of the tidal frame from mean sea level (MSL) to the level of the highest astronomical tide, which generally corresponds to the highest elevation at which mangroves can survive[22]. This gives rise to what is termed a wetland's 'elevation capital', or the potential of an intertidal wetland to remain within a suitable inundation regime at that site (that is, above MSL) despite subsiding relative to local SLR[23]. For example, mangrove forests occupying high intertidal sites that have a 10-m tidal range (such as the Kimberly coast of Australia) would need to lose up to 5 m of elevation capital to reach MSL. In contrast, high intertidal sites with a tidal range of 1 m (such as the Caribbean and parts of Indonesia) would have to lose only 0.5 m of elevation to put the entire contemporary forest at or below MSL. Assuming that mangrove forest species cannot persist below approximately MSL, we estimate the time to inundation and thus loss of the forest by using tidal range as a surrogate for the elevation capital within the ecosystem.

Over the range of elevation deficits within our data set, we estimated the time until complete submergence of the forest at sites with varying tidal range (and thus varying elevation capital). This model, which subtracts elevation from the elevation capital over time, assumes constant rates of SLR. Assuming an elevation deficit of 20 mm yr^{-1} (that is, sea level rising 20 mm yr^{-1} faster than mangrove surface elevation gain), which occurs at some of our sites owing to high local rates of SLR and shallow subsidence (for example, Indonesia), we project complete submergence of the forests in 100 years wherever tidal ranges are less than 4 m (Extended Data Fig. 2). At an elevation deficit of 6 mm yr^{-1} (the mean elevation deficit for our sites with elevation deficits), we

©2015 Macmillan Publishers Limited. All rights reserved

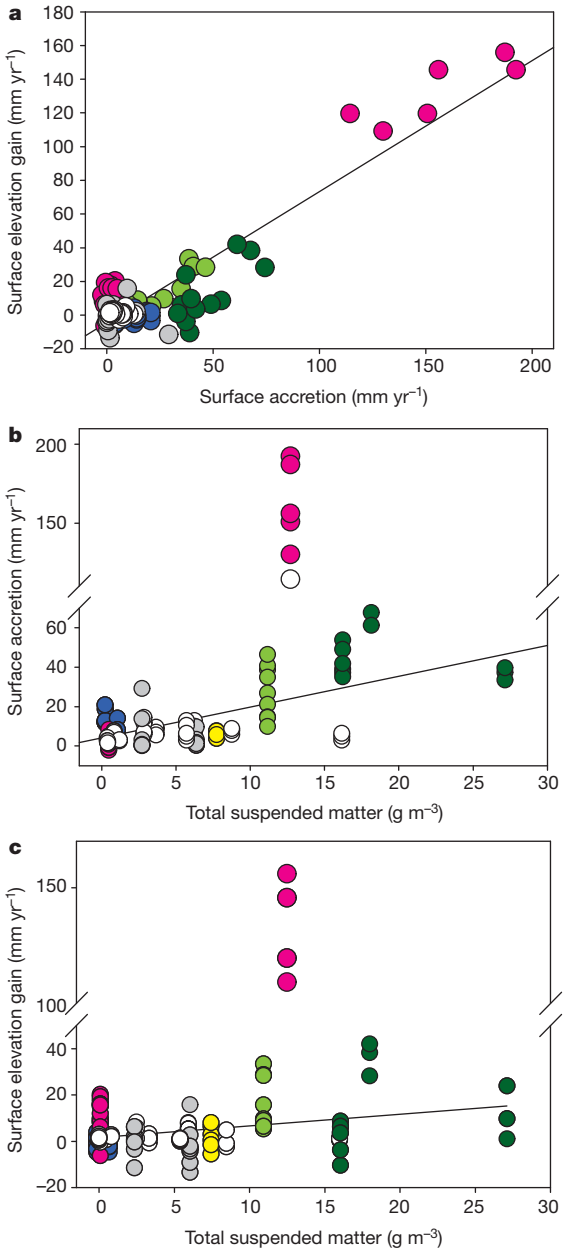


Figure 2 | The relationship between mangrove soil-surface elevation gains and sediment availability. **a**–**c**, Relationships between soil-surface elevation gains and accretion on the soil surface (**a**), accretion on the soil surface and average annual TSM derived from MERIS satellite imagery (**b**), and surface elevation gains and average annual TSM (**c**). Data points are coloured as follows: pink, Indonesia; dark green, Vietnam; light green, New Zealand; yellow, western Australia; dark blue, Micronesia; grey, Singapore; white, eastern Australia. Solid lines are linear regressions: **a**, (surface elevation gain) = (−4.44 ± 0.95) + (0.78 ± 0.03) × (surface accretion), $R^2 = 0.849$, $P < 0.0001$, F test (for overall significance of the linear regression); **b**, (surface accretion) = (4.15 ± 1.08) + (1.57 ± 0.15) × TSM, $R^2 = 0.443$, $P < 0.0001$, F test (excluding data from Porong, Indonesia); **c**, (surface elevation gain) = (1.38 ± 0.83) + (0.51 ± 0.11) × TSM, $R^2 = 0.122$, $P < 0.0001$, F test (excluding data from Porong, Indonesia); the indicated uncertainties are standard errors. Source Data for this figure are available online.

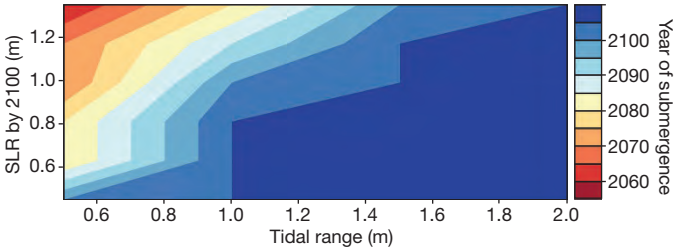


Figure 3 | Year in which mangroves are predicted to be submerged at sites with low (<2.5 g m^{-3}) sediment availability over variation in tidal range and rates of SLR. The darkest blue region indicates no submergence predicted within the modelling time frame (until 2100). At high sediment supply (>2.5 g m^{-3}), mangrove forests were not predicted to be submerged by 2100. See Methods for further details.

estimate it would take 100–300 years for high intertidal forests to be lower than MSL, while at low elevation deficits (1 mm yr^{-1}) the forests may persist for thousands of years. The palaeorecord is consistent with high levels of persistence of mangroves through time when rates of SLR are low to moderate (that is, low levels of elevation deficits). For example, in Belize there is evidence that mangrove forests persisted for long intervals over the Holocene epoch during periods when rates of SLR were less than 5 mm yr^{-1} (ref. 15). Additionally, there is evidence that high intertidal mangrove forests in northern Australia persisted for thousands of years despite relatively high rates of SLR[14]. However, evidence of overwhelming flooding and loss of mangrove forests is also evident during past rapid rises in sea level[14].

To synthesize the effects of sediment supply and accelerating rates of SLR (and corresponding elevation deficits) on the fate of mangrove forests, we formulated a second model that assessed the probable time to submergence of mangrove forests over the range of observed rates of surface elevation gains with no landward migration and over a range of tidal amplitudes. According to the model, mangrove forests are likely to persist at sites with high tidal range even with high rates of SLR and low levels of sediment availability (Fig. 3), consistent with palaeo-observations[14] and theory[16,18]. However, at sites with low tidal range, forests will be vulnerable by 2080 at moderate SLR (0.8 m by 2100).

We cannot estimate the absolute extent of losses of mangrove cover over the region because measurements of mangrove forest elevation in the region are too coarse; however, our model provides a semi-empirical indication of the conditions under which mangrove loss is likely with SLR and locations where management of sediment supply and space for landward migration are vital to ensure mangrove forests survive into the future. Our model indicates that the outlook for mangrove forests in some locations is poor under relatively low rates of SLR—the Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathway 6 (RCP6) scenario—with submergence of mangroves by 2070 predicted in the Gulf of Thailand, the southeast coast of Sumatra, the north coasts of Java and Papua New Guinea and the Solomon Islands (Fig. 4). In contrast, the outlook for the persistence of mangroves into the future is more positive in east Africa, the Bay of Bengal, eastern Borneo and northwestern Australia, where there are relatively large tidal ranges and/or higher sediment supply.

Our model does not account for long-term and nonlinear feedbacks within the system where elevation deficits may be enhanced or reduced, for example, through episodic high-wave-energy events that cause erosion[24], degradation of forests[25], other stochastic events such as intense storms that may alter hydrology or deliver sediment pulses[26], or changes in ocean circulation that may influence regional rates of SLR[7]. The frequency and intensity of these events are predicted to increase under climate-change scenarios[2], and all of these factors will influence the length of time before forest submergence and loss. Our model also does not include subsidence (or uplift) that occurs below the SET benchmark[9], which in some locations may strongly influence the time until submergence. But shifts in the way sediment is managed, and reversing forest degradation and thus enhancing organic matter inputs to sediments may extend the persistence of mangroves for hundreds of years (for example, reducing elevation deficits by 6 mm yr^{-1} extended the time until submergence from 83 years to 167 years for sites with a 2-m tidal range). In coastal and estuarine systems with reduced upstream sediment inputs due to human modifications[27], the potential

©2015 Macmillan Publishers Limited. All rights reserved

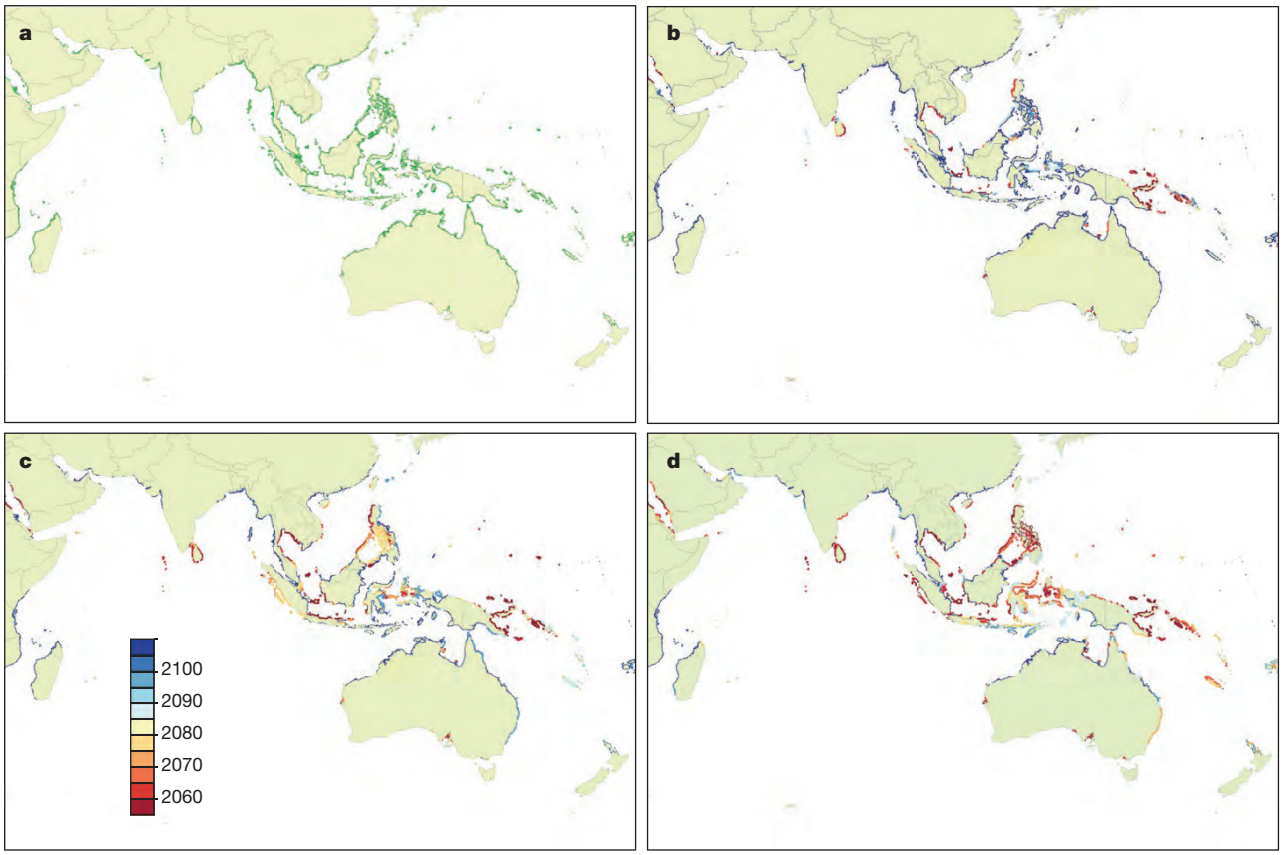


Figure 4 | Mangrove forest distribution in the Indo-Pacific region. **a**, Dark green areas indicate current mangrove forests. **b**–**d**, Predicted decade of mangrove forest submergence, indicated by the colour scale in **c**, for IPCC RCP6 (0.48 m SLR by 2100) (**b**), RCP8.5 (0.63 m SLR by 2100) (**c**), and a more extreme scenario (1.4 m SLR by 2100) (**d**). The darkest blue region indicates no submergence predicted within the modelling time frame (until 2100). The model assumes landward migration of mangrove forests is not possible.

for eco-geomorphic feedbacks that delay the onset of mangrove-forest loss is diminished.

Data from our network of sites indicate that the fate of mangroves in the Indo-Pacific with SLR is strongly linked to the availability of suspended matter, which is important for increases in soil-surface elevation and enables mangroves to maintain their elevation within the tidal frame above MSL. The importance of sediment supply for the resilience of mangrove forests in the face of SLR has been inferred from the palaeontological record[14] and from recent observed changes in mangrove coasts where sediment supply has been reduced, owing to damming of rivers[27]. In Thailand, there has been an 80% reduction of sediment supply in the Chao Phraya River delta, which, in combination with surface subsidence caused by groundwater extraction, has resulted in kilometres of mangrove shoreline retreat[28]. Within the Mekong River system, planned construction of dams and reductions in sediment supply[28] will have a devastating effect on the local coastal sediment budget and the long-term persistence of mangrove forests. Management of the coast and particularly of the river systems that deliver much of the sediment to the region is therefore vital for the survival of mangrove forests. Although sediment supply at some sites may be maintained as a legacy of prior forest clearing of catchments (which leads to erosion of soil), the restriction of sediment supply caused by the building of dams is a major issue that will contribute to mangrove losses in the future.

More than half the mangrove forests we studied have already lost elevation relative to sea level. With constant rates of SLR where tidal ranges are large and sediment supplies are maintained, mangrove forests in the upper intertidal zone may survive thousands of years before they are threatened by submergence. However, under moderate emissions scenarios (for example, IPCC RCP6) at sites with low tidal ranges and low sediment supply, mangrove forests may be lost by 2080. Our work emphasizes the urgent need to plan for the maintenance of sediment supply in river systems that are expected to be heavily modified and dammed in the future, to reverse forest degradation that reduces organic matter inputs and to plan for the landward migration of mangrove forests to higher elevations in locations where sediment supply is expected to be restricted.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 28 January; accepted 26 August 2015.
Published online 14 October 2015.

1. Nicholls, R. J. & Cazenave, A. Sea-level rise and its impact on coastal zones. *Science* **328,** 1517–1520 (2010).
2. Woodruff, J. D., Irish, J. L. & Camargo, S. J. Coastal flooding by tropical cyclones and sea-level rise. *Nature* **504,** 44–52 (2013).
3. Kirwan, M. L. & Megonigal, J. P. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* **504,** 53–60 (2013).
4. Giri, C. *et al.* Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecol. Biogeogr.* **20,** 154–159 (2011).
5. Milliman, J. D. & Farnsworth, K. L. *River Discharge to the Coastal Ocean: A Global Synthesis* (Cambridge Univ. Press, 2011).
6. Church, J. A. *et al.* in *Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker, T. F. *et al.*) Ch. 13 (Cambridge Univ. Press, 2013).
7. Stammer, D. *et al.* Causes for contemporary regional sea level changes. *Annu. Rev. Mar. Sci.* **5,** 21–46 (2013).
8. Cahoon, D. R. *et al.* High-precision measurements of wetland sediment elevation: I. Recent improvements to the sedimentation-erosion table. *J. Sediment. Res.* **72,** 730–733 (2002).

©2015 Macmillan Publishers Limited. All rights reserved

9. Callaway, J. C., Cahoon, D. R. & Lynch, J. C. in *Methods in Biogeochemistry of Wetlands* (eds DeLaune, R. D. *et al.*) 901–917 (Soil Science Society of America, 2013).
10. Webb, E. L. *et al.* A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. *Nature Clim. Change* **3,** 458–465 (2013).
11. Costanza, R. *et al.* Changes in the global value of ecosystem services. *Global Environ. Change* **26,** 152–158 (2014).
12. Brander, L. M. *et al.* Ecosystem service values for mangroves in Southeast Asia: a meta-analysis and value transfer application. *Ecosyst. Services* **1,** 62–69 (2012).
13. Ball, M. C. Ecophysiology of mangroves. *Trees Struct. Funct.* **2,** 129–142 (1988).
14. Woodroffe, C. D. Response of tide-dominated mangrove shorelines in Northern Australia to anticipated sea-level rise. *Earth Surf. Proc.. Land.* **20,** 65–85 (1995).
15. McKee, K. L., Cahoon, D. R. & Feller, I. C. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecol. Biogeogr.* **16,** 545–556 (2007).
16. Kirwan, M. L. & Murray, A. B. A coupled geomorphic and ecological model of tidal marsh evolution. *Proc. Natl Acad. Sci. USA* **104,** 6118–6122 (2007).
17. Jennerjahn, T. C. *et al.* Environmental impact of mud volcano inputs on the anthropogenically altered Porong River and Madura Strait coastal waters, Java, Indonesia. *Estuar. Coast. Shelf Sci.* **130,** 152–160 (2013).
18. Fagherazzi, S. *et al.* Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. *Rev. Geophys.* **50,** RG1002 (2012).
19. Krauss, K. W. *et al.* How mangrove forests adjust to rising sea level. *New Phytol.* **202,** 19–34 (2014).
20. Saintilan, N. *et al.* Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biol.* **20,** 147–157 (2014).
21. Black, R., Bennett, S. R. G., Thomas, S. M. & Beddington, J. R. Climate change: migration as adaptation. *Nature* **478,** 447–449 (2011).
22. Alongi, D. M. Present state and future of the world's mangrove forests. *Environ. Conserv.* **29,** 331–349 (2002).
23. Cahoon, D. R. & Guntenspergen, G. R. Climate change, sea-level rise, and coastal wetlands. *Nat. Wetl. Newslett.* **32,** 8–12 (2010).
24. Winterwerp, J. C. *et al.* Defining eco-morphodynamic requirements for rehabilitating eroding mangrove-mud coasts. *Wetlands* **33,** 515–526 (2013).
25. Lang'at, J. K. S. *et al.* Rapid losses of surface elevation following tree girdling and cutting in tropical mangroves. *PLoS ONE* **9,** e107868 (2014).
26. Cahoon, D. R. A review of major storm impacts on coastal wetland elevations. *Estuar. Coast.* **29,** 889–898 (2006).
27. Giosan, L., Syvitski, J., Constantinescu, S. & Day, J. Climate change: protect the world's deltas. *Nature* **516,** 31–33 (2014).
28. Kondolf, G. M., Rubin, Z. K. & Minear, J. T. Dams on the Mekong: cumulative sediment starvation. *Water Resour. Res.* **50,** 5158–5169 (2014).

Supplementary Information is available in the online version of the paper.

Acknowledgements The Global Change Institute at The University of Queensland supported this collaboration, as did the Australian Research Council SuperScience grant number FS100100024 to the Australia Sea Level Rise Partnerships. D.R.C., G.R.G. and K.W.K. acknowledge support from the US Geological Survey Climate and Land Use Research and Development Program. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Author Contributions All authors participated in a collaborative workshop or contributed field data, contributed to the conceptualization of models and edited the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to C.E.L. (c.lovelock@uq.edu.au).

©2015 **Macmillan Publishers Limited. All rights reserved**

METHODS

SET–MH method description. The SET and the later-developed rod-SET consist of a benchmark rod driven in sections through the soil profile to resistance, often to 10–25-m depth in the soil or to when bedrock is reached (Fig. 1b). After installation of the benchmark rod, a portable horizontal arm is attached, and fixed points (usually four positions around the top of the rod) are used to measure the distance to the substrate surface using a series of vertical pins lowered to the soil surface (Fig. 1b). Total surface height measurements have confidence intervals of ±1.3 mm (ref. 8). SET data are usually complemented with monitoring of accretion on the soil surface using artificial soil marker horizons typically made of feldspar, sand or other resistant material, which simultaneously allows users to quantify rates of vertical surface accretion (that is, sediment deposition; Fig. 1b). The complete SET–MH installation provides observations of net surface elevation change above the benchmark depth as well as accretion on the surface of the wetland. These values may be compared to infer whether surface or subsurface processes are contributing to surface elevation gains. For example, if accretion on the soil surface is equivalent to surface elevation gain, then accretion on the soil surface, whether of mineral or organic origin, is the major process contributing to elevation gain. However, if elevation gains are less than surface accretion, then shallow subsidence of the soil volume is inferred (Extended Data Fig. 1). Conversely, if elevation gains are greater than surface accretion, then expansion of the subsurface soil profile is inferred, which may be due to root growth[8,9,15,23]. Over many sites it has been repeatedly shown that vertical accretion on the soil surface is not a valid substitute for surface elevation change and that the complete set-up is necessary to identify the contribution of surface and shallow subsurface processes to surface elevation change at a specific site[15,23,26]. Repeated measurements allow description of net surface elevation change, which can be integrated with region-specific relative SLR (for example, tide-gauge data; see Supplementary Information) to determine whether the surface elevation of mangroves has kept pace with SLR over that time period.

Analysis of variation in surface elevation. Linear regression was used to describe the relationships between: (1) surface elevation gains and accretion of sediment on the soil surface; (2) accretion on the surface and TSM; and (3) surface elevation gains and TSM. Forms of these relationships are given in the legend of Fig. 2.

The relative influence (in per cent) of predictor variables on surface elevation change (in millimetres per year) was analysed using boosted regression tree (BRT) models[29] developed using data from 153 observations and 10 predictors, with a tree complexity of 5 and learning rate of 0.005. We developed three models using three different measures of sea-level variation at each site (Supplementary Table 1): the long-term rate of SLR at tide gauges (model 1); the rates of sea-level change over the period of the surface elevation gain measurements at tide gauges (model 2); and the rates of sea-level change based on satellite altimetry (model 3). On the basis of cross-validation, the mean percentages (s.e.m.) of deviance explained by models 1–3 are 44.8% (±10.5%), 38.2% (±9.3%) and 40.9% (±8.9%), respectively. BRT modelling was done with *R* version 3.0.2 using packages *dismo* and *gbm*. The BRTs were built with a 10-fold cross-validation optimization, with a Gaussian distribution for surface elevation change. Stochasticity (bag fraction) was set to 0.5. The final models were fitted with 5,850 trees. Geomorphological setting followed the classifications of ref. 30: river delta, tidal, lagoon or carbonate island. Ecological habitat followed the classifications of ref. 31: fringe, scrub, hammock, basin, overwash or riverine. Dominant tree genera were *Avicennia, Rhizophora, Sonneratia*; mangrove forests were classified as mixed forests at sites where no single genera was dominant.

Estimating time to submergence. Years to submergence over variation in tidal range was estimated by summing annual elevation deficits (Extended Data Fig. 2). Elevation deficit is the difference between the rate of local SLR and the rates of surface elevation gain. Where elevation deficits in our data were observed ($N = 103$), mean elevation deficit over our sites was 6 mm yr^{-1} (dashed line in Extended Data Fig. 2). Extended Data Fig. 2 shows the years to submergence (on a logarithmic scale) of the highest intertidal mangrove forest over variation in tidal range (microtidal, blue; mesotidal, yellow; macrotidal, red), for a range of elevation deficits (1–20 mm yr^{-1}); see Extended Data Fig. 2.

Model to predict the year of submergence of mangrove ecosystems. A model to predict the year of submergence of mangrove ecosystems subject to accelerating rates of SLR was developed for various physical environmental contexts. The model was based on the observed rates of mangrove surface elevation change as a function of rate of SLR, suspended sediment availability and tidal range. The model was run from 2010 to 2100 in 10-year time steps (see Extended Data Fig. 3 for a summary of the modelling process).

The vertical range of mangrove distribution was assumed to be the upper 50% of the tidal range[22]. For example, if the tidal range was 1 m, the vertical distribution of mangroves was assumed to be 0.5 m. Assuming that mangroves were at their upper vertical limit of their range at the start of the simulations, the time until net elevation loss was equivalent to 50% of the magnitude of tidal range (in metres) was calculated as the time to mangrove submergence. In each time step, elevation deficit was calculated as the magnitude of SLR minus the magnitude of surface elevation gain. Total elevation deficit over the 90-year simulation was calculated by summing the accumulated elevation deficits.

Elevation gain (in millimetres per year) caused by sediment accumulation for particular SLR and suspended-sediment scenarios was calculated according to the observed surface elevation data. The slope and intercept of linear models relating elevation gain to rate of SLR are given in Extended Data Table 2. The relationship between surface elevation gain and rate of SLR (in millimetres per year) was established for two TSM classes: low (<2.5 g m^{-3}) and high (>2.5 g m^{-3}). Linear regression was used to establish the functional forms of the relationships between surface elevation gain and the rate of SLR.

Scenarios of tidal ranges from 0.5 m to 2.0 m in 0.5-m increments were examined (4 total). Six SLR trajectories were simulated for a total of 24 simulations. The starting rate of SLR for each trajectory was 3 mm yr^{-1}, equivalent to the current rate of global average SLR. The rate of change of sea-level increase was varied by 0.5 mm yr^{-1} in decadal time steps for the six trajectories: SLR increased by 0.5 mm yr^{-1} each decade in the first trajectory, 1 mm yr^{-1} in the second, 1.5 mm yr^{-1} in the third and so on, up to 3.0 mm yr^{-1} each decade in the last trajectory. The resultant magnitudes of sea-level change for the six trajectories were 0.45 m, 0.63 m, 0.81 m, 0.99 m, 1.17 m and 1.35 m by 2100. The model was run for each of the tide-range ($N = 4$) and SLR ($N = 6$) trajectory combinations, for each of the sediment availability scenarios (low and high), for a total of 48 simulations.

We then created spatial layers of the model. The TSM layer was classified as high (>2.5 g m^{-3}) or low (<2.5 g m^{-3}). The tidal-range layer was sourced from the FES2012 tidal model package distributed by AVISO, with support from CNES (http://www.aviso.altimetry.fr/)[32]. We ran the model for each pixel that contains mangroves, as indicated by the data presented in ref. 4, for three SLR scenarios (RCP6.5, RCP8.5 and a higher, 1.4-m SLR by 2100 scenario based on ref. 33).

There are a number of assumptions and limitations to this approach. First, we assumed that mangroves commenced the simulations at the upper vertical limit of their range. Therefore, mangroves at lower vertical extents would submerge earlier and the model is an optimistic estimate of time until submergence. Second, while feedbacks between surface elevation change and other environmental features (sediment supply, vertical location in the tidal frame and so on) were not explicitly incorporated, they were implicitly included as they would have contributed to the observed SET data upon which the model was built. Third, we assumed that mangroves would be submerged when they reached MSL (50% of the tidal range). However, mangroves may be able to persist beyond this time (that is, there may be a time lag), owing to physiological tolerance and acclimatization. If this time lag were to exist, then it would extend the time frame for which mangroves would be expected to survive after submergence. Lastly, the model does not consider the area of habitat, or predict when new habitat would become available.

Time scales of soil surface elevation records. The timescale of SET measurements is relatively short compared to the timescales of ecosystem change in response to SLR; therefore, to assess whether SET measurements are representative of longer term rates of surface elevation change we took two approaches. The first uses SET records of differing lengths to compare shorter- and longer-term rates. The second compares SET elevation gains with those inferred from ^{210}Pb dating of sediment cores (over the scale of decades) for the few sites where sediment dating and SET data are available.

To assess whether the length of the SET record is likely to influence our results, surface elevation gains measured over longer periods (mean record length of 5.5 years) were compared to those over shorter periods (mean record length of 2.1 years) for three sites (New Zealand, $N = 3$; Micronesia, $N = 13$; Moreton Bay, Australia, $N = 18$). Longer-term and shorter-term rates were highly correlated ($R^2 = 0.59$) with a slope of 0.90 ± 0.13 which was not statistically different from 1 ($t = 0.769$, $P = 0.45$) (Extended Data Fig. 4). The lengths of the SET records were not correlated with surface elevation gain, surface accretion, shallow subsidence or elevation deficits relative to SLR. Six SETs in Micronesia have now been monitored for 16.6 years. At this site, surface elevation gains at 16.6 years were correlated with surface elevation gains at 6.6 years: (surface elevation at 16.6 yr) = −0.16 + (0.36 ± 0.12) × (surface elevation at 6.6 yr), $R^2 = 0.59$. Thus, in Micronesia, the long-term elevation gain was approximately 40% of the short-term rate, indicating compaction of the sediment profile over time. ^{210}Pb dating of sediment cores and SET data are available for the New Zealand site and also for locations on the east coast of Australia. In New Zealand, sediment accumulation rates measured using SETs and those using ^{210}Pb (from the 1960s to the present) are similar[34]. In Moreton Bay, the mean rate of mangrove sediment accumulation using ^{210}Pb was 1.2 ± 0.9 mm yr^{-1}, which is lower, but in the range of that observed using SETs in similar habitats (1.7 ± 0.5 mm yr^{-1}; ref. 35); in southeastern Australia, ^{210}Pb was 1.7 ± 0.3 mm yr^{-1}, which is higher than that observed using SETs (0.72 ± 0.49 mm

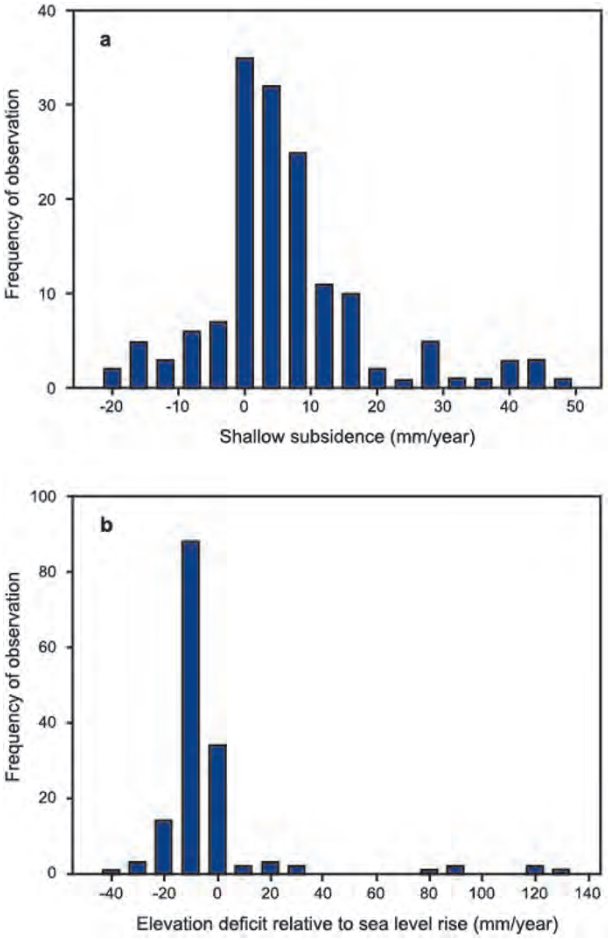
©2015 Macmillan Publishers Limited. All rights reserved

yr^{-1}; ref. 35). Additionally, rates of surface elevation gain measured with SETs in the Caribbean and Florida are broadly consistent with sediment accumulation rates derived from ^{14}C dating[15] and ^{210}Pb dating[36]. The study in Florida[36] found sediment accumulation based on ^{210}Pb was on average 81% of that measured using 2.5-yr SET records. Compaction can be caused by loss of pore space due to dewatering and grain packing, and compression and decomposition of organic matter, which may not occur linearly over time[37]. Variation in sediment characteristics are likely to lead to variable rates of compaction over the Indo-Pacific region. If high rates of compaction are typical, then our short-term rates may over-estimate surface elevation gains for the region.

Total suspended matter in coastal waters. In this study we used level-3-processed TSM data at 4-km resolution and binned monthly (data freely available from http://hermes.acri.fr/). TSM concentration was derived from the MERIS instrument on the European Space Agency's (ESA) Envisat satellite (390–1,040 nm). TSM in coastal waters is an indicator of suspended sediments associated with river run-off and resuspension and is useful in both estuarine and reef lagoon waters[38]. Data products were processed and validated as part of the ESA's DUE GlobColour Global Ocean Colour for Carbon Cycle Research project (for more information on data processing see http://www.globcolour.info/CDR_Docs/GlobCOLOUR_PUG.pdf). The resulting raster grid was displayed in the plate-carrée projection. TSM was extracted using the open-source software BEAM VISAT (http://www.brockmann-consult.de/cms/web/beam/; ESA), using the TSM value of the pixel containing, or closest to, the SET site. For 24 sites, we used data from the pixel containing the SET site (that is, within 4 km of the site); 3 sites were 1 pixel distant and 3 sites were greater than 1 pixel distant (2 pixels for Kooragang Island, 5 pixels for Quail and 17 pixels for Porong). The Porong region has limited data availability owing to high cloud cover. An annual mean for 2011, where data from all sites was available, was calculated by averaging TSM pixel data for January, April, July and October. In other years, TSM from many sites were missing from the data set. We used mean annual data in 2011 to assess relationships between sediment accretion and TSM. Comparison of TSM values over the different years the data were available (since 2002) found that spatial differences were consistent over years. The relationship between mean TSM in 2011 and mean over the available record is shown in Extended Data Fig. 5. The linear regression of this relationship is (mean TSM in 2011) $= (1.38 \pm 0.94) + (0.58 \pm 0.08) \times$ (mean TSM over all available years), $R^2 = 0.64$, $P < 0.0001$, F test, where the indicated uncertainties are standard errors.

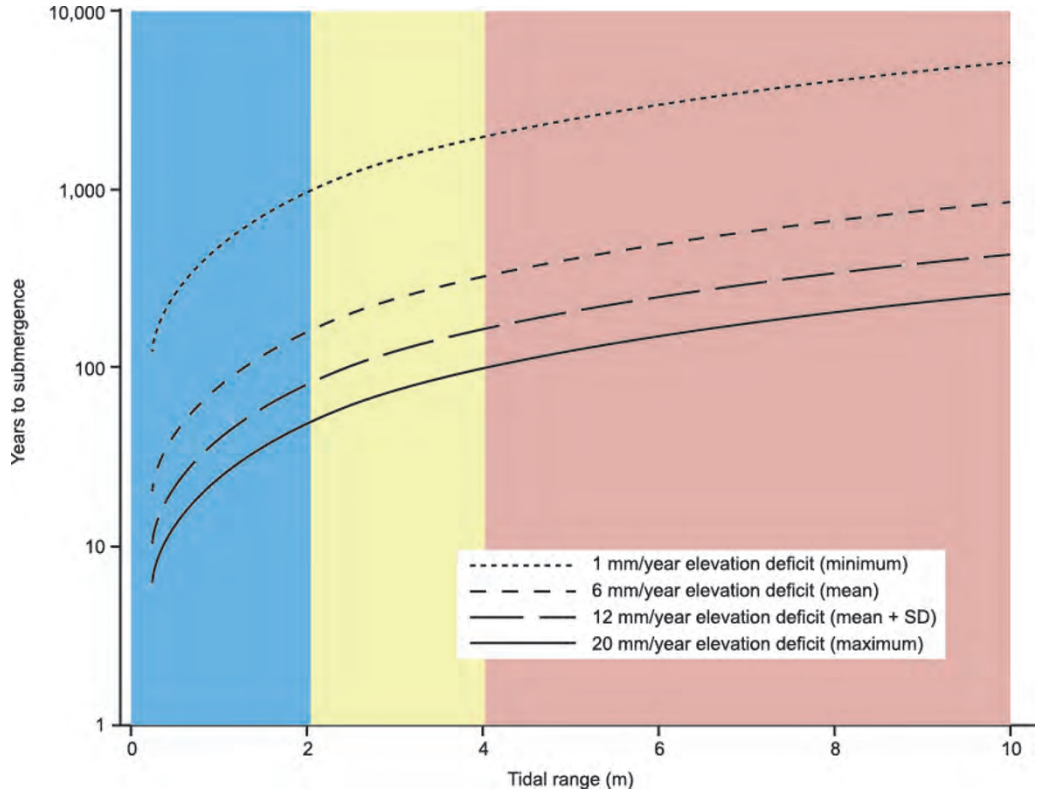
29. Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J. Anim. Ecol.* **77,** 802–813 (2008).
30. Woodroffe, C. in *Tropical Mangrove Ecosystems* (eds Robertson, A. I. & Alongi, D. M.) Ch. 2 (American Geophysical Union, 1993).
31. Lugo, A. I. & Snedaker, S. C. The ecology of mangroves. *Annu. Rev. Ecol. Syst.* **5,** 39–64 (1974).
32. Carrère, L., Lyard, F., Cancet, M., Guillot, A. & Roblou, L. FES 2012: a new global tidal model taking advantage of nearly 20 years of altimetry. In *Proc. 20 years of Progress in Radar Altimetry Symp.* ESA SP-710 (2012).
33. Horton, B. P., Rahmstorf, S., Engelhart, S. E. & Kemp, A. C. Expert assessment of sea-level rise by AD 2100 and AD 2300. *Quat. Sci. Rev.* **84,** 1–6 (2014).
34. Swales, A., Bentley, S. J. & Lovelock, C. E. Mangrove-forest evolution in a sediment-rich estuarine system: opportunists or agents of geomorphic change? *Earth Surf. Proc. Land.* **40,** 1672–1687 (2015).
35. Rogers, K., Saintilan, N. & Heijnis, H. Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence and sea level rise. *Estuaries* **28,** 551–559 (2005).
36. Cahoon, D. R. & Lynch, J. C. Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, U.S.A. *Mangroves Salt Marshes* **1,** 173–186 (1997).
37. Woodroffe, C. D. *et al.* Mangrove sedimentation and response to relative sea-level rise. *Annu. Rev. Mar. Sci.* Preprint at http://www.annualreviews.org/doi/abs/10.1146/annurev-marine-122414-034025.
38. Blondeau-Patissier, D. *et al.* ESA-MERIS 10-year mission reveals contrasting phytoplankton bloom dynamics in two tropical regions of Northern Australia. *Remote Sens.* **6,** 2963–2988 (2014).

©2015 Macmillan Publishers Limited. All rights reserved



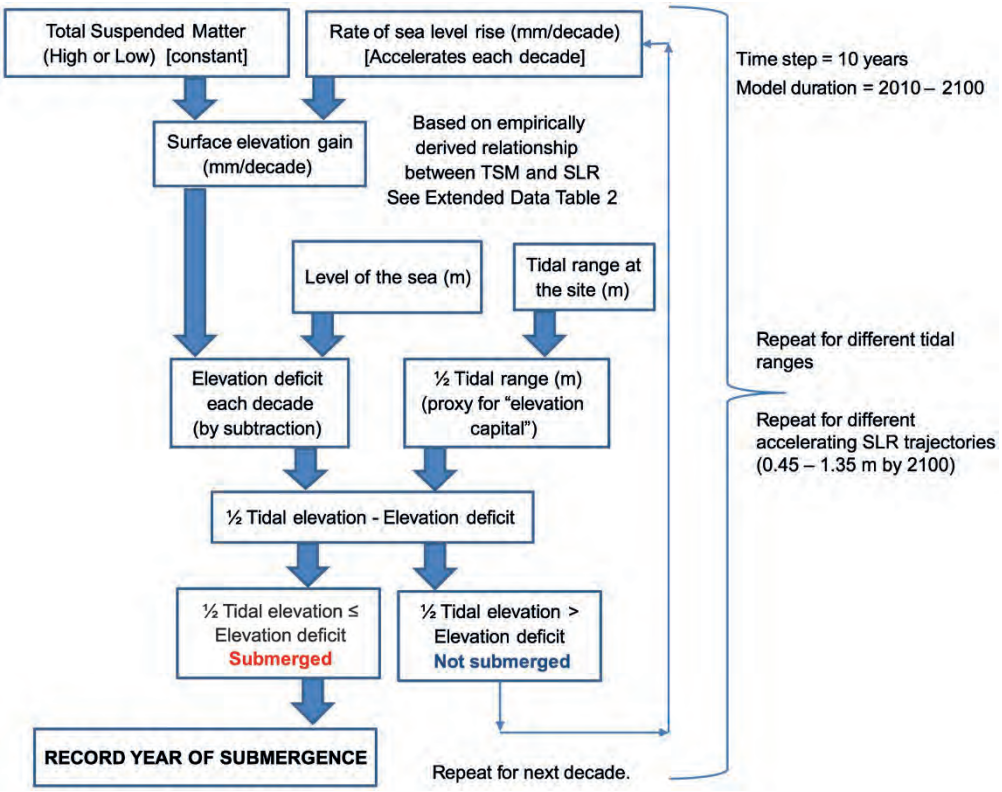
Extended Data Figure 1 | Frequency distributions of values of shallow subsidence and elevation deficits. **a**, The frequency distribution of shallow subsidence over all the SET sites, calculated as (surface accretion) − (surface elevation gain). (The data presented here are available online from the Source Data of Fig. 2). **b**, The frequency distribution of surface elevation deficits relative to SLR from tide gauges (see Supplementary Table 1).

©2015 Macmillan Publishers Limited. All rights reserved



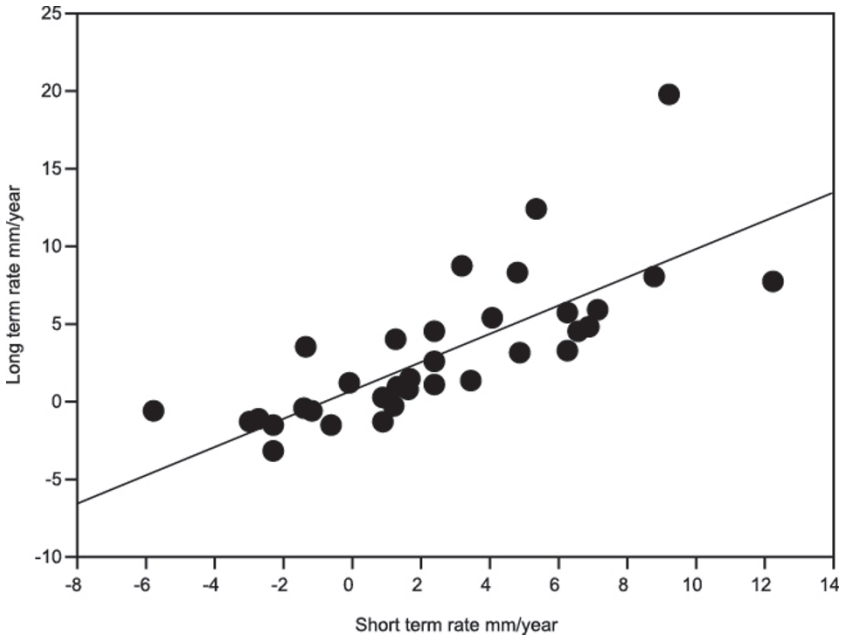
Extended Data Figure 2 | Years until submergence (logarithmic scale) of the highest intertidal mangrove forest over variation in tidal range and for a range of elevation deficits. The elevation deficit is the difference between the rate of local SLR and the rate of surface elevation gain. Submergence is assumed to occur when the cumulative elevation deficit is equivalent to the elevation capital (defined as half the tidal range). The mean elevation deficit in our study was 6 mm yr^{-1} (dashed line); other elevation deficits shown are 12 mm yr^{-1} (mean + SD = 6 + 6.3; long-dashed line), 1 mm yr^{-1} (minimum; dotted line) and 20 mm yr^{-1} (maximum; solid line). Categories of tidal range are coloured blue for microtidal, yellow for mesotidal and red for macrotidal.

©2015 Macmillan Publishers Limited. All rights reserved



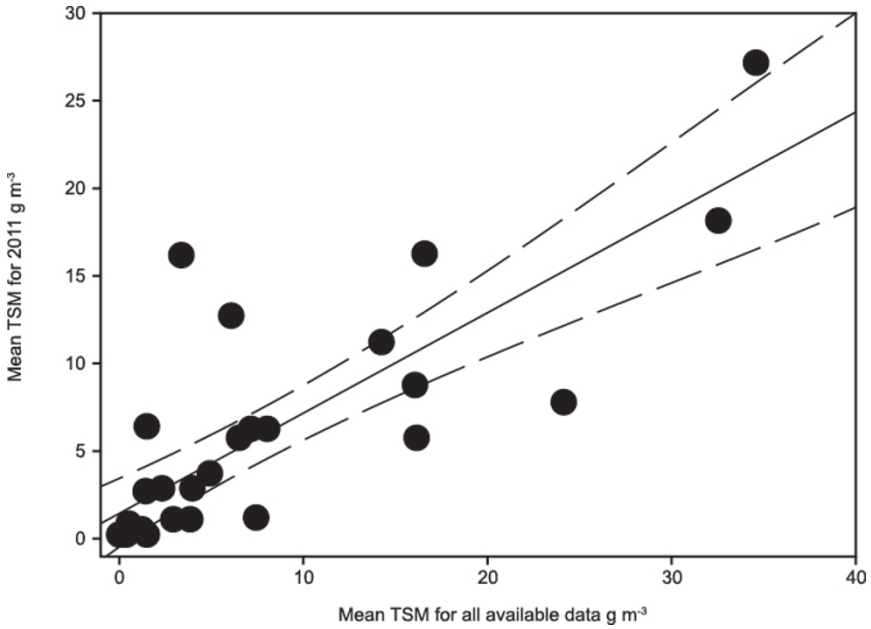
Extended Data Figure 3 | Schematic summary of the modelling process for estimating the decade of submergence of mangrove forests with SLR.

©2015 Macmillan Publishers Limited. All rights reserved



Extended Data Figure 4 | Comparison of surface elevation gains measured over longer and shorter periods for three sites. The three sites are New Zealand ($N = 3$), Micronesia ($N = 13$) and Moreton Bay, Australia ($N = 18$). The long-term mean record length is 5.5 years; the short-term mean record length is 2.1 years. Longer-term and shorter-term rates were highly correlated ($R^2 = 0.59$) with a slope of 0.90 ± 0.13, which is not statistically different from 1 ($t = 0.769$, $P = 0.45$).

©2015 Macmillan Publishers Limited. All rights reserved



Extended Data Figure 5 | The relationship between mean TSM in 2011 over the available TSM record (2002–2011). In 2011, all sites were represented in the MERIS data set. The linear regression (solid line) of this relationship is (mean TSM in 2011) = (1.38 ± 0.94) + (0.58 ± 0.08) × (mean TSM over all available years), $R^2 = 0.64$, $P < 0.0001$, F test, where the indicated uncertainties are standard errors. Dashed lines are 95% confidence intervals.

©2015 Macmillan Publishers Limited. All rights reserved

Extended Data Table 1 | Summary of the relative influence of predictor variables on surface elevation change for BRT models

Model predictor	Relative Influence (%)
Model 1	
Total Suspended Matter (annual mean) g m^{-3}	36.47
Sea level change at tide gauge (mm/year)	29.32
Longitude	8.81
Geomorphological setting	7.19
Ecological habitat	5.36
Latitude	5.20
Dominant tree genera	3.68
Annual rainfall (mm)	2.84
Tidal range (m)	1.12
Model 2	
Total Suspended Matter (annual mean) g m^{-3}	37.40
Sea level change during the SET measurement (mm/year)	30.00
Longitude	8.56
Geomorphological setting	6.99
Ecological habitat	5.82
Latitude	4.00
Dominant tree genera	4.08
Annual rainfall (mm)	2.12
Tidal range (m)	1.06
Model 3	
Total Suspended Matter (annual mean) g m^{-3}	53.38
Sea level change from satellite altimetry (mm/year)	3.02
Longitude	14.22
Geomorphological setting	6.77
Ecological habitat	5.08
Latitude	4.97
Dominant tree genera	5.72
Annual rainfall (mm)	3.17
Tidal range (m)	3.66

See Methods for descriptions of the different models and predictors.

©2015 Macmillan Publishers Limited. All rights reserved

Extended Data Table 2 | Parameters used in the model for estimating time to submergence of mangrove forests for different sediment availability (classes of TSM).

Sediment availability classes	Slope	Standard error of estimate	Intercept	Standard error of estimate	R^2
Low (<2.5 g m^{-3})	0.36	0.04	0.29	0.53	0.45
High (>2.5 g m^{-3})	5.84	0.28	-24.6	2.49	0.85

The model is described in Extended Data Fig. 3. TSM values were obtained from MERIS data; see Methods. The parameters describe the linear regression relating surface elevation gain (in millimetres per year) to SLR (in millimetres per year) for two sediment availability bins, averaged over all tidal ranges; see Fig. 3.

©2015 Macmillan Publishers Limited. All rights reserved

Processes Influencing Autocompaction Modulate Coastal Wetland Surface Elevation Adjustment With Sea-Level Rise

Rogers, Kerrylee; Saintilan, Neil

ProQuest document link

ABSTRACT (ENGLISH)

The fate of coastal wetlands and their ecosystem services is dependent upon maintaining substrate elevations within a tidal frame that is influenced by sea-level rise. Development and application of morphodynamic models has been limited as few empirical studies have measured the contribution of key processes to surface elevation change, including mineral and organic matter addition, autocompaction of accumulating sediments and deep subsidence. Accordingly, many models presume that substrates are in equilibrium with relative sea-level rise and the composition of substrates are relatively homogenous. A 20-year record of surface elevation change and vertical accretion from a large tidal embayment in Australia coupled with analyses of inundation frequency and the character of sediments that have accumulated above mean sea level was analysed to investigate processes influencing surface elevation adjustment. This study confirms the varying contribution of addition, decomposition and compression of organic material, and mineral sediment consolidation, resulting in autocompaction that is proportional to the overburden of accumulating sediments. These processes operate concurrently and are influenced by sediment supply and hydrodynamic energy. Vertical accretion was linearly related to accommodation space. Surface elevation change was related to vertical accretion and substrate organic matter, indicated by carbon storage above mean sea level, and conformed to models that initially increase and then decrease as accommodation space diminishes. Rates of surface elevation change were largely found to be in equilibrium with sea-level rise measured at the nearest tide gauge, which was estimated at 3.5 mm y-1 over the period of measurements. As creation of new accommodation space with sea-level rise is contrary to the longer-term history of relative sea-level stability in Australia since the mid-Holocene, striking stratigraphic variation arises with deeper sediments dominated by mineral sands and surficial sediments increasingly fine grained and having higher carbon storage. As the sediment character of substrates was found to influence rates of surface elevation gain, we caution against the unqualified use of models derived from the northern hemisphere where substrates have continuously adjusted to sea-level rise and sediment character is likely to be more homogenous.

FULL TEXT

Introduction

The influence of accelerating sea-level rise (SLR) (Church et al., 2013) on tidal dynamics has directed attention to the fate of saline coastal wetlands and the ecosystem services they provide (Reed, 1990; Morris et al., 2002; Krauss et al., 2014). The response of coastal wetlands to SLR is dependent upon feedbacks between hydrodynamics, sedimentation, plant productivity, sediment diagenesis, and organic matter decomposition (Pethick, 1981; Allen, 2000; Morris et al., 2002; Alongi, 2008). These feedbacks influence wetland substrate elevations and are important when considering the fate of coastal wetlands exposed to rising sea level. As such, there has been increasing focus on measuring and parameterizing processes contributing to elevation adjustment (see reviews by Fagherazzi et al., 2012; Wiberg et al., 2020). Allen (2000) conceptualized a relatively simple one dimensional model describing substrate elevation adjustment relative to a moving tidal frame that is influenced by SLR (ΔE). In this model, the change in tidal position of a wetland surface is attributed to the addition of mineral sediment (ΔS_{min}) and organic material (ΔS_{org}), and the degree of change due to autocompaction (ΔP). Critically, this adjustment is relative to the

additional vertical space created by SLR for sediment accumulation (ΔM). The term “accommodation space” is used to describe the vertical space for mineral and sediment accumulation. In the context of this model, the variable ΔM incorporates available accommodation space created by both eustatic, tectonic and isostatic processes influencing relative SLR, whilst ΔP describes the additional accommodation space created by autocompaction.

ΔE=ΔSmin+ΔSorg−ΔP−ΔM(1) ΔE=ΔSmin+ΔSorg-ΔP-ΔM(1)

Resolving spatial and temporal patterns in surface elevation change is crucial for developing and validating morphodynamic models of the response of coastal wetlands to a shifting tidal frame as sea level rises, and some efforts have been directed toward this task. Early empirical studies found that accretion was proportional to tidal position and proposed that this was due to negative feedbacks between these factors; the ensuing outcome of negative feedbacks was proposed to be an asymptote in substrate elevations as they age (Kestner, 1975; Pethick, 1981). Subsequent empirical models described sedimentation in the context of inundation depth and distances to sediment sources, such as creeks and channels, with functions taking an exponential (Temmerman et al., 2003) or linear form (Krone, 1987; French, 1993). Physical models built upon Exner’s equation of conservation of mass applied advection diffusion equations (Rinaldo et al., 1999) that could be modified to account for distances to sediment sources. As empirical data of processes contributing to surface elevation change became available, models have evolved and increased in complexity. The empirically developed model of Morris et al. (2002) ascribed surface elevation change to both organic matter addition and mineral sediment addition that was proportional to depth below mean high tide and organic matter addition was parameterized as a function of the standing density of plant biomass or above ground productivity. The productivity function was expressed as a second order polynomial that describes the relationship between productivity of *Spartina alterniflora* and depth below mean high tide, and coefficients describe the tolerance of vegetation to inundation and the inundation depth of peak productivity. Application of a modified form of Exner’s equation by Marani et al. (2013) quantified sediment deposition on the basis of settling velocity, bulk density and sediment porosity, and was governed by hydrodynamic transport regulated by tidal flooding. It also allowed for the rate of organic matter production to be modulated by compaction and decomposition processes, and incorporated the varying tolerance of different species to inundation and associated feedbacks with organic matter addition to substrates. The Organic-Inorganic Marsh Accretion and Stratigraphy-Numerical (OIMAS-N) model (Mudd et al., 2009) takes a one-dimensional form and simulates the evolution of a sediment column with SLR. It specifically incorporates organic matter addition, decay of three carbon pools (refractory, fast labile, and slow labile), inorganic sedimentation, and compaction. The model is parameterized so that organic matter declines linearly away from the surface and is proportional to above-ground biomass (as per Morris et al., 2002) and inorganic sedimentation is linearly related to and inundation. Compaction is a function of void space and the compressibility of substrate material of varying fabric (i.e., mineral or organic) and size (i.e., sand and silt). The Wetland Accretion Rate Model of Ecosystem Resilience (WARMER) model (Swanson et al., 2014; Thorne et al., 2018) has a similar structure and incorporates mineral sediment accretion, organic matter addition and decomposition and compaction. Mineral sediment is parameterized to increase linearly with increasing inundation depth, organic matter addition follows Morris et al. (2002), organic matter decomposition declines exponentially from the surface, and compaction varies with sediment porosity (as per Callaway et al., 1996).

Currently there is general agreement that net vertical accretion, arising from mineral sedimentation and erosion, is a function of accommodation space. This is commonly and expressed in models on the basis of elevation or depth below mean high tide and related to energy pathways that transport sediment for deposition or erosion (Fagherazzi et al., 2012). Model functions variably take a linear form (for example Krone, 1987; French, 1993) or exponential form (for example Temmerman et al., 2003). Organic matter accretion may also be expressed as a function of accommodation space, either linearly (D’Alpaos et al., 2007), or as a second-order polynomial with peak productivity delimited by the vertical distribution of vegetation (Morris et al., 2002). However, there is less agreement on attribution of the post-depositional behavior of mineral and organic matter in substrates (Wiberg et al., 2020; Zhang et al., 2020).

Empirical data and associated models are commonly derived from wetlands of the mid-Atlantic coasts of the United

States and Europe, southern coasts of the North Sea, and Pacific coasts of the United States, where wetlands have been adjusting to relative sea-level rise (RSLR) for millennia (Fagherazzi et al., 2012; Wiberg et al., 2020). These locations, often termed intermediate-field locations due to their proximity to extensive areas of land-based ice, have been undergoing vertical land movement due to glacio-isostatic adjustment (Murray-Wallace and Woodroffe, 2014; Khan et al., 2015). This adjustment has contributed to ongoing RSLR throughout the Holocene, despite relatively stable eustatic sea levels over the past ~7,000 years. Holocene sea level records at intermediate-field locations contrast far-field locations, predominantly in the southern hemisphere, where sea level records generally exhibit a mid-Holocene highstand (the timing and magnitude is spatially variable) before falling to present levels over the past few millennia. Rogers et al. (2019) proposed that movement of the tidal frame relative to land surfaces at intermediate-field locations over the past few millennia promotes preservation of organic matter and creation of new accommodation space. Conversely, sea-level stability, or a fall following a highstand, promotes decomposition of organic matter and accommodation space becomes increasingly limited (Rogers et al., 2019). This hypothesis was confirmed in global-scale analyses of carbon content within saltmarsh sediments, which found carbon content is generally lower at far-field locations than intermediate-field locations, and carbon is generally concentrated near the active rooting zone of saltmarsh vegetation at far field locations. The predominance of models derived from intermediate-field empirical data may be problematic when applied to the southern hemisphere as they commonly presume substrates are relatively homogenous with little variation in stratigraphy, or that elevations gain corresponds to RSLR. Empirical data from a range of settings, particularly in the southern hemisphere where there are considerable data gaps, are needed to fully elucidate controls on coastal wetland evolution under SLR.

This paper seeks to address some of these data gaps by analyzing a 20-year observational record of surface elevation change, vertical accretion and by deduction, autocompaction of wetland surfaces from a tidal embayment in southern Australia. Westernport Bay, located east of Melbourne, has a complex intertidal vegetation composition that includes zones dominated by mangroves, saltbush, herbaceous saltmarsh and rushes. Differentiation of processes contributing to autocompaction, namely addition/decomposition of organic matter, compression of organic matter and consolidation of mineral sediments was facilitated by analyses of substrate composition. The overall aim of this study was to conceptualize processes contributing to surface elevation adjustment with SLR. The specific objectives were to:

i) identify processes influencing surface morphodynamics that account for variation in substrate characteristics, autocompaction and vertical accretion;

ii) validate existing modeling approaches by applying functions of varying structure (i.e., linear, exponential, peak models) to develop relationships between vertical accretion, surface elevation change, autocompaction, and indicators of tidal position (i.e., elevation and inundation frequency); and

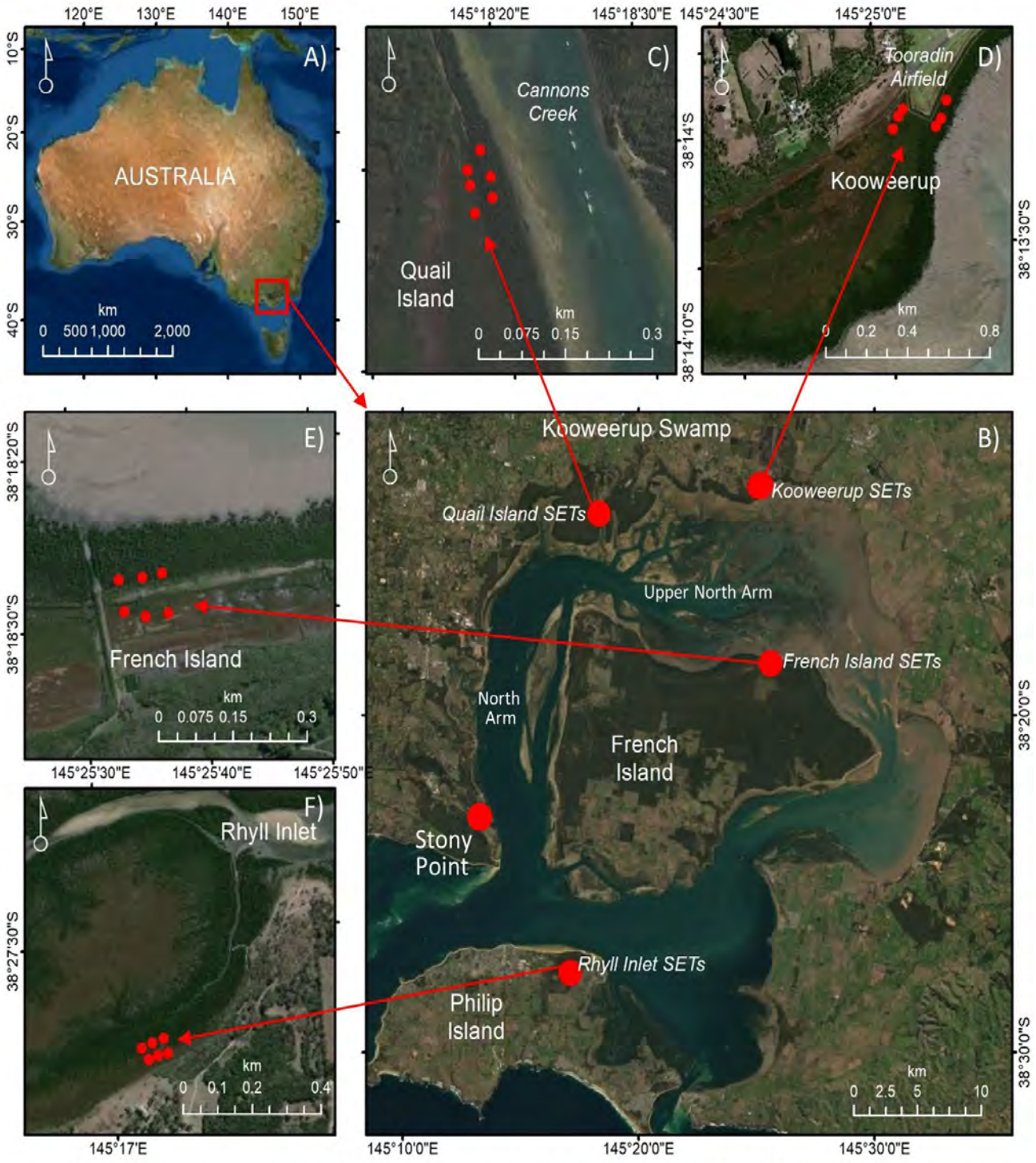
iii) verify whether surface elevation change is in equilibrium with the shifting tidal frame.

Materials and Methods

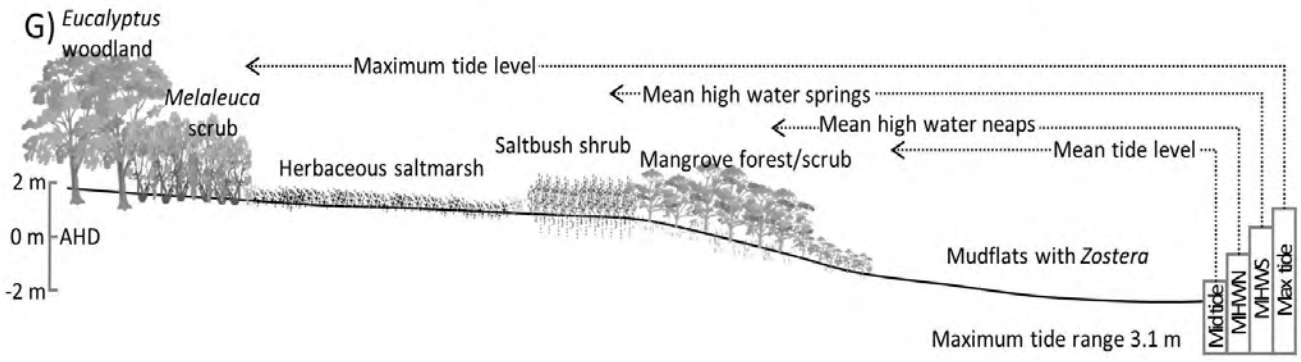
Study Site and Design

Westernport Bay (38°21′S, 145°13′E) is a large coastal embayment (~680 km^2). It drains a catchment area of 3,433 km^2 and is located east of Melbourne Victoria, Australia (Figure 1). The region is relatively tectonically and isostatically stable and vertical land movement of tide gauges is negligible (White et al., 2014; Khan et al., 2015). Post-glacial sea level is reported to have increased to a highstand of 1–1.5 m above present levels approximately 6,900 cal. yr BP before falling to present levels after 2,000 cal. yr BP (Lewis et al., 2013; Dougherty et al., 2019). The region is also prone to periodic drought associated with negative phases of the Southern Oscillation, and an increase in the frequency of positive phases of the Southern Annular Mode and the Indian Ocean Dipole (Dey et al., 2019). The influence of drought on rainfall has been associated with changes in substrate elevations of coastal wetlands around Westernport Bay (Rogers et al., 2005b).

FIGURE 1



Service Layer Credits: Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community



Enlarge this image.

Westernport Bay has two entrances to Bass Strait; the constriction of the eastern entrance near San Remo causes tides to propagate relatively freely through the Western entrance, clockwise around French Island until they

converge with anticlockwise tidal movement. The tidal regime is semi diurnal with a tidal range of up to 3.1 m. Significant tidal amplification occurs along the upper North Arm of Westernport Bay (Water Technology, 2014). Despite its size, the embayment is relatively shallow and tides comprise approximately 30% of the total volume at high tide (Lee in Boon et al., 2011). Westernport Bay includes extensive intertidal flats (~270 km^2) that supports mangrove and saltmarsh communities along its low energy intertidal shorelines, estimated to cover approximately 12.3 and 10.9 km^2, respectively (Boon et al., 2011). These wetlands comprise a lower elevation mangrove zone that supports the cold tolerant mangrove, *Avicennia marina*, which is near its most latitudinal limit at this location. The upper intertidal zone also supports a dense thicket of saltmarsh shrubs of the genus *Tecticornia* and a landward zone of herbs, grasses and sedges that are regarded to be highly diverse (Boon et al., 2011).

Rogers et al. (2005b) presented results from a network of surface elevation tables (SET) and marker horizons (MH) established in 2000. These SETs were established to provide quantitative information on the dynamics of mangrove and saltmarsh vegetation and changes in rates of sedimentation and surface elevation. This network comprised 24 SET-MH stations in a nested design whereby six SETs were co-located at French Island, Kooweerup, Quail Island, and Rhyll (Figure 1). At each location, SETs were positioned in groups of three within structurally similar vegetation; three were located in the mangrove zone, lower in the tidal frame, and three were located in herbaceous saltmarsh zones higher in the tidal frame. Some saltmarsh SET locations have become increasingly dominated by *Tecticornia* over the 20 year analysis period, particularly at Kooweerup (*pers. obs.*). This paper provides an updated analysis from this network.

Inundation Frequencies and Water Levels

Analyses of variation in water levels associated with tidal inundation at co-located mangrove and saltmarsh SETs at each study site were undertaken using hobo water level loggers. The vertical and horizontal position of each SET and hobo water level logger was determined using RTK-GPS during field campaigns. All vertical positions are henceforth reported according to the Australian height datum (AHD). The frequency of inundation was determined for each logger on the basis of whether the logger was inundated for each 15 min logging increment over the logging period; logging periods exceeded 6 months at each study site and included highest high spring tides. The nearest tide gauge is managed by the local port authority and is located at Stony Point (Station no. 586268). This gauge underwent repositioning in 2017, and to control for inaccuracies that may arise from moving the tide gauge, processed data was only used for the period of August 1981 to July 2017. Processed data was converted to AHD. Maximum daily water level from each logger (logged at 15-min intervals) and the Stony Point tide gauge (logged at 6-min intervals) was compared to identify tidal modification at study sites. The maximum, minimum and mean recorded water level recorded at the tide gauge at Stony Point over the period of water-level logging was also determined. This facilitated the development of a relationship between elevation and inundation frequency. To do so, the elevations above the maximum water level were presumed to be rarely inundated; elevations below the minimum water level were presumed to be inundated 100% of the time, whilst the mean water level was presumed to represent the elevation with an inundation frequency of 50%. Inundation frequencies were plotted against elevation and the best model was used to determine a relationship between elevation and inundation frequencies. This model was used to determine inundation frequency of each SET-MH monitoring station and core locations. Processed minimum, mean and maximum monthly water-level data for the Stony Point tide gauge was also accessed for the full record length. Conversion of this data to be relative to AHD meant the position of SETs and the tidal frame were determined using the same datum. This processed tide gauge data underwent additional processing to remove any months where data gaps were greater than 10% of the gauging frequency each month. Linear regressions were used to identify the rate of change in minimum, mean, and maximum monthly water levels for the full record length. As intertidal vegetation is typically positioned above mean sea level, mean and maximum linear regressions were subsequently used to indicate change in intertidal vegetation tidal position.

Sediment Characterization

Sediment cores of approximately 1.5 m length were collected in 2017. Cores were collected adjacent to mangrove and saltmarsh SET monitoring stations at each study site. Cores were extracted in aluminum tube of 75 mm

diameter. The degree of sediment compaction that occurred during core collection was determined and cores were capped to ensure they remained continuous and intact. Cores were placed in cold storage at 4°C until sample preparation was undertaken. The position of each core at the time of extraction was determined using an RTK-GPS. Sediment cores were split longitudinally and half of the core was subsampled at intervals of 2 cm for the upper 10 cm of sediment, every 5 cm to 1 m depth and every 10 cm below 1 m depth for further analysis. The remaining core was placed in storage. Grain size of each sample was determined (μm) using a Malvern Mastersizer 2000 laser diffractometer. To determine dry bulk density (g cm^{-3}), samples were oven dried to constant weight at 60°C. Dry sample weight was determined and bulk density (BD) was estimated as the ratio of dry sample mass to wet sample volume. Each sample was then homogenized by grinding to a fine powder using a Retsch three-dimensional vibrator mill (Type-MM-2: Haan, Germany). Samples were analyzed for percentage carbon (%C) using dry combustion techniques by the Environmental Analysis Laboratory at Southern Cross University.

Sediment profiles were developed that characterized grainsize, bulk density and carbon content for each core. Core depths were calibrated to AHD to facilitate comparisons on the basis of elevation. Depth constrained cluster analysis was undertaken for grainsize fraction, bulk density and carbon content in R using the Rioja package. The depth of clusters, with respect to AHD were used to identify consistent patterns between study sites. Total carbon content in the upper 30 cm was quantified to indicate near surface carbon content of each core. Total carbon content was also quantified for sediments positioned between 0 m AHD (approximating MSL) and the wetland surface to represent carbon storage across the vertical distribution of intertidal vegetation. ANOVAs were undertaken on both estimates of carbon in the upper 30 cm and above MSL to identify statistical differences between cores extracted from mangrove and saltmarsh. C content above MSL was standardized for the volume of sediment above MSL; this characterized the C content per meter of substrate (i.e., g cm^{-2} m^{-1}). Linear regression analyses were undertaken to establish relationships between C content either in the upper 30 cm, C content above MSL (i.e., above 0 m AHD), standardized C content, and elevation and inundation frequency.

Surface Elevation Morphodynamics

SET-MH techniques were used to characterize surface elevation morphodynamics and SETs were established in Westernport Bay in 2000 (Rogers et al., 2005b). The SET acts as a stable benchmark against which measurements in substrate elevation change can be determined (Cahoon et al., 2002). Each SET monitoring station includes a platform that protects substrates from compression and compaction during installation and whilst taking measurements. At each SET monitoring station, a vertical benchmark pole was inserted to the point of refusal and extends to substrate depths of up to 6 m. The original SET design was used in this study and is composed of a horizontal arm that is positioned on the vertical benchmark pole; this horizontal arm is positioned in the same location using a spirit level. A plate at the end of the horizontal arm accommodates pins that are lowered to the wetland surface, and the height of each pin above the horizontal plate is measured. At each SET monitoring station, measurements of nine pins are taken in four arm directions; this generated 36 measurements of substrate elevation at each monitoring station. Repeated measurements of the height of pins above the horizontal plate were taken in four arm directions at each station. This provided time-series data of relative surface elevation change for each pin. This large dataset was subsequently reduced to determine the mean relative surface elevation change for each SET monitoring station at each measurement time. Measurements of SET elevation using an RTK-GPS allowed measurements of surface elevation change to be calibrated to AHD and for distances to the wetland edge and main channel at Rhyll to be calculated. Due to the multi-decadal period of measurements, some benchmark poles had undergone corrosion or were damaged by debris. In some cases, damage became substantial enough that the benchmark was no longer regarded to be stable. This was evident for one mangrove SET at Quail Island and one saltmarsh SET at Kooweerup. Deficits in funding limited the capacity to undertake annual measurements. Measurements were taken initially in October 2000 and repeated measurements were taken in November 2001, November 2003, December 2009, May 2015, April 2016, May 2017, December 2018, and November 2019. Feldspar marker horizons were established in three replicate plots of 50 cm ×50 cm at the margins of each SET monitoring station platform when baseline measurements were undertaken in 2000. When subsequent SET

measurements were taken, mini cores were extracted from each MH plot and the vertical increase in sediment that had accumulated above the MH was determined. This provided time-series data of vertical accretion at each plot; this data was subsequently reduced to indicate vertical accretion at each monitoring station over time. The MH is prone to loss due to dispersal associated with bioturbation and tides (Cahoon and Turner, 1989). Over the study period, the ability to detect MH diminished and results were reported only when the MH could be detected; this was particularly apparent for mangrove MH.

Statistical Analyses of Surface Elevation Morphodynamics

Linear regression analyses of surface elevation change and vertical accretion were undertaken to determine mean rates of surface elevation change and vertical accretion for each SET-MH monitoring station. Analyses of coefficient of determination (r^2) and rates of change were undertaken to determine confidence in linear regression analyses of rates of vertical accretion and surface elevation change. Results of surface elevation change at one SET monitoring station in the mangrove at Quail Island was excluded from subsequent analyses due to damage.

Subsequent analyses were undertaken to identify processes influencing rates of surface elevation change (i.e., $\Delta S_{min} + \Delta S_{org} - \triangle P$). Linear regression analyses were undertaken to determine the relationship between rates of surface elevation gain, vertical accretion and available accommodation space; the elevation of SET-MH monitoring stations and modeled inundation frequency was used to indicate accommodation space. These relationships were assessed on the basis of coefficient of determination and Akaike information criterion with correction for small sample sizes (AICc). An exponential model that relates accretion to elevation, and distances to sediment sources (i.e., wetland edge and main channel) was also applied to measurements of vertical accretion using elevation and also substituting inundation for elevation (Temmerman et al., 2003). This model describes sedimentation rates on the basis of depth below mean high tide (H), distance to nearest creek edge (Dc), and marsh edge (De), and parameters (k, l, m, n), and has the form indicated in equation 2. Parameters were solved on the basis of 1,000 iterations until convergence was achieved at a significance level of 0.05.

Sedimentationrate=kelH·emDc·enDe(2) Sedimentationrate=kelH·emDc·enDe(2)

For measurements of surface elevation change, we also investigated whether peaks associated with organic matter production were evident in rates of surface elevation change. As surface elevation change describes the combined influence of surface accretion and processes operating within the substrate, it was not appropriate to fit a second order polynomial, as per Morris et al. (2002). Rather, best-fit Gaussian and Lorentzian peak models were applied to the relationship between surface elevation change, and elevation and inundation; care was taken to recognize zonation by generating a peak for mangrove and saltmarsh surface elevation change.

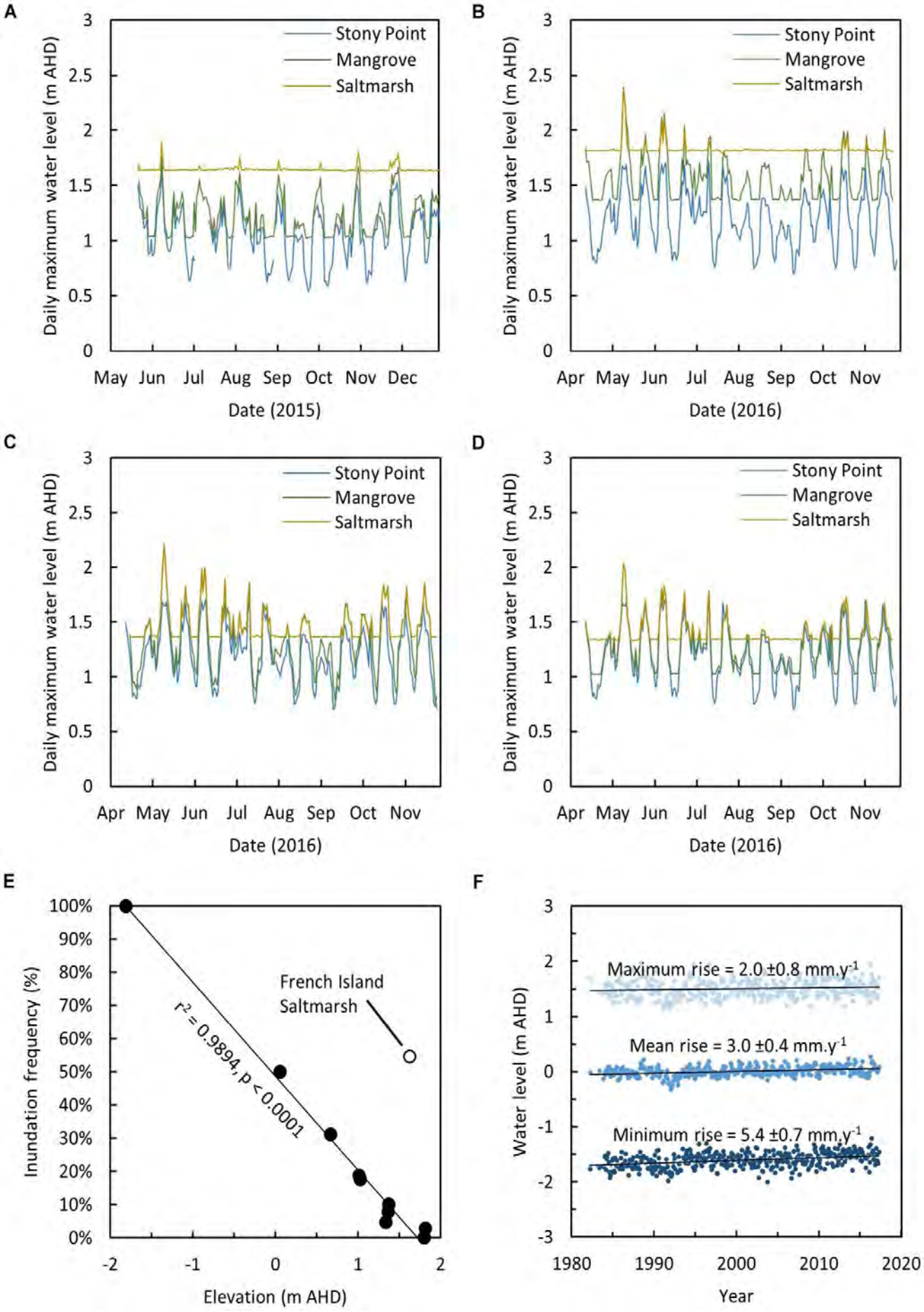
A two-way paired *t*-test was undertaken to determine whether rates of surface elevation change differed from rates of vertical accretion at each SET-MH monitoring station. The deficit between rates of vertical accretion (i.e., ΔS_{min}) and surface elevation change, which incorporates the combined influence of sediment consolidation, organic matter addition/decomposition and compression (i.e., $\Delta S_{org} - \triangle P$) was determined; for simplicity this was termed autocompaction. Autocompaction error was determined by propagating errors in rates of surface elevation change and vertical accretion. Linear regression analyses were undertaken to establish relationships between rates of surface elevation change, vertical accretion, autocompaction and substrate organic matter, using carbon storage above MSL to indicate volume of organic matter. A mixed model linear regression analysis was undertaken to determine the relationship between surface elevation change, vertical accretion and substrate carbon storage above MSL, with the hypothesis confirmed on the basis of coefficient of determination and *p*-value.

Equilibrium Analysis: Changing Tidal Position

Maintenance of tidal position (i.e., $\Delta E = 0$) indicates that the wetland substrate is adjusting in equilibrium with increasing accommodation space created by RSLR and autocompaction (i.e., $\Delta S_{min} + \Delta S_{org} - -\Delta P - -\Delta M$). Analyses of maximum, mean and minimum monthly water levels confirmed that rates of change to boundaries defining intertidal vegetation accommodation space were not consistent; that is, the rate of rise of mean water level was higher than the rate of rise of maximum water level between 1981 and 2017 (see Figure 2F). A more sophisticated approach for measuring changes to the tidal frame was required prior to assessing changes to tidal position. Changes to the tidal

frame relevant to intertidal vegetation (i.e., from mean water level to maximum water level) was defined at each time step. The relative increase in substrate elevation was then defined as the difference between the substrate surface elevation and mean water level at each time step. By deduction, change in tidal position (i.e., ΔE) was determined as the difference between the rate of change in the tidal frame and relative substrate elevation at each time step. All measurements were made relative to AHD. Accordingly, values near zero were presumed to indicate maintenance of tidal positions, positive values indicate an increase in tidal position and negative values indicate decreasing tidal position. To account for any errors in SET measurements and subsequent analyses, a buffer of ±2 mm y^{-1} was applied to all values, particularly when determining values near zero Values exceeding 2 mm y^{-1} were regarded to be increasing their position in the tidal frame and values lower than −2 mm y^{-1} were regarded to be decreasing their position in the tidal frame.

FIGURE 2



Enlarge this image.

Variation in tidal position (i.e., ΔE) should be interpreted in the context of available accommodation space or substrate elevation, particularly as mineral vertical accretion and organic matter accumulation (i.e., $\Delta S_{min} + \Delta S_{org}$) are

likely to vary on the basis of accommodation space. Hence, rates of change in tidal position were compared to substrate elevation at the time of last SET measurement. This also provided the capacity to determine the elevation at which substrate elevation gain corresponded to the rate of increase in accommodation space, or the equilibrium elevation. The mean elevation of all values where tidal position was maintained (i.e., $\Delta E = 0 \pm 2$ mm y^{-1}) were used to approximate the equilibrium elevation range across Westernport Bay.

The longer-term resilience of locations where tidal positions were diminishing were estimated by projecting observed surface elevation change, mean water level and maximum water level trajectories. Resilience was presumed to be exhausted when substrate elevations were less than mean water level, as this elevation delimits the lower boundary of mangrove vegetation and inundation frequencies at lower elevations are presumed to be beyond the physiological tolerance of mangroves. This analysis does not incorporate anticipated projections in SLR or loss of tidal position due to erosion rates beyond that already incorporated in rates of surface elevation change.

Results

Inundation Frequencies and Increasing Water Levels

Inundation frequency was variable between study site logging locations, but was generally higher in the mangrove where substrate elevations are lower than in the saltmarsh (Supplementary Figure 1). The saltmarsh SETs at French Island were the only exception where inundation frequency was estimated at approximately 55%. This high inundation frequency was attributed to ponding of water within areas that were previously used as a salt works and that has since been abandoned. The maximum tidal height at Stony Point was less than the maximum inundation height recorded at each study site (Figures 2A–D), and the timing of maximum water level at all study sites coincided with the tidal peak recorded at Stony Point. The deviation between tidal height at study sites and the Stony Point tide gauge increased as the tidal height increased, indicating significant amplification of tides as they propagate around French Island and along the Upper North Arm. This was most prominent in the mangrove at Kooweerup where tides on 10 May 2016 were amplified to an elevation of 2.388 m AHD and was markedly greater than the maximum tide gauge height of 1.652 m AHD on the same day. The observed pattern of amplification of tides was consistent with analyses of spatial variation in the mean high water springs tidal plane throughout Westernport Bay (Water Technology, 2014).

Inundation frequency was anomalously high in the saltmarsh at French Island, whilst tidal peaks were attenuated. Analyses focused on areas where salt ponds had been abandoned, and earthworks associated with salt generation remain evident in aerial photography, and likely influence both drainage of the saltmarsh and tidal incursion into the saltmarsh. A linear relationship was established between surface elevation and inundation frequency when inundation patterns in the saltmarsh at French Island were excluded ($r^2 = 0.9894$, AICc = −31.8384, $p < 0.0001$, Figure 2E). The relationship remains significant when the saltmarsh at French Island was included in the analysis ($r^2 = 0.7358$, AICc = −1.2417, $p < 0.0001$).

Mean water level at Stony Point tide gauge increased at a rate of 3.0 ±0.4 mm y^{-1} over the ~40 years of tide gauge records and increased at a higher rate than the monthly maximum water level (2.0 ±0.8 mm y^{-1}). This implies a decrease in the vertical space between mean water level and maximum water level over the tide gauge period (Figure 2F); crucially, this is the component of accommodation space occupied by intertidal vegetation. However, since 2000 when SET-MH were established, monthly maximum water level (3.5 ±2.3 mm y^{-1}) increased at approximately the same rate as monthly mean water level (3.5 ±1.2 mm y^{-1}).

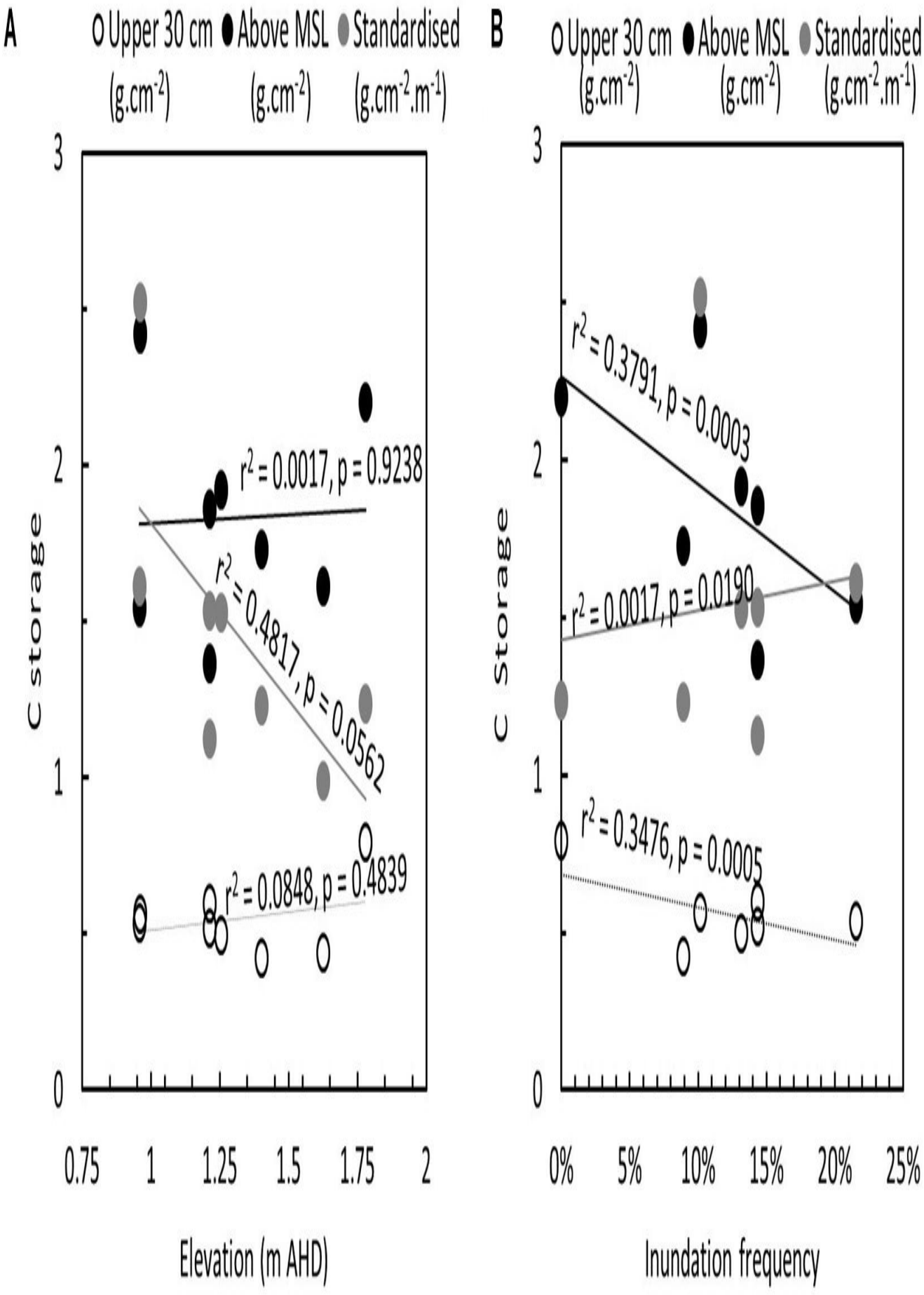
Sediment Characterization

For most cores, sediments increasingly comprised sand fractions at lower elevations beyond approximately 0.8 m AHD (Supplementary Figures 2–5). The inverse pattern was evident in the saltmarsh core at Rhyll where the grainsize was finer at depths of 0.4–1.0 m AHD and then increased at depths below approximately 0.4 m AHD. Above 0.8 m AHD, sediments were typically finer grained, and sediments from the saltmarsh at Rhyll exhibited a tendency toward finer grain sizes with increasing elevation in the core. Bulk density reflected this pattern of increasing grain size as elevation decreased with sediments typically becoming less bulky toward the surface. Carbon content was generally higher in the topmost-cluster where grainsize was typically smaller, and diminished to

negligible volumes at depths corresponding to mean sea level (i.e., approximately 0 m AHD). Anomalous carbon peaks were evident in some cores, and these sediment depths clustered separately.

Overall, C stock increased with elevation within the core, decreased with inundation frequency and was generally higher in the saltmarsh; however, the density of C was greater in the mangrove and increased with inundation frequency. No statistical difference was found in total C content in cores extracted from mangrove and saltmarsh for C in the upper 30 cm (p = 0.3528) where living root material dominates. There was also no statistical difference in C to MSL (p = 0.6001), and this is likely due to the greater sediment volume above mean sea level in the saltmarsh than the mangrove. As inundation frequency was disproportionately high despite the high elevation of the saltmarsh at French Island, subsequent analyses of relationships between C content and elevation and inundation excluded data from the saltmarsh at French Island. C content in the upper 30 cm (r^2 = 0.1309, p = 0.3784) and above MSL (r^2 = 0.1779, p = 0.2980) were positively related to elevation. Standardized C content was negatively related to elevation (r^2 = 0.2870, p = 0.1703), confirming a greater concentration of C within mangrove dominated sediments (Figure 3A). The inverse pattern was evident for relationships with inundation frequency. C content in the upper 30 cm (r^2 = 0.3476, p = 0.0005) and above MSL (r^2 = 0.3791, p = 0.0003) was negatively related to inundation frequency. Standardized C content was positively correlated to inundation frequency (r^2 = 0.0017, p = 0.0190), although the relationship was weak when French Island study sites were excluded (Figure 3B).

FIGURE 3



Enlarge this image.

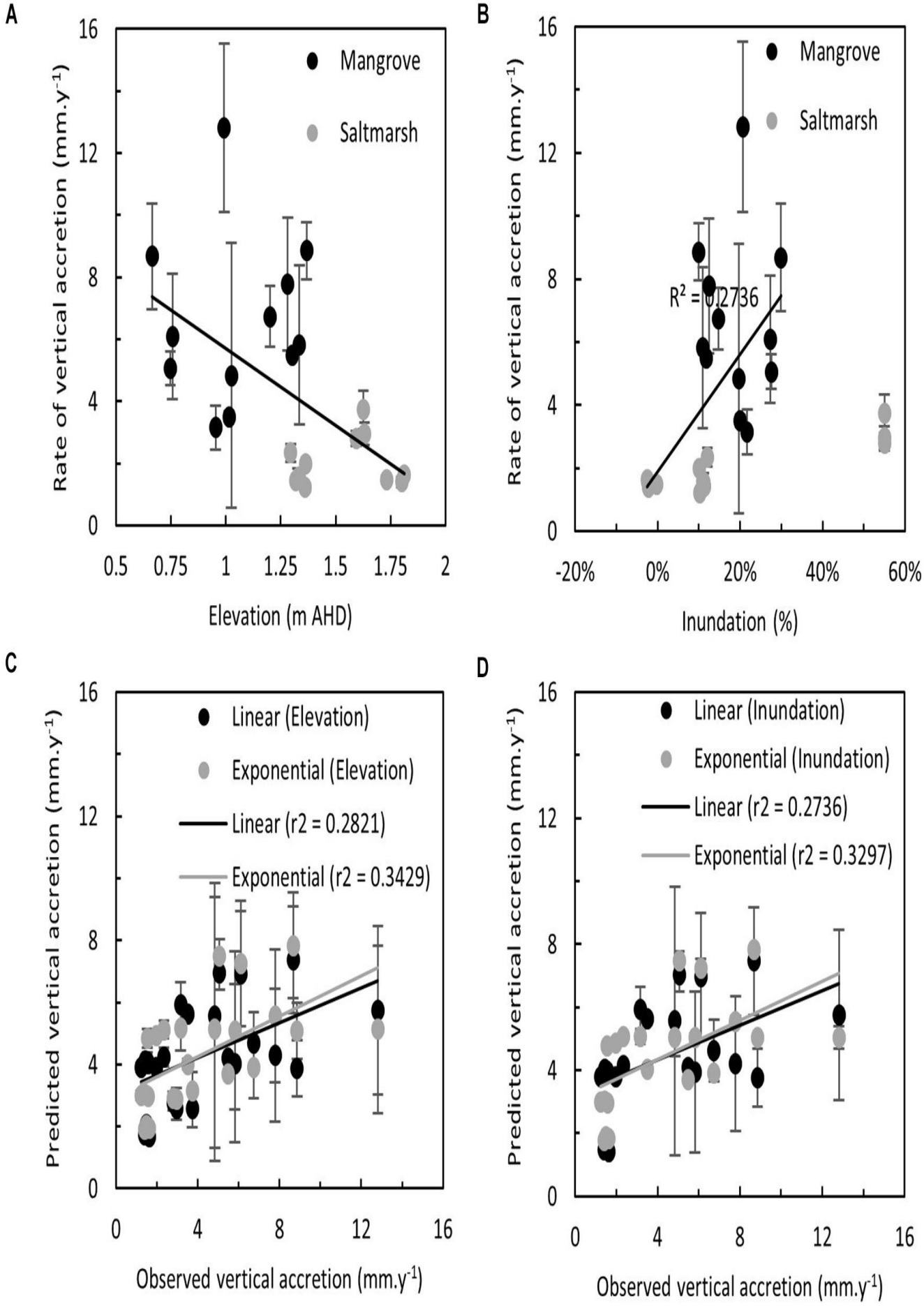
Surface Elevation Morphodynamics

Vertical accretion trends were reasonably well-modeled using linear regression analyses over time, with analyses

indicating that 96% of SETs had r^2-values exceeding 0.5 (Supplementary Table 1); however there was considerable loss of feldspar marker horizons at mangrove SETs due to bioturbation. Similarly, surface elevation change was modeled with reasonable confidence using linear regression analyses and 75% of SETs exhibited r^2 >0.5. Where the coefficient of determination was less than 0.5, surface elevation change was negligible (<1 mm y^{-1}) (Supplementary Table 1 and Supplementary Figure 6). Based on patterns of vertical accretion or surface elevation over time (Supplementary Figures 7–10), low r^2-values and insignificant *p*-values were regarded to be indicative of little vertical accretion or surface elevation change and were therefore included in subsequent analyses. Rates of change for the saltmarsh at French Island were excluded from analyses involving inundation as pooling of water within abandoned ponds was regarded to be unrepresentative of other saltmarsh locations in Westernport Bay.

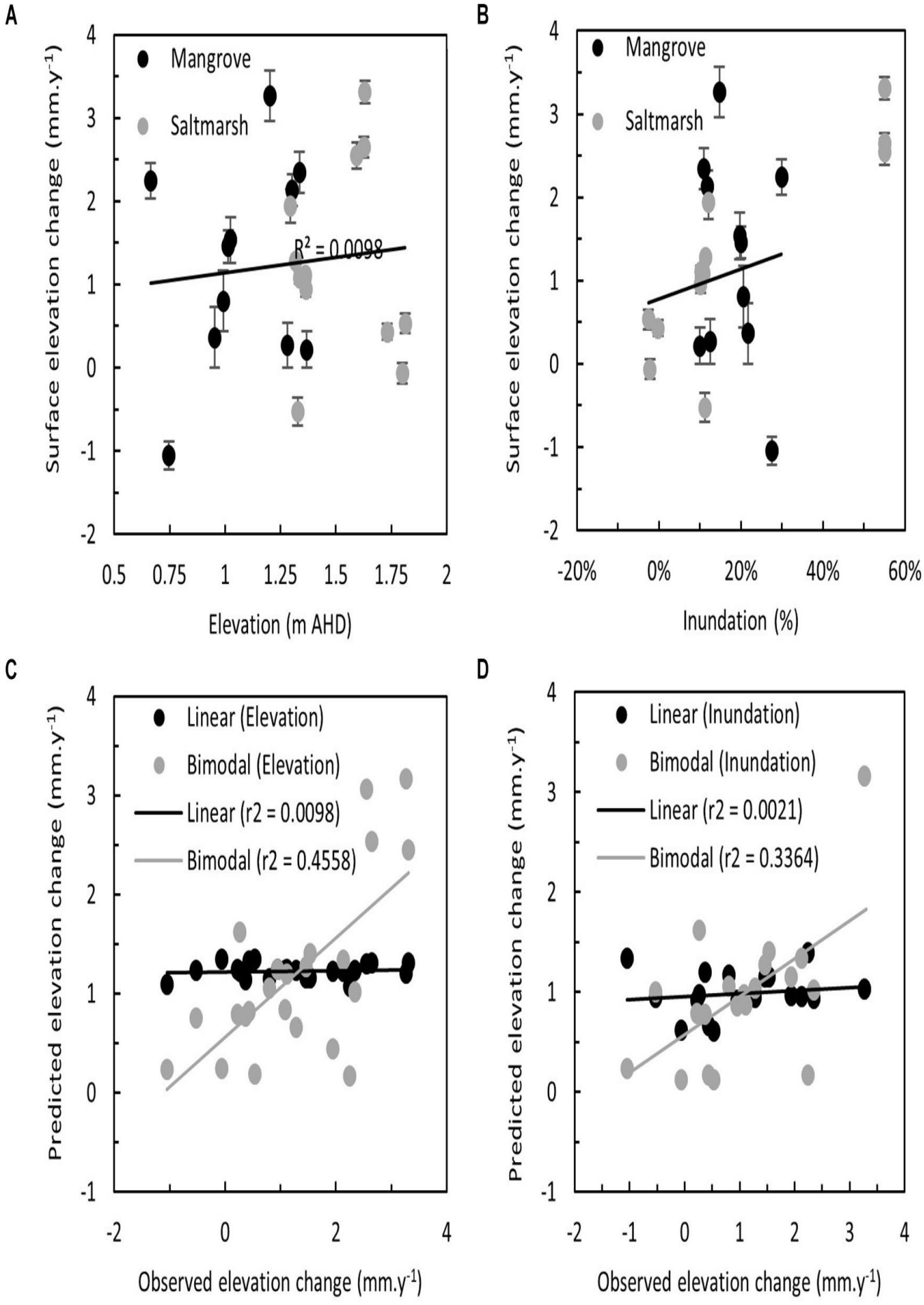
Temporal variation in vertical accretion was particularly evident in the mangrove zone and this was likely related to bioturbation of MH and the shorter duration over which they were detectable. Irrespectively, vertical accretion was linearly related to elevation (Figure 4A, r^2 = 0.2821, p = 0.0076) and inundation (Figure 4B, r^2 = 0.2736, p = 0.0150). This relationship was improved with an exponential model (as per Temmerman et al., 2003) that accounted for distances to sediment sources for both elevation (Figure 4C, r^2 = 0.3429, p = 0.0026) and inundation (Figure 4D, r^2 = 0.3297, p = 0.0065). The strength of these relationships was not maintained in linear regression analyses relating rates of surface elevation change to elevation (Figure 5A, r^2 = 0.0098, p = 0.6530) or inundation (Figure 5B, r^2 = 0.0021, p = 0.5317). Lorentzian peak models provided the best fit when mangrove surface elevation change was related to elevation (r^2 = 0.3022, AICc = 45.67) or inundation (r^2 = 0.3022, AICc = 45.67), whilst Gaussian peak models provided the best fit when saltmarsh surface elevation change was related to elevation (r^2 = 0.6070, AICc = 38.33) or inundation (r^2 = 0.2414, AICc = 34.66). When both peak models were merged to provide a bimodal distribution the fit markedly improved upon linear models for elevation (Figure 5C, r^2 = 0.4558, p = 0.0004) or inundation (Figure 5D, r^2 = 0.3364, p = 0.0073).

FIGURE 4



Enlarge this image.

FIGURE 5

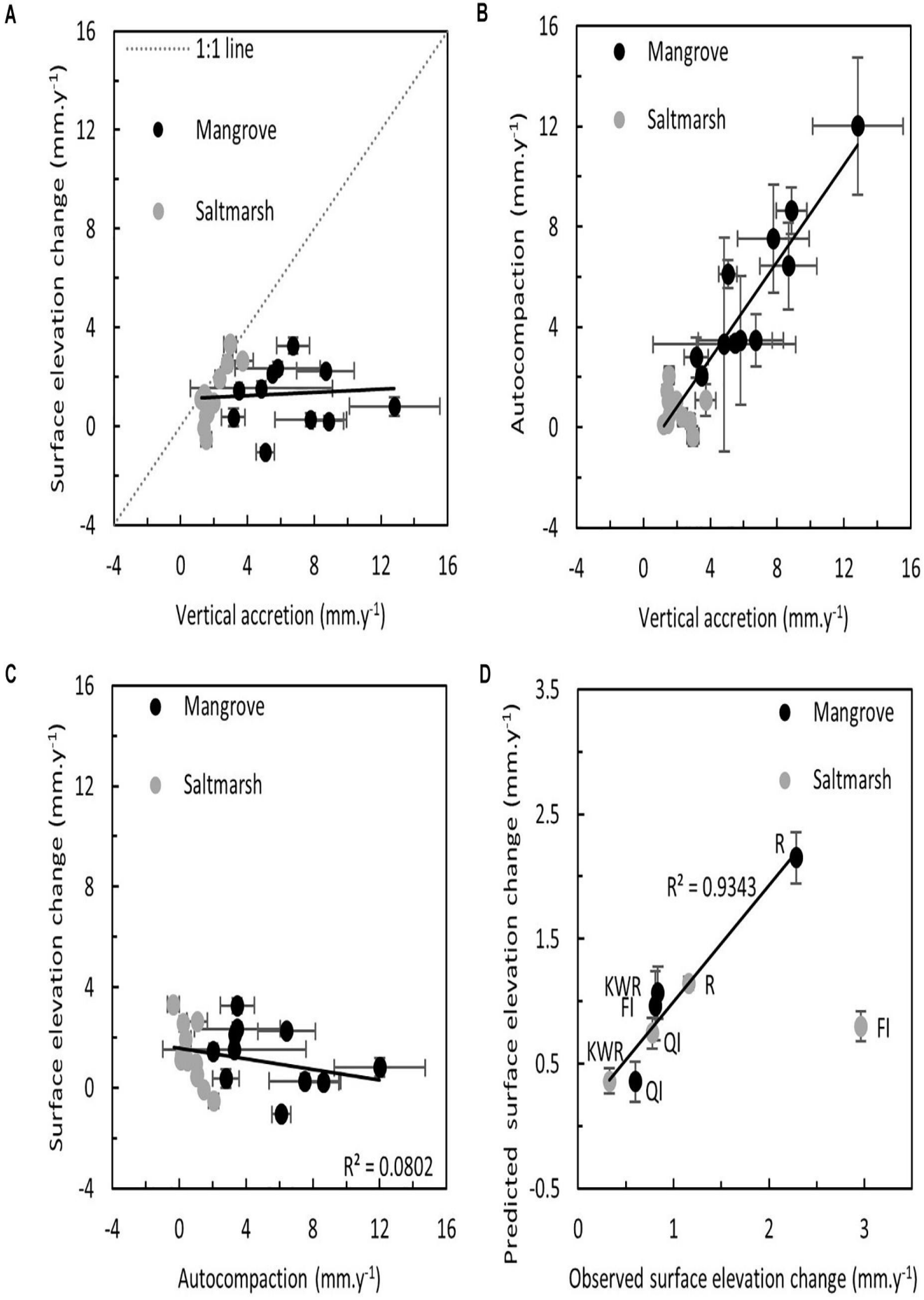


Enlarge this image.

Paired *t*-test confirmed rates of surface elevation change were statistically different to rates of vertical accretion (Figure 6A, r^2 = 0.0076, p = 0.6927). Differences between vertical accretion and surface elevation change were

attributed to autocompaction operating on both mineral and organic material. Vertical accretion was related autocompaction (Figure 6B, r^2 = 0.8632, p <0.0001). However, this did not translate to a similar correlation with surface elevation change (Figure 6C, r^2 = 0.0802, p = 0.1905). Processes modulating the relationship between vertical accretion and accommodation space were influential, but were not related to accommodation space. Mixed model linear regression analysis, which excluded anomalous values at French Island saltmarsh, confirmed the contribution of vertical accretion and substrate organic matter (indicated by carbon storage above MSL) to surface elevation change (Figure 6D, r^2 = 0.9343, p = 0.0280).

FIGURE 6

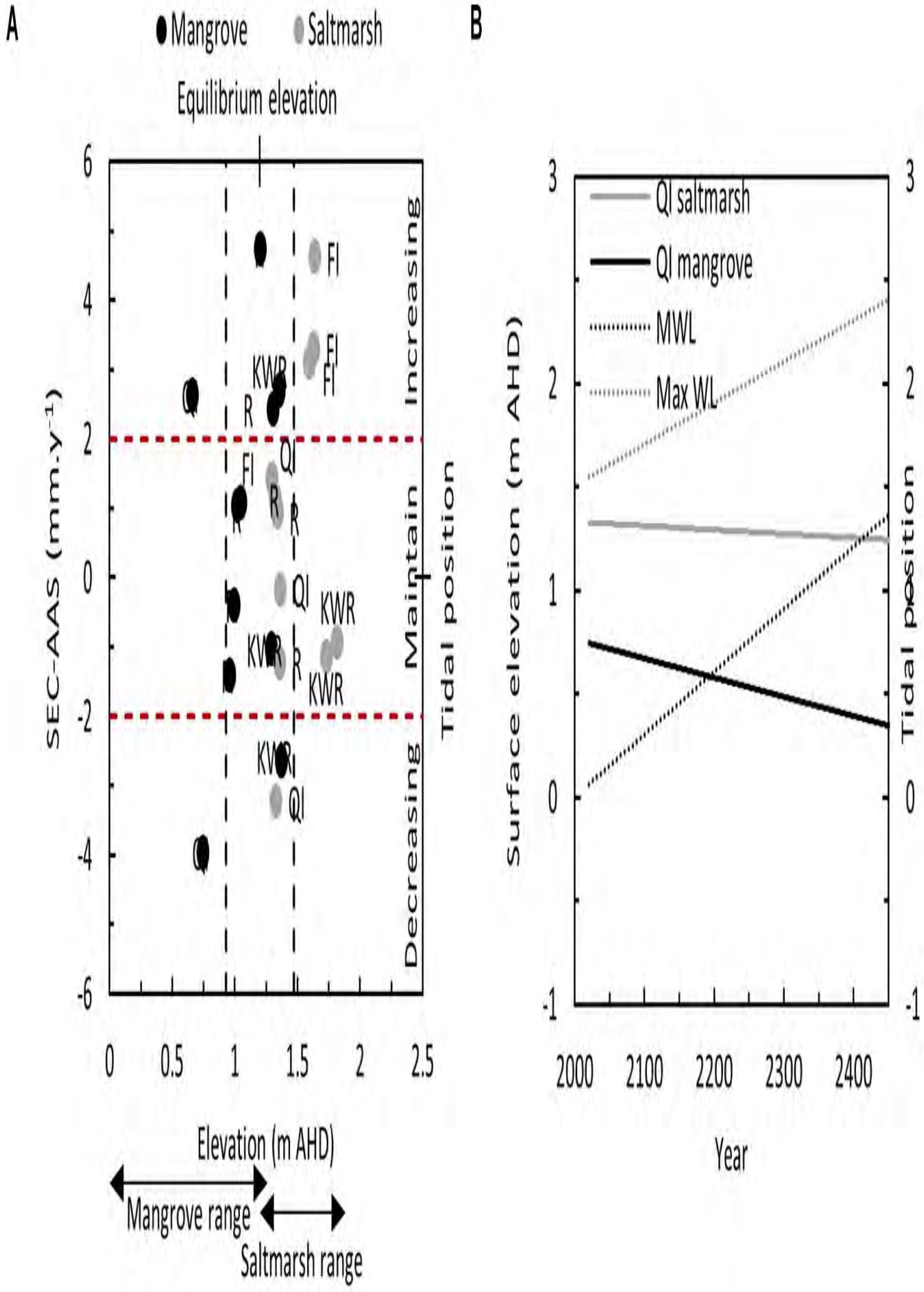


Enlarge this image.

Equilibrium Analysis: Changing Tidal Position

Most SET locations exhibited a surface elevation gain that ensured that tidal position was maintained under

observed rates of RSLR; few locations exhibited a marked decline in tidal position or an increase tidal position (Figure 7A). The equilibrium elevation at which changes to the tidal frame corresponded to an increase in substrate elevation was centered around 1.2 ±0.3 m. This value is remarkably close to estimated mean high water springs tidal plane, reported to be at an elevation of 1.15 m (Water Technology, 2014), and the height at which mangroves give way to saltmarsh vegetation and both vegetation types may occur (Water Technology, 2014). A mangrove SET at Kooweerup exhibited a decline in tidal position that is of little concern given its elevated position in the tidal frame (corresponds to saltmarsh tidal positions). A mangrove and a saltmarsh SET at Quail Island also exhibited a decline in tidal position; these SETs are positioned at the lower end of the vertical distribution for mangrove and saltmarsh, respectively. Given the declining tidal position of the mangrove SET at Quail Island, and the increasing tidal position of the other mangrove SET at Quail Island, it is probable that the location adjacent to the creek draining Kooweerup Swamp (i.e., Cannons Creek) provides considerable hydrodynamic energy that is highly variable, even at the scale of distances between SET monitoring stations. The declining saltmarsh SET remains positioned relatively high in the tidal frame. However, should it continue to loose elevation and the tidal frame shifts according to current rates, this location may transition to being mangrove dominated. Projections indicate that this is not likely to occur until approximately the year 2190 under current rates of change (Figure 7B).
FIGURE 7



Enlarge this image.

Discussion

Processes Influencing Morphodynamics

This study confirmed that wetland surfaces positioned lower in the tidal frame were inundated more frequently, which provided additional opportunities for sediments to be removed from suspension and deposited on wetland surfaces. The role of tidal inundation in facilitating vertical accretion within the vegetated intertidal zone has been established for mangroves and saltmarshes (Pethick, 1981; Rogers et al., 2005a; Kirwan and Megonigal, 2013). However, this observed pattern did not translate into a similar degree of surface elevation gain as processes influencing substrate organic matter and mineral sediment volume caused significant autocompaction and modulated the degree of elevation gain. More specifically, no relationship was found between surface elevation gain, substrate elevation or inundation frequency. This deviation was attributed to processes that alter the substrate volume and contribute to autocompaction. These processes, including decomposition/addition of organic material, consolidation of mineral sediments and compression of organic material, do not operate linearly with inundation. Higher carbon storage toward surfaces in most cores implies that there is some degree of organic matter turnover near substrate surfaces with living vegetation contributing new organic material to substrates as decomposition occurs. The outcome of this is net accumulation of organic material at wetland surfaces. Depletion of carbon away from the rooting zone of *in situ* vegetation was particularly evident in saltmarsh cores (except Kooweerup saltmarsh), where rooting zones are generally shallower and deeper organic material is likely to have had considerably more time for decomposition. This decomposition of older organic material is consistent with global-scale analyses that relate depleted carbon storage in saltmarshes of the southern hemisphere to relatively stable sea levels since the mid-Holocene (Rogers et al., 2019). The compensatory role of organic matter addition was further validated by relatively high rates of surface elevation change in the mangrove zone at Rhyll being associated with high substrate carbon storage and relatively low rates of autocompaction, despite modest vertical accretion.

The degree of autocompaction that occurred was positively related to the degree of vertical accretion on wetland surfaces, indicating that either recently deposited sediments underwent significant consolidation and/or the overburden of accumulating material contributed to deeper consolidation and compression of organic matter. As autocompaction is measured on the basis of changes occurring below marker horizons, processes of autocompaction are operating on mineral sediments below marker horizons and that accumulated prior to the commencement of this study. Autocompaction is regarded to be asymptotic and there is a limit to the reduction in substrate volume that can be achieved (Allen, 2000). Additionally, larger grain sizes are more resistant to consolidation (Bandini and Sathiskumar, 2009). The general trend of increasing grain size with depth below 0.8 m AHD implies consolidation largely operates on sediments above 0.8 m. The predominance of silt and clay grain sizes near wetland surfaces provides further support that consolidation is likely to dominate surface sediments. Paradoxically and unlike other locations, the saltmarsh at Rhyll exhibited both low rates of autocompaction and vertical accretion. This was attributed to the predominance of sand fractions at the surface that are resistant to consolidation. Low rates of surface elevation change, high rates of autocompaction and high substrate carbon content in the saltmarsh at Kooweerup imply that compression of organic material may be the primary process contributing to autocompaction at this location. Despite this autocompaction, substantial substrate carbon and low bulk density was quantified in the upper 40 cm of sediments, indicating that vertical growth of the saltmarsh was more recently associated with organic matter addition. Due to the relatively high position of the saltmarsh at this location and low inundation frequency, compression of this thickness of organic material is critical for maintaining substrates within the vertical range of accommodation space, else accommodation space will become exhausted and terrestrialization of vegetation cover may occur.

The varying contribution of addition, decomposition and compression of organic material, and mineral sediment consolidation to autocompaction limits the capacity to develop relationships between trajectories of surface elevation change and accommodation space. This problem was predicted by Allen (2000) who recognized the difficulty in realistically modeling autocompaction of Holocene coastal deposits due to the diversity and complexity of process involved and the environmental context. However, this is contrary to the structure of many existing empirical and physical models. Many models either presume processes causing autocompaction operate solely on organic material through decomposition (For example, Zhang et al., 2020), are implicitly incorporated in models of net

surface elevation change (Morris et al., 2002; Rogers et al., 2012), or apply a constant rate of autocompaction irrespective of tidal position (For example, Marani et al., 2013). There are exceptions: the WARMER (Swanson et al., 2014) model includes parameters of mineral sediment accretion, organic matter addition and decomposition, and compaction; and OIMAS-N (Mudd et al., 2009) includes parameters of mineral and organic matter addition, decay of carbon pools and compaction. This study confirms that sandy substrates tend to undergo less autocompaction than substrates where surface sediments are largely fine grained. The upward fining of sediments within substrates (with the exception of Rhyll saltmarsh) indicates that grain size of accreting material and associated resistance to consolidation is positively related to available accommodation space. Given the elevation at which sandy and carbon-depleted sediments have typically accumulated in wetland substrates (i.e., <0.8 m AHD, though some peaks in carbon are preserved at lower elevations, particularly in mangrove-dominated locations), it is probable that the high-energy conditions required for sand deposition occurred some time ago. If this is the case, most of the autocompaction that could have occurred on these sediments is nearing completion.

Conceptualizing Processes of Autocompaction

The physical, biological and chemical processes contributing to autocompaction operate across different timescales (Allen, 2000). However as these processes are asymptotic, we propose that the bulk of autocompaction at Westernport Bay occurs in sediments either above approximately 0.8 m AHD or corresponding to the active rooting zone of mangrove vegetation. Autocompaction is also dependent upon the proportion of organic material in substrates, sediment characteristics and prior rates of surface elevation gain. We identify four critical factors that influence the degree of autocompaction: rooting depths of vegetation, sediment characteristics, rates of surface elevation gain, and vegetation distribution changes.

i) Rooting depths of vegetation: Whilst mangrove species diversity is low at Westernport Bay, saltmarsh species diversity is extraordinarily high with discernible zones dominated by saltbush, highly diverse herbaceous saltmarsh, and landward rushes. The varying rooting depth of this vegetation influences whether addition of organic material to substrates exceeds processes of decomposition. In this study, mangrove cores typically exhibited deeper zones of higher carbon storage near the surface, whilst the surficial zones of higher carbon storage at saltmarsh locations were typically shallower (i.e., with the exception of the saltmarsh at Kooweerup). Despite herbaceous saltmarshes generally having shallower, carbon-rich surficial zones, their overall deeper sediment columns above MSL (i.e., 0 m AHD) resulted in carbon storage above MSL being relatively consistent across the intertidal gradient. However, it is feasible to characterize the variation in rooting depths associated with optimal tidal positions to generate multi-peak models of organic matter addition, as was coarsely undertaken in this study by merging peak models to relate surface elevation change to elevation and inundation.

ii) Sediment characteristics: Supply of high volumes of fine-grained sediments generates a larger volume of substrate that is prone to processes of sediment consolidation. This was particularly evident in mangrove cores as they generally exhibited high accretion rates and greater silt to sand ratios in surficial sediments. The exception was Quail Island mangrove locations where sands dominated most of the substrate. The dominance of sands at wetlands surfaces attests to higher energy conditions and the possibility of erosion. The supply and subsequent deposition of sediments are hydro-dynamically governed and improvements on hydrodynamic models such that they account for sediment characteristics and their contribution to processes of autocompaction could be considered.

iii) Rates of surface elevation gain: Surface elevation gain, achieved through either organic matter and/or mineral sediment addition exceeding the rate of autocompaction, creates conditions favorable for increasing tidal position of wetland surfaces. When this occurs rapidly, either rooting zones of vegetation are transposed vertically, or lateral vegetation transitions occur (e.g., replacement of mangrove by saltmarsh) with a corresponding change in the depth of the active root zone. In both situations, the overall outcome is an increase in the depth of surficial carbon-rich zones until the deeper zones associated with prior root zones undergoes decomposition. High rates of vertical accretion may transition substrate elevations rapidly from lower positions in the tidal frame to optimal positions for organic matter addition (as per Morris et al., 2002), although the inverse may also occur. Whilst deeper active rooting zones will be increasingly abandoned and exposed to processes of decomposition, insufficient time may

have passed for processes of decomposition and compression of organic material and consolidation of mineral sediments to significantly influence autocompaction. Increases in the height of the tidal frame with RSLR has been related to greater carbon storage (McKee et al., 2007; Toscano et al., 2018), and is likely facilitated by increasing exposure to anaerobic conditions (Rogers et al., 2019). It is feasible that this process may have resulted in instances of increasing tidal positions at "equilibrium elevations" as occurred for mangrove locations at Rhyll and Kooweerup, and for saltmarsh locations at French Island.

iv) Vegetation distribution changes: Changes in tidal position of vegetation may occur when surface elevation gain does not correspond to changes to the tidal frame with RSLR. As mangroves at Westernport Bay are positioned at lower tidal positions and have relatively deep rooting zones, and herbaceous saltmarsh positioned at higher tidal positions has shallower rooting zones, vegetation encroachment upon herbaceous saltmarsh may promote rapid addition of organic material to substrates. When this occurs, surficial carbon stocks may markedly increase and offset processes of autocompaction occurring deeper in the substrate. There is substantial evidence in southeastern Australia and elsewhere (Doughty et al., 2016; Kelleway et al., 2016) of increasing surficial carbon storage as mangroves have encroached upon saltmarsh over the past few decades. In Westernport Bay, this process is further promoted as the intermediary saltbush zone dominated by *Tecticornia arbuscula* grows to heights of approximately 2 m (*pers. obs.*), and are likely to have deeper rooting zones than herbaceous saltmarsh. This subsidy may be critical for achieving the high rates of surface elevation change in mangrove locations at Rhyll where relatively recent encroachment of mangrove along the nearby tidal creek and across formerly saltmarsh-dominated surfaces has been documented (Rogers et al., 2005b; Whitt et al., 2020).

Validation of Model Structure

Processes of net vertical accretion are typically related to accommodation space and our analyses confirmed this; minor improvements in vertical accretion model fit were achieved when distances to sediment sources were incorporated according to an exponential function, as per Temmerman et al. (2003). Whether accretion behaves linearly or exponentially is of little consequence when accommodation space becomes limited at high tidal positions (i.e., in saltmarsh) as modeled values converge, as demonstrated by Mogensen and Rogers (2018). Nevertheless, it is particularly important at lower tidal positions where differences between values derived from linear or exponential models can be significant. Unfortunately, preservation of marker horizons in mangrove zones at Westernport Bay was poor due to bioturbation and this markedly reduced confidence and increased variability in vertical accretion data. Hence, our ability to discern optimal model functions for vertical accretion was limited. Complementary analyses of sedimentation derived from measurements of ^{210}Pb activity in sediments and using a time for space substitution indicate that peak models (Gaussian or Lorentzian) improved predictive ability (Rogers et al. in prep). More specifically, peak models can account for lower rates of sedimentation when accommodation space and hydrodynamic energy is high, accelerating sedimentation as accommodation space infills, and decelerating sedimentation as accommodation space becomes limited.

The linear relationship between vertical accretion and autocompaction indicates that autocompaction may also behave according to an inundation depth/frequency-constrained model; models may be either peak or linear in behavior. Disaggregating processes contributing to autocompaction that operate on organic and mineral material in substrates requires further investigation of intertidal variation in the behavior of these processes. Stratigraphic controls on compression were related to accommodation space with sandy, compression-resistant sediments dominating when accommodation space was high, and conforms closest to the OIMAS-N model structure of Mudd et al. (2009). Due to the greater complexity of vegetation at Westernport Bay, more information is needed to describe the vertical distribution of vegetation within the tidal frame, rooting depths of *in situ* vegetation, and time-depth dependence of decomposition. Application of merged peak models to describe surface elevation change within mangrove and saltmarsh zones indicate that quantifying the range and peak productivity of vegetation may correlate with the full range of processes operating on organic matter that modulates surface elevation change. Irrespective of these data gaps, our data indicates that processes influencing surface elevation change are largely depth constrained, and their behavior is more likely to conform with peak model structures rather than linear. There

remains considerable scope to calibrate this data against OIMAS-N model to characterize changing tidal position and substrate carbon storage.

Equilibrium Analysis

Given the relatively recent change in trajectory of sea level across the southern hemisphere, it was feasible that equilibration of processes to recent SLR may be lagging. Additionally, there remains some concern that short-term datasets, such as those derived from SET-MH approaches, may not have sufficient temporal range to characterize surface elevation trajectories with confidence (Breithaupt et al., 2018; Wiberg et al., 2020). There was a surprising degree of confidence in elevation trajectories over the 20-year analysis period. We found that relatively few locations exhibited surface elevation trajectories beyond that required to maintain tidal positions (i.e., 0 ±2 mm y^{-1}). This implies that presumptions of equilibrium may not be misplaced, particularly when models are parameterized using high confidence data that is not influenced by perturbations operating over shorter timescales. Mean trajectories of elevation change and vertical accretion in this study were generally within the error range of rates reported in the earlier study of Rogers et al. (2005b); with the exception of rates of surface elevation change at French Island, and surface elevation change in the mangroves at Quail Island. We recommend analyses of confidence in trajectories before model application, as undertaken in this study and others (Jankowski et al., 2017).

Some locations that exhibited an increase in tidal position were associated with relatively recent transition of mangrove into saltmarsh (i.e., Rhyll mangrove locations were saltmarsh prior to the commencement of this study). Organic matter addition to substrates achieved by vegetation encroachment plays a critical role in increasing substrate surface elevations. Hydrological alterations in the saltmarsh at French Island appeared to provide a productivity subsidy and improve sediment-trapping efficiency, resulting in an increase in tidal position beyond that expected for its elevation. Increasing hydrodynamic energy along the creek draining Kooweerup Swamp and adjacent to Quail Island (i.e., Cannons Creek) may be influencing lateral movement of sediment on the eastern shores of Quail Island and contributing to declines in tidal positions at this location (Figure 1). The dominance of larger grain sizes in sediments and relatively low rates of vertical accretion at Quail Island indicate that hydrodynamic energy is generally too high for finer grain sediment deposition within the mangrove zone. Hydrodynamic modeling will be critical for conceptualizing the restructuring of shorelines of Quail Island and other locations where hydrodynamic energy is changing.

The analysis of equilibrium elevation undertaken in this study intriguingly indicated an equilibrium elevation corresponding to both the height of mean high tide and the approximate elevation that the mangrove niche transitions into the saltmarsh niche. The reported equilibrium elevation of 1.2 m is approximately 0.3 m below the upper boundary of accommodation space and where only ~15% of total accommodation space remains for sediment accumulation. Saltmarsh is evidently a climax intertidal community in this region, and mangroves are a pioneering community. However, it would be misplaced to describe mangroves as “land-builders,” as proposed by Bird (1971, 1986) following work in Westernport Bay. This is because mineral sediment supply to create an intertidal surface at an elevation suitable for mangroves is a critical precursor for their establishment. This was confirmed in this study by the predominance of sandy substrates with little organic material at elevations at or below MSL. Accordingly, the most critical component of “land-building” is related to sediment supply, driven by hydrodynamic energy, and occurs prior to mangrove establishment. Commentary from Spenceley (1987) implied that there was not enough evidence to confirm that sedimentation would not have occurred in the absence of mangroves and proposed that sediment characteristics, prevailing energy conditions and faunal activity may be more critical for erosion and deposition than the presence of pneumatophores at Westernport Bay. Spenceley (1987) lamented the absence of more data and research into the role of mangrove roots in promoting mineral sediment deposition, and unfortunately, little has changed in subsequent years.

Projected acceleration in SLR (Oppenheimer et al., 2019) is proposed to deepen equilibrium elevations (Fagherazzi et al., 2012) and should this occur mangroves forests will increasingly dominate the intertidal zone of Westernport Bay by encroaching upon adjacent saltmarsh. Mangrove forests may eventually give way to un-vegetated mudflat and subtidal elevations should SLR acceleration exceed the capacity for maintaining equilibrium elevations. There is

substantial evidence that this is already occurring with mangrove encroachment of saltmarsh well-documented in Westernport Bay (Rogers et al., 2005b; Whitt et al., 2020). Management efforts to maintain the areal distribution of saltmarsh and limit mangrove encroachment should recognize the subsidizing effect mangroves provide by adding considerably more organic material to substrates than herbaceous saltmarsh vegetation. Actions that limit expansion, such as controlling propagule dispersal and removing seedlings, may be detrimental and promote the development of ponds and open water within saltmarshes (Coleman et al., 2021).

Conclusion

This study established that a range of processes influence autocompaction; these processes vary spatially, are proportional to vertical accretion, and can feasibly be modeled with reference to accommodation space or depth below high water. Surface elevation change was related to vertical accretion and substrate organic matter, as indicated by carbon storage above mean sea level. Additionally, surface elevations do not adjust linearly with accommodation space and peak model structures will likely improve model performance. More research is required to improve characterization of model structures; however, it may be reasonable to presume equilibration with current rates of SLR providing models are parameterized with highly accurate data.

We propose that the outcomes of this study can only be achieved by analyzing processes of surface elevation change at locations with a longer history of stable or falling sea level, as occurred in much of the southern hemisphere over the mid- to late-Holocene. Relatively stable sea levels over the past 7,000 years provided favorable conditions for estuarine infill and this has been demonstrated in numerous studies (Woodroffe et al., 1993, 2000; Hashimoto et al., 2006; Kennedy et al., 2021). Since the mid-Holocene, processes influencing autocompaction operating on older/deeper sediments have had more time to reach completion and this is evident by depleted carbon stocks in saltmarsh sediments below 0.8 m AHD. This provides local-scale confirmation of the global-scale pattern of lower saltmarsh carbon stocks along coastlines where sea level was relatively stable throughout the mid- to late-Holocene (Rogers et al., 2019).

Recent increases in sea level are contrary to antecedent conditions and new accommodation space is now being created for mineral and organic material accumulation. Striking stratigraphic variation is generated as new accommodation space infills with mineral and organic material above older strata that have undergone processes of autocompaction and are increasingly dominated by mineral sediments. The sediment character of these new strata subsequently influences the degree of surface elevation occurring today. This stratigraphy contrasts locations where wetlands are exposed to a longer history of rising sea levels and creation of new accommodation space, as conditions influencing vertical accretion and processes of autocompaction are more likely to equilibrate, and the homogeneity of substrates will be higher. Considerably more research is required in the southern hemisphere to characterize spatial variation in processes influencing surface elevation change to improve and validate model structures and confidently parameterize models. We caution the use of models derived from the northern hemisphere, particularly those that presume constant rates of autocompaction or linear behavior of surface elevation change.

Data Availability Statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

Author Contributions

KR and NS undertook data collection, analysis, and writing. This has been a collaborative research project since its inception. Both authors contributed to the article and approved the submitted version.

Funding

The Victorian Government provided financial support to establish this research in 2000 and subsequent funding in 2017 to maintain research continuity and deliver knowledge that assists with management of coastal wetlands of Westernport Bay. KR received an Australian Research Council Future Fellowship (FT130100532) that provided financial support for measurements and sediment analyses from 2014 to 2018.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgments

We acknowledge the custodians of the Western Port area, the Bunurong (Boonerwrung) people of the Kulin Nation. We recognize the contribution of field and laboratory assistants in undertaking this work; over 20 years of analysis there are too many to mention but we remember every field trip fondly. Special thanks given to Lawrance Ferns who has supported this research and the Victorian Government who has provided financial support with the initial establishment and recent measurements.

Supplementary Material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.694039/full#supplementary-material

References

Allen, J. R. L. (2000). Morphodynamics of holocene salt marshes: a review sketch from the Atlantic and Southern North sea coasts of Europe. *Quat. Sci. Rev.* 19, 1155–1231. doi: 10.1016/s0277-3791(99)00034-7

Alongi, D. M. (2008). Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. *Estuar. Coast. Shelf Sci.* 76, 1–13. doi: 10.1016/j.ecss.2007.08.024

Bandini, P., and Sathiskumar, S. (2009). Effects of silt content and void ratio on the saturated hydraulic conductivity and compressibility of sand-silt mixtures. *J. Geotech. Geoenviron. Eng.* 135, 1976–1980. doi: 10.1061/(asce)gt.1943-5606.0000177

Bird, E. C. F. (1971). Mangroves as land builders. *Vic. Nat.* 88, 189–197.

Bird, E. C. F. (1986). Mangroves and intertidal morphology in Westernport Bay, Victoria, Australia. *Mar. Geol.* 69, 251–271. doi: 10.1016/0025-3227(86)90042-3

Boon, P. I., Allen, T., Brook, J., Carr, G., Frood, D., Harty, C., et al. (2011). "Mangroves and coastal saltmarsh of Victoria: distribution, condition, threats and management," (Melbourne, VIC: Institute for Sustainability and Innovation, Victoria University).

Breithaupt, J. L., Smoak, J. M., Byrne, R. H., Waters, M. N., Moyer, R. P., and Sanders, C. J. (2018). Avoiding timescale bias in assessments of coastal wetland vertical change. *Limnol. Oceanogr.* 63, S447–S495.

Cahoon, D. R., Lynch, J. C., Hensel, P., Boumans, R., Perez, B. C., Segura, B., et al. (2002). High-precision measurements of wetland sediment elevation: i. recent improvements to the sedimentation-erosion table. *J. Sediment. Res.* 72, 730–733. doi: 10.1306/020702720730

Cahoon, D. R., and Turner, R. E. (1989). Accretion and canal impacts in a rapidly subsiding wetland II. Feldspar marker horizon technique. *Estuaries* 12, 260–268. doi: 10.2307/1351905

Callaway, J., Nyman, J., and Delaune, R. D. (1996). Sediment accretion in coastal wetlands: a review and a simulation model of processes. *Curr. Top. Wetl. Biogeochem.* 2, 2–23.

Church, J. A., Clark, P. U., Cazenave, A., Gregory, J. M., Jevrejeva, S., Levermann, A., et al. (2013). "Sea level change," in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, et al. (Cambridge: Cambridge University Press).

Coleman, D. J., Rogers, K., Corbett, D. R., Owers, C. J., and Kirwan, M. L. (2021). The geomorphic impact of mangrove encroachment in an Australian salt marsh. *Estuar. Coast. Shelf Sci.* 251:107238. doi: 10.1016/j.ecss.2021.107238

D'Alpaos, A., Lanzoni, S., Marani, M., and Rinaldo, A. (2007). Landscape evolution in tidal embayments: modeling the interplay of erosion, sedimentation, and vegetation dynamics. *J. Geophys. Res.* 112, 1–17. doi: 10.1007/978-1-4615-0575-4_1

Dey, R., Lewis, S. C., Arblaster, J. M., and Abram, N. J. (2019). A review of past and projected changes in Australia's rainfall. *Wiley Interdiscip. Rev. Clim. Change* 10:e577.

Dougherty, A. J., Thomas, Z. A., Fogwill, C., Hogg, A., Palmer, J., Rainsley, E., et al. (2019). Redating the earliest

evidence of the mid-holocene relative sea-level highstand in Australia and implications for global sea-level rise. *Plos one* 14:e0218430. doi: 10.1371/journal.pone.0218430
Doughty, C. L., Langley, J. A., Walker, W. S., Feller, I. C., Schaub, R., and Chapman, S. K. (2016). Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuar. Coasts* 39, 385–396. doi: 10.1007/s12237-015-9993-8
Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenspergen, G. R., Temmerman, S., D'alpaos, A., et al. (2012). Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. *Rev. Geophys.* 50:RG1002.
French, J. R. (1993). Numerical simulation of vertical marsh growth and adjustment to accelerated sea-level rise, North Norfolk, U.K. *Earth Surf. Process. Landf.* 18, 63–81. doi: 10.1002/esp.3290180105
Hashimoto, T. R., Saintilan, N., and Haberle, S. G. (2006). Mid-holocene development of mangrove communities featuring rhizophoraceae and geomorphic change in the richmond river estuary, New South Wales, Australia. *Geogr. Res.* 44, 63–76. doi: 10.1111/j.1745-5871.2006.00360.x
Jankowski, K. L., Törnqvist, T. E., and Fernandes, A. M. (2017). Vulnerability of Louisiana's coastal wetlands to present-day rates of relative sea-level rise. *Nat. Commun.* 8:14792.
Kelleway, J. J., Saintilan, N., Macreadie, P. I., Skilbeck, C. G., Zawadzki, A., and Ralph, P. J. (2016). Seventy years of continuous encroachment substantially increases 'blue carbon'capacity as mangroves replace intertidal salt marshes. *Glob. Change Biol.* 22, 1097–1109. doi: 10.1111/gcb.13158
Kennedy, D., Wong, V., and Jacobsen, G. J. (2021). Holocene infill of the Anglesea Estuary, Victoria: a keep-up estuary in a geologically constrained environment. *Aust. J. Earth Sci.* doi: 10.1080/08120099.2021.1879266 [Epub ahead of print].
Kestner, F. J. (1975). The loose-boundary regime of the wash. *Geogr. J.* 141, 388–414. doi: 10.2307/1796474
Khan, N. S., Ashe, E., Shaw, T. A., Vacchi, M., Walker, J., Peltier, W. R., et al. (2015). Holocene relative sea-level changes from near-, intermediate-, and far-field locations. *Curr. Clim. Change Rep.* 1, 247–262. doi: 10.1007/s40641-015-0029-z
Kirwan, M. L., and Megonigal, J. P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504, 53–60. doi: 10.1038/nature12856
Krauss, K. W., Mckee, K. L., Lovelock, C. E., Cahoon, D. R., Saintilan, N., Reef, R., et al. (2014). How mangrove forests adjust to rising sea level. *New Phytol.* 202, 19–34. doi: 10.1111/nph.12605
Krone, R. B. (1987). "A method for simulating historic marsh elevations," in *Coastal Sediments '87*, ed. N. C. Krause (New Orleans, LA: American Society of Civil Engineers).
Lewis, S. E., Sloss, C. R., Murray-Wallace, C. V., Woodroffe, C. D., and Smithers, S. G. (2013). Post-glacial sea-level changes around the Australian margin: a review. *Quat. Sci. Rev.* 74, 115–138. doi: 10.1016/j.quascirev.2012.09.006
Marani, M., Da Lio, C., and D'alpaos, A. (2013). Vegetation engineers marsh morphology through multiple competing stable states. *Proc. Natl. Acad. Sci. U.S.A.* 110, 3259–3263. doi: 10.1073/pnas.1218327110
McKee, K. L., Cahoon, D. R., and Feller, I. C. (2007). Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Glob. Ecol. Biogeogr.* 16, 545–556. doi: 10.1111/j.1466-8238.2007.00317.x
Mogensen, L., and Rogers, K. (2018). Validation and comparison of a model of the effect of sea-level rise on coastal wetlands. *Sci. Rep.* 8:1369.
Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B., and Cahoon, D. R. (2002). Responses of coastal wetlands to rising sea-levels. *Ecology* 83, 2869–2877. doi: 10.1890/0012-9658(2002)083[2869:rocwtr]2.0.co;2
Mudd, S. M., Howell, S. M., and Morris, J. T. (2009). Impact of dynamic feedbacks between sedimentation, sea-level rise, and biomass production on near-surface marsh stratigraphy and carbon accumulation. *Estuar. Coast. Shelf Sci.* 82, 377–389. doi: 10.1016/j.ecss.2009.01.028
Murray-Wallace, C. V., and Woodroffe, C. D. (2014). *Quaternary Sea-Level Changes: A Global Perspective.* Cambridge: Cambridge University Press.
Oppenheimer, M., Glavovic, B., Hinkel, J., Van De Wal, R., Magnan, A. K., Abd-Elgawad, A., et al. (2019). "Chapter

4: sea level rise and implications for low lying islands, coasts and communities," in *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*, eds H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, et al. (Geneva: Intergovenmental Panel on Climate Change).
Pethick, J. S. (1981). Long-term accretion rates on tidal salt marshes. *J. Sediment. Res.* 51, 571–577.
Reed, D. J. (1990). The impact of sea-level rise on coastal salt marshes. *Prog. Phys. Geogr.* 14, 465–481. doi: 10.1177/030913339001400403
Rinaldo, A., Fagherazzi, S., Lanzoni, S., Marani, M., and Dietrich, W. E. (1999). Tidal networks: 2. watershed delineation and comparative network morphology. *Water Res. Res.* 35, 3905–3917. doi: 10.1029/1999wr900237
Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., et al. (2019). Wetland carbon storage controlled by millennialscale variation in relative sea-level rise. *Nature* 567, 91–95. doi: 10.1038/s41586-019-0951-7
Rogers, K., Saintilan, N., and Cahoon, D. (2005a). Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetl. Ecol. Manag.* 13, 587–598. doi: 10.1007/s11273-004-0003-3
Rogers, K., Saintilan, N., and Copeland, C. (2012). Modelling wetland surface elevation and its application to forecasting the effects of sea-level rise on estuarine wetlands. *Ecol. Model.* 244, 148–157. doi: 10.1016/j.ecolmodel.2012.06.014
Rogers, K., Saintilan, N., and Heijnis, H. (2005b). Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence and sea level rise. *Estuaries* 28, 551–559. doi: 10.1007/bf02696066
Spenceley, A. P. (1987). Mangroves and intertidal morphology in Westernport Bay, Victoria, Australia —Comment. *Mar. Geol.* 77, 327–330. doi: 10.1016/0025-3227(87)90121-6
Swanson, K. M., Drexler, J. Z., Schoellhamer, D. H., Thorne, K. M., Casazza, M. L., Overton, C. T., et al. (2014). Wetland accretion rate model of ecosystem resilience (WARMER) and its application to habitat sustainability for endangered species in the San Francisco estuary. *Estuar. Coasts* 37, 476–492. doi: 10.1007/s12237-013-9694-0
Temmerman, S., Govers, G., Wartel, S., and Meire, P. (2003). Spatial and temporal factors controlling short-term sedimentation in a salt and freshwater tidal marsh, scheldt estuary, Belgium, SW Netherlands. *Earth Surf. Process. Landf.* 28, 739–755. doi: 10.1002/esp.495
Thorne, K., Macdonald, G., Guntenspergen, G., Ambrose, R., Buffington, K., Dugger, B., et al. (2018). US Pacific coastal wetland resilience and vulnerability to sea-level rise. *Sci. Adv.* 4:eaao3270. doi: 10.1126/sciadv.aao3270
Toscano, M. A., Gonzalez, J. L., and Whelan, K. R. T. (2018). Calibrated density profiles of Caribbean mangrove peat sequences from computed tomography for assessment of peat preservation, compaction, and impacts on sea-level reconstructions. *Quat. Res.* 89:201. doi: 10.1017/qua.2017.101
Water Technology (2014). *Western Port Local Coastal Hazard Assessment. Inundation Hazards Report 04 (R04).* Melbourne, VIC: Melbourne Water Technology.
White, N. J., Haigh, I. D., Church, J. A., Koen, T., Watson, C. S., Pritchard, T. R., et al. (2014). Australian sea levels—trends, regional variability and influencing factors. *Earth Sci. Rev.* 136, 155–174. doi: 10.1016/j.earscirev.2014.05.011
Whitt, A. A., Coleman, R., Lovelock, C. E., Gillies, C., Ierodiaconou, D., Liyanapathirana, M., et al. (2020). March of the mangroves: drivers of encroachment into southern temperate saltmarsh. *Estuar. Coast. Shelf Sci.* 240:106776. doi: 10.1016/j.ecss.2020.106776
Wiberg, P. L., Fagherazzi, S., and Kirwan, M. L. (2020). Improving predictions of salt marsh evolution through better integration of data and models. *Ann. Rev. Mar. Sci.* 12, 389–413. doi: 10.1146/annurev-marine-010419-010610
Woodroffe, C. D., Mulrennan, M. E., and Chappell, J. (1993). Estuarine infill and coastal progradation, Southern van Diemen Gulf, Northern Australia. *Sediment. Geol.* 83, 257–275. doi: 10.1016/0037-0738(93)90016-x
Woodroffe, C. W., Buman, M., Kawase, K., and Umitsu, M. (2000). Estuarine infill and formation of Deltaic Plains, Shoalhaven River. *Wetlands* 18, 72–84. doi: 10.31646/wa.232
Zhang, Y., Rowland, J. C., Xu, C., Wolfram, P. J., Svyatsky, D., Moulton, J. D., et al. (2020). Understanding the eco-geomorphologic feedback of coastal marsh under sea level rise: vegetation dynamic representations, processes

interaction, and parametric sensitivity. *J. Geophys. Res. Earth Surf.* 125:e2020JF005729.

AuthorAffiliation

Kerrylee Rogers[1*] and Neil Saintilan[2]

* [1]School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW, Australia

* [2]Department of Earth and Environmental Science, Macquarie University, Sydney, NSW, Australia

DETAILS

Subject:	Holocene; Hydrodynamics; Substrates; Models; Organic matter; Soil erosion; Mean sea level; Sea level; Productivity; Ecosystem services; Decomposition; Sediments; Wetlands; Sea level changes; Coasts; Tide gauges; Aquatic ecosystems; Vegetation; Accretion; Accumulation; Carbon; Stability; Carbon sequestration; Accommodation; Compression; Sedimentation &deposition; Sediment; Carbon capture and storage
Business indexing term:	Subject: Productivity
Location:	United States--US
Identifier / keyword:	Accommodation space; Coastal wetland; Sea level; Sea level rise; Sedimentation; Vertical accretion; subsidence; consolidation; Surface elevation tables (SET); Marker horizons
Publication title:	Frontiers in Marine Science; Lausanne
Publication year:	2021
Publication date:	Jul 21, 2021
Section:	ORIGINAL RESEARCH article
Publisher:	Frontiers Research Foundation
Place of publication:	Lausanne
Country of publication:	Switzerland, Lausanne
Publication subject:	Earth Sciences--Oceanography
e-ISSN:	2296-7745
Source type:	Scholarly Journal
Language of publication:	English
Document type:	Journal Article
Publication history :	
Online publication date:	0001-01-01

Milestone dates:	2021-04-12 (Received); 2021-06-16 (Accepted); 2021-07-21 (Published)
Publication history :	
First posting date:	01 Jan 0001
DOI:	https://doi.org/10.3389/fmars.2021.694039
ProQuest document ID:	2553614540
Document URL:	https://simsrad.net.ocs.mq.edu.au/login?url=https://www.proquest.com/scholarly-journals/processes-influencing-autocompaction-modulate/docview/2553614540/se-2?accountid=12219
Copyright:	© 2021. This work is licensed under http://creativecommons.org/licenses/by/4.0/ (the “License”). Notwithstanding the ProQuest Terms and Condition s, you may use this content in accordance with the terms of the License.
Last updated:	2024-05-09
Database:	Publicly Available Content Database,SciTech Premium Collection

LINKS

Database copyright © 2024 ProQuest LLC. All rights reserved.

Terms and Conditions Contact ProQuest

Estuarine, Coastal and Shelf Science 302 (2024) 108776

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Living root contributions dominate vertical accretion, but not carbon burial, in two SE Australian tidal wetlands

Yujie Sun [a], Kerrylee Rogers [b], Kirti K. Lal [c], Neil Saintilan [a,*]

[a] School of Natural Sciences, Macquarie University, Sydney, Australia
[b] School of Life and Atmospheric Sciences, University of Wollongong, Wollongong, Australia
[c] Science, Economics and Insights Division, NSW Department of Climate Change, Energy, the Environment and Water, Lidcombe, NSW 2141, Australia

ARTICLE INFO

Submission date: November 2023

Keywords:
Mangrove
Saltmarsh
organic carbon
Surface elevation
Root carbon

ABSTRACT

Organic matter derived from allochthonous and autochthonous sources makes an important contribution to the accumulation and burial of "blue carbon" in tidal wetlands. Organic matter accretion is also a mechanism by which tidal marshes and mangroves adjust vertically to the pressure of sea-level rise, through feedbacks between marsh autotrophic productivity and hydroperiod. However, the separate contributions of inorganic matter, detrital organic matter and living roots to marsh accretion have rarely been documented. We used a network of Surface Elevation Table-Marker Horizon (SET-MH) stations SE Australia as a benchmark against which the accumulation of inorganic, organic and living root material was measured. Established in 2000–2002, the SET-MH stations allowed for sampling accretion and elevation gain in mangrove and saltmarsh in fluvial and marine sand geomorphic settings. We found living root material to be the dominant contributor to the volume of accretion above feldspar marker horizons and elevation gain over the 20-year experimental period. However, detrital organic matter, being of lower bulk density than living roots, contributed most to carbon burial. Higher rates of accretion and elevation gain were associated with higher contributions of pore volume, and lower contributions of inorganic matter. The rate of subsidence increased with accretion and was lower where inorganic matter contributions to mass were higher. The results highlight the importance of biological and hydrological contributions to accretion and elevation gain in a region subject to riverine minerogenic inputs.

1. Introduction

Globally, mangroves and saltmarshes provide approximately US$ 24.8 trillion in ecosystem services annually, including water quality improvement, habitat to plants and invertebrate communities, fisheries preservation, and flood protection (Costanza et al. 2014; Friess et al., 2020). Coastal wetland ecosystems also contribute to greenhouse gas emission offsets (so-called "blue carbon") and mitigate climate change impacts by storing CO_2 in the biomass and sediments (Sasmito et al. 2020; Watanabe et al. 2019). Coastal wetlands store about 10–24 Pg carbon in their sediments and biomass and their annual carbon sequestration is about 30–70 Tg C per year globally, among the highest on the earth on a unit area basis (Duarte et al. 2005; Atwood et al., 2020; Bertram et al., 2021). Due to their bio-geochemical conditions and microbial composition, the decomposition process of organic matter is largely constrained in saturated, saline soils, and the accumulated organic carbon in these habitats can be stored over long timescales, potentially millennia (Kelleway et al., 2017; Kelleway et al. 2016a; McLeod et al. 2011). Therefore, promoting coastal vegetation conservation and restoration has become an emerging pathway to mitigate carbon emissions and coastal habitats are quantitatively and qualitatively important for carbon management (Sandi et al. 2021; Alongi, 2020). Australian coastal wetlands, which have been recognised as a global blue carbon hotspot, store up to ~35% of the global tidal marsh soil organic carbon (C_{org}) stock and ~5% of the global mangrove soil C_{org} stock, presenting significant blue carbon storage capacity (Serrano et al. 2019).

Despite their significance, coastal wetlands have long been threatened by anthropogenic impacts (Rogers et al. 2016; Friess et al., 2019; Goldberg et al., 2020), which threatens their contribution to carbon sequestration (Adame et al., 2021). Due to their low-lying position, coastal wetlands are extremely vulnerable to increasing sea level, and SLR has been identified as one of the most significant threats to coastal ecosystems (Lovelock et al. 2015a; Cahoon et al. 2021; Saintilan et al.,

* Corresponding author.
E-mail address: neil.saintilan@mq.edu.au (N. Saintilan).

https://doi.org/10.1016/j.ecss.2024.108776
Received 17 November 2023; Received in revised form 6 March 2024; Accepted 19 April 2024
Available online 24 April 2024
0272-7714/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

2023). The IPCC 6th Assessment Working Group 1 report (Arias et al., 2021) projected that it is virtually certain that global mean sea level will continue rising over the 21st century, and the global mean sea level (GMSL) is projected to rise 0.28–0.55m (likely range) by 2100 under the very low GHG (Greenhouse Gas) emission scenario (SSP 1–1.9) and 0.63–1.01m (likely range) under the very high GHG emissions scenario (SSP5-8.5) relative to the 1995–2014 average (medium confidence).

Wetland sediment vertical accretion usually contains both organic matter (OM), including living roots and non-living detrital organic materials (both allochthonous and autochthonous), and mineral components, and their relative contribution to wetland elevation gain differs across coastal landscapes (Howard et al., 2020; Morris et al., 2016). Bricker-Urso et al. (1989) found that while sediment dry mass accumulation in Rhode Island marshes was mainly controlled by inorganic input, sediment volume gain was mostly contributed by organic inputs and their associated water content. While feedbacks between sea-level rise and minerogenic sediment can promote wetland resilience (French, 2006), the supply of allochthonous minerogenic sediments in not unlimited, and the role of organic accumulation can be essential for wetland sediment accumulation (FitzGerald and Hughes, 2019). Under rising sea level, the increased accommodation associated with greater flooding depth and flooded area require an increase in the accumulation rate if wetlands are to remain *in situ* (Törnquivst et al., 2021). On coastlines increasingly impacted by catchment dams and other hydrological control structures that can limit sediment supply to coastal wetlands, the delivery of the requisite sediment is impeded (Lovelock et al., 2015a; Lui et al., 2021), and in this context greater organic inputs are required to offset the increased accommodation associated with of sea-level rise.

Recognition of the biotic contribution to wetland vertical building is therefore critical for wetland vulnerability analysis (McKee et al., 2007; McKee, 2011). Several studies have demonstrated that organic matter (OM) accumulation can be the critical influence over wetland survival under SLR in areas with little sediment supply (McKee et al. 2007; Morris et al., 2016). Radiocarbon dating has shown that the vertical development in some sediment-deficient environments was almost entirely driven by plant organic matter accumulation (Cahoon et al., 2021). For example, McKee et al. (2007) concluded that without roots and other organic material inputs, tidal wetlands in Caribbean will be submerged by the rising sea-level. McKee (2011) further highlighted the importance of root and benthic mat development to mangrove vertical adjustment in the Caribbean. Allen et al. (2021) found that the organic contribution was higher than inorganic inputs in 12 out of 15 sites in a Chesapeake Bay Sub-estuary. Further, when considering the associated water content, they estimated that organic matter contributes 91%–98% of wetland accretion within the estuary.

Wetlands subject to sea-level rise during the mid-to late-Holocene have higher levels of organic carbon than wetlands exposed to relatively stable sea-levels, suggesting that stable sea levels favour decomposition over preservation (Rogers et al., 2019). Increased flooding frequency and duration in recent decades as also led to increased mangrove root contributions to accretion in some locations (Marx et al., 2020, Breithaupt et al. 2017). As the rate of sea level rises, root production and autochthonous carbon may make stronger contributions to elevation gain where rates of sediment supply do not meet the sediment demand created by sea-level rise, and predictive models will require these processes to be more adequately represented.

Nevertheless, the volumetric contribution of roots to vertical accretion within coastal wetlands has not been widely documented and the findings are equivocal. Cahoon et al. (2006) measured the contribution of root volume to vertical accretion by using root in-growth bags and converting the mass to volume, and found a significant correlation between elevation change and root production. However, (Lovelock et al, 2015b) used root in-growth bags to conclude that there was no significant relationship between root growth and wetland surface elevation gains in Morton Bay, Queensland; although the root contribution to soil volume and subsidence was influenced by the season and the side of bay, which presented differences in sediment turbidity, nutrients, and sediment texture. Ampuero Reyes and Chmura (2022) measured live root and rhizome volume for common saltmarsh species in the St Lawrence estuary, Quebec, using mass displacement. They found the volume of living root material to be substantially greater than implied by mass, due to the very low bulk density of root aerenchyma. *Spartina alterniflora, S. patens*, and *Phragmites australis* had live plant material volume/mass relationships of 8.1, 7.2, and 5.1 times higher than the 1.1 g m^{-3} commonly used to convert the mass contribution of saltmarsh roots to volume change (Bricker-Urso et al., 1989; Turner et al., 2002; Wang et al., 2017).

In this study we quantify the composition of sediments accumulating above feldspar marker horizons in saltmarsh and mangrove vegetation communities, measuring the volume of living roots, organic matter mineral sediment and their rate of surface accumulation. The feldspar marker horizons were first established in 2000–2002, allowing an assessment of the constituents of accretion over two decades under rising sea-levels. We test the hypothesis that material accumulating above marker horizons over this ~20-year period consists primarily of allochthonous mineral sediment, as suggested by recent models of regional and continental-scale accretion models (Kirwan et al., 2016; Coleman et al., 2022). All feldspar marker horizons were associated with Surface Elevation Tables (SETs) installed at the same time. The SET is a standard method used to measure elevation changes in wetlands against a benchmark rod driven into the marsh to ~6–20 m depth) (Webb et al., 2013; Cahoon et al. 2020). We use a subset of a network SET-MHs established in SE Australia to firstly, quantify the proportional contributions of living roots, non-living organic matter and mineral sediment to mangrove and saltmarsh accumulation, and second, to test whether variation in the proportional contributions of these components is associated with variation in surface elevation gain and shallow subsidence, defined as compaction between the base of the SET rod and the feldspar horizon.

2. Methods

2.1. Study sites

We selected two sites characterised by fine fluvial sediment (Homebush Bay on the Parramatta River (Rogers et al.,2005a, 2005b); and Kooragang Island on the Hunter River (Rogers et al., 2013). Similar dominant species were found across the two sites, with the grey mangrove *Avicennia marina* dominating the mangrove vegetation, and the saltmarsh consisting largely of the *Salicornia quinqueflora/Sporobolus virginicus* association (Saintilan et al., 2013).

In each site, surface elevation change and vertical accretion above a feldspar horizon was quantified using Surface Elevation Table-Marker Horizon (SET-MH) installations established two decades prior (2000–2002). The SET-MH is a benchmark survey rod and associated artificial marker horizon (Cahoon et al., 2002), allowing for highly accurate and standardised estimates of accretion rate and elevation change between sampling locations (Webb et al., 2013). We retrieved soil cores immediately adjacent to feldspar marker horizons for sediment analysis. In SE Australia, mangroves occur approximately between mean high water and mean high water spring tides, and saltmarsh between mean high water spring tides and the highest astronomical tides. SET-MH stations were installed in replicates of 3 in the mangrove and saltmarsh at each of the four locations. At the Homebush Bay site, a distinct mangrove-saltmarsh ecotone existed, and an additional 3 replicate SET-MH stations were sampled in this “mixed” zone (see Table 1).

2.2. Vertical accretion and elevation gain

At each SET station, measurements of nine pins were taken in four arm directions, generating 36 measurements of substation elevation for

Table 1
Sampling site characteristics of vertical accretion and elevation change were measured with the SET-MH (Surface Elevation Table – Marker Horizon) method. Surface elevation tables were used to determine the surface elevation change for all sites relative to the base of the benchmark rod (driven to refusal at 4–6 m depth). At each installation, three replicate feldspar marker horizon plots were used to measure soil vertical accretion (VA). Upper-level subsidence was then calculated as the difference between soil vertical accretion and elevation change.

Study site	Geographic locations	Geomorphic setting	Dominant mangrove	Dominant saltmarsh	Period of SET measurement
Homebush Bay	151°04′E, 33°50′S	Riverine	Avicennia marina	Salicornia quinqueflora Sporobolus virginicus Juncus krausii	February 2000–September 2020
Kooragang Island	151°48′ E, 32°55′S	Riverine	A. marina	S. virginicus S.quinqueflora	January 2002–December 2020

each monitoring station. Those measurements were then averaged to a mean value for each station. Feldspar marker horizons were installed in three replicate 0.25 m^2 plots at the perimeter of each SET station. A total of 81 feldspar marker horizons were read across study sites, comprising three replicates in each SET station.

2.3. Soil sample collection

Soil sampling was conducted between December 2020 to October 2021. As our analyses of accretion data suggested that no site had greater than 10 cm of accretion since installation, sampling was conducted to this depth only. At each SET site, three sediment cores of 10 cm depth were extracted from immediately adjacent to each felspar plot, giving a total of 81 samples. The cores were extracted using in a PVC tube (9 cm diameter * 10 cm length) inserted into the marsh adjacent to the feldspar marker horizon and removed using a shovel. We found that due to the high width to depth ratio of the tube, sediment compaction was negligible (the interior core surface was flush with the exterior surface prior to extraction). Tubes were then sealed and transported on ice and stored in a cool room until sample preparation could be undertaken.

2.4. Laboratory methods

We sectioned the cores horizontally at the depth of the adjacent feldspar horizon, which allowed us to standardize the duration of accretion sampled across sites. This sample was then sectioned vertically, and half the sample (sample A) was used to quantify dry bulk density, as outlined in Fig. 1. The remaining half (sample B) was used to quantify the components contributing to accretion. These were categorised as: (a) the mass and volume of visible root material; (b) the loss on ignition (LOI), excluding the visible root material already extracted, providing the mass of non-bulk root organic matter; and (c) the mass and volume of the inorganic sediment remaining following LOI. From this we deduced the volume of non-bulk root organic matter.

To measure the dry bulk density, a known volume of sediment (from sample A) was oven-dried to constant weight. Dry bulk density was calculated as dry weight divided by the initial wet volume (Nyman et al., 1990). Sample B was immersed in a graduated measuring cylinder containing 1000 ml water, the displacement being recorded as bulk volume (being the volume of all components of the sample except for interstitial air (Lorenz et al., 1994; Robert et al., 2019). Sample B was then washed in the beaker to separate visible roots, which were manually picked using tweezers. The visible root material was weighed after the removal of surface water, and the volume was measured using the

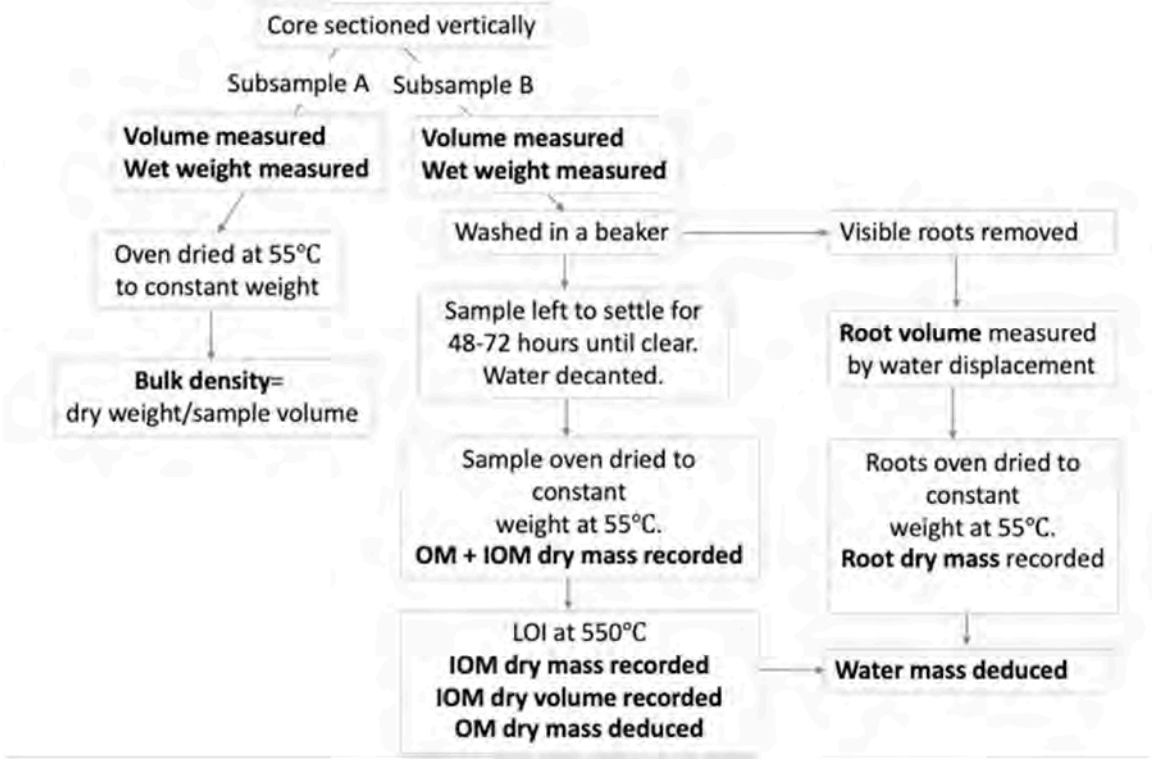


Fig. 1. Sample preparation workflow and analysis.

water displacement technique previously described. Ampuero Reyes and Chmura (2022) found this technique to compare well with computer-aided tomography (CT) imaging (Blum and Davey, 2013) and root-scanning software (Pang et al., 2011), though may miss very fine roots. The remaining sample (inorganic and detrital organic material) was allowed to settle for three to five days before decanting the water. The wet subsample was then oven-dried to constant weight, and volume and mass recorded. The separation of the organic and inorganic matter was achieved by conducting LOI at 550 °C for 3 h (Heiri et al., 2001; Breithaupt et al., 2017) (see Table 1).

2.5. Statistical analyses

For each sampling episode at each SET station, 36 surface elevation readings were generated (nine for each of four arm orientation). Outliers (pins clearly influenced local topographic features such as crab burrows and pneumatophores) were removed from analyses. The corrected data were used to determine the linear surface elevation trend for each SET station. The linear trend in sediment accumulation above the feldspar horizons was determined from the average of the three marker horizon plots at each SET from each time of reading. In some cases the feldspar horizons were lost over time (most probably due to bioturbation) and extrapolations to current depth were made on the basis of linear trends, as indicated in Table 2.

Two-way Analysis of Variance was performed in R studio (Bolker, 2008) to examine whether there were significant differences between vegetation types (mangrove, saltmarsh) and study locations on the volumetric contribution of roots, organic matter and inorganic matter. The ANOVA tests assumed that the comparison groups have the same variance (assumption of homogeneity of variance). Subsequently, Tukey's tests were used to identify significant differences between individual sampling locations. Regression analyses were performed to determine whether the relationship between the proportional contributions (both mass and volumetrically) of roots, organic matter and inorganic matter and the rate of vertical accretion, elevation gain and subsidence were significant for both mangroves and saltmarshes.

3. Results

3.1. Surface elevation change, vertical accretion, and subsidence

The rate of accretion was higher in mangrove than saltmarsh at all sites (Table 2). Shallow subsidence, defined as soil contraction between the base of the SET benchmark rod and the feldspar horizon, occurred in 11 of 15 SETs and was proportional to the rate of accretion.

3.2. Contributions of roots, organic matter and inorganic matter to accretion by mass and volume

Overall, inorganic matter contributed the most to the mass of material accreting above the feldspar horizons (Fig. 2; Table S1), excluding interstitial water. By contrast, roots and organic matter mass contributions were relatively low at all sites, contributing no more than 10% of the total accretion mass.

While inorganic material dominated mass accretion, the expansion of volume above the feldspar horizons occurred within a matrix structurally supported by living root material. Interstitial space within the sediment provided the largest contribution to volume above the feldspar horizon (49.3% ± 7.5%), followed by visible roots (34.3% ± 5.8%), inorganic sediment (12.8% ± 6.3%), and detrital organic matter (3.6% ± 2.0%). At all sites root volume was the most significant solid component contributing to accretion above the marker horizons (Fig. 3; Table S1). By contrast OM had relatively low volumetric contribution above the marker horizons at all sites, with contributions between 1.7% and 5.7%, despite making a greater contribution to organic mass accumulation in nearly all settings.

No significant difference was identified between mangrove and saltmarsh vegetation in the volumetric contribution of roots (ANOVA $p = 0.95$) or organic carbon (ANOVA $p = 0.98$) or inorganic matter (ANOVA $p = 0.71$) to accretion volume, nor were consistent differences found between sites in the contribution of these constituents: (ANOVA $p = 0.45$ for root volume contribution; $p = 0.98$ for organic carbon; $p = 0.60$ for inorganic matter contribution to volume).

3.3. Contributions of roots, organic matter and inorganic matter to accretion, elevation change and subsidence

In common with wetlands elsewhere in SE Australia (Rogers and Saintilan, 2021) and globally (Saintilan et al., 2022), increased accretion rates were associated with increased rates of upper level subsidence (Fig. 4a). The analysis of soil constituents provides some insights into the drivers of this association. Regression analyses showed that the proportional volumetric contribution of inorganic matter negatively correlated with accretion above the marker horizon ($p < 0.008$, $r^2 = 0.45$; Fig. 4b), and the proportional contribution of non-root solid components (inorganic + organic) were strongly and inversely correlated with accretion ($p < 0.001$, $r^2 = 0.74$; Fig. 4c). Conversely, higher proportional pore volume contributions were associated with higher rates of accretion (Fig. 4d). With the decrease in the proportion of inorganic matter under high rates of accretion, the rate of subsidence also increases (Fig. 4e). Data on elevation gain reflected this, with higher rates of elevation gain associated with lower proportional contributions of all solid state constituents (inorganic matter, organic matter and

Table 2
Rates of elevation change and vertical accretion across sampling sites.

Location	Vegetation	Site	Surface elevation change		Vertical accretion		Shallow Subsidence
			Cumulative (mm)	Linear rate (mm yr^{-1})	Cumulative (mm)	Linear rate (mm yr^{-1})	Linear rate (mm yr^{-1})
Homebush	Mangrove	M1	55.3	3.28	78.0	2.92	0.40
		M2	65.2	2.66	91.7	3.43	0.15
		M3	57.8	2.48	86.0	2.88	0.22
	Saltmarsh	S1	17.5	2.65	38.7	1.06	−1.59
		S2	15.1	3.42	24.7	1.50	−1.92
		S3	19.7	2.50	26.3	1.93	−0.57
	Mixed	Mx1	29.6	3.45	65.3	2.65	−0.80
		Mx2	27.6	2.43	79.1	5.09	2.66
		Mx3	29.1	1.91	83.7	3.79	1.87
Kooragang	Mangrove	M1	47.5	2.48	58.6	2.96	0.47
		M2	39.3	2.04	51.9	2.45	0.40
		M3	34.9	1.68	64.3	3.25	1.57
	Saltmarsh	S1	26.3	1.34	29.2	1.83	0.49
		S2	23.3	1.23	34.1	2.00	0.77
		S3	37.5	1.46	29.4	1.50	0.04

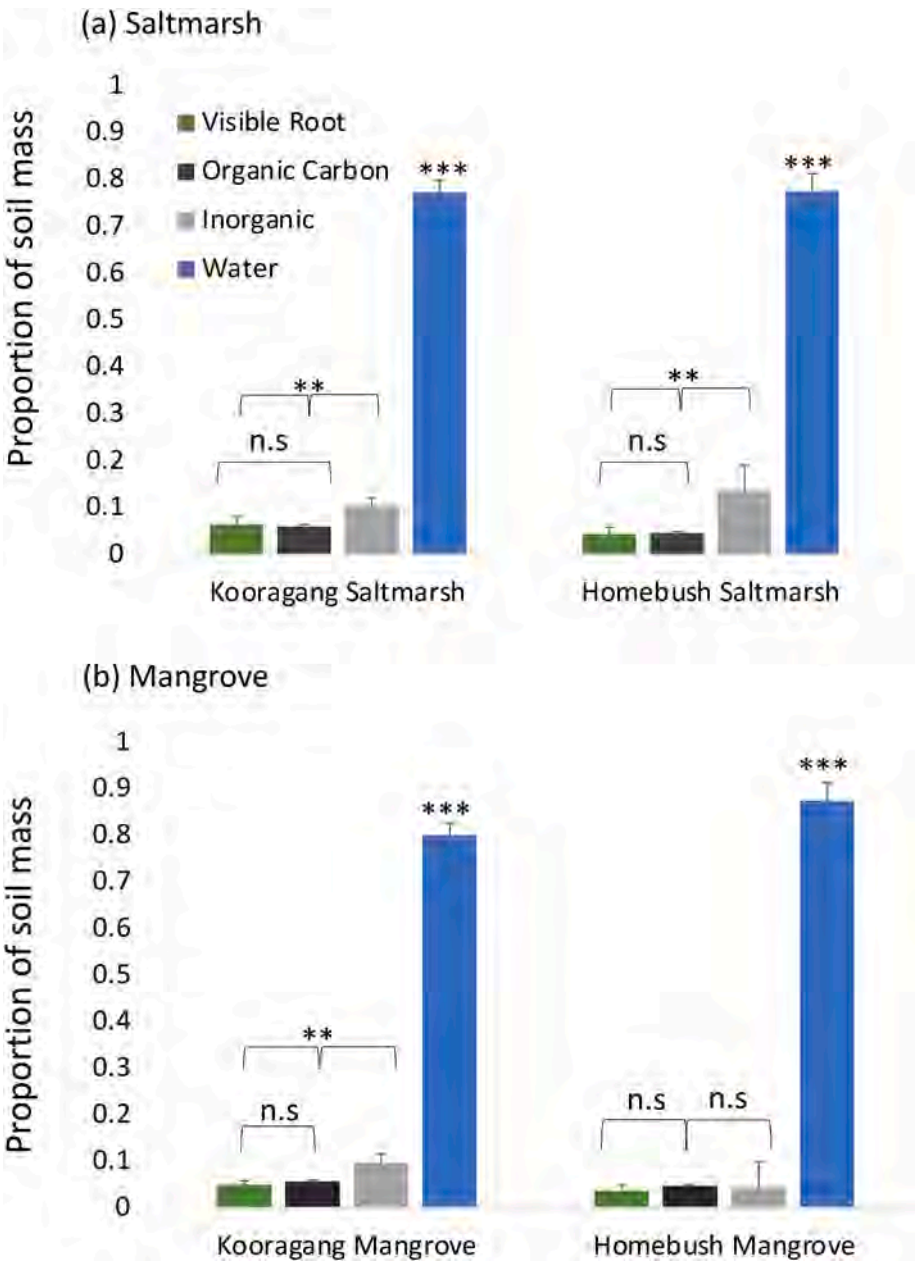


Fig. 2. The proportional wet mass contribution of living roots, other organic matter, and inorganic matter to the mass of accreted material above feldspar horizons. The remaining mass consisted of interstitial water.

living root mass: Fig. 5a and b).

4. Discussion

The results show the potential of combining Surface Elevation Table-Marker Horizon readings with measurement of the components of accretion above the marker horizons to clarify processes responsible for accretion, elevation gain and upper level subsidence. The sites chosen for this analysis lie within riverine settings in eastern Australia, and we hypothesised that allochthonous sediment inputs might be important in controlling accretion and elevation gain. Our results showed that in both sites living root material made a considerably greater contribution.

Counter to our assumption, higher rates of elevation amongst the 15 SETs sampled were associated with lower proportional mass contributions of all components sampled (Fig. 5). Reflecting this finding was the higher pore-space contribution to volume in more rapidly accreting sites, and lower volume contributions of inorganic sediment. This contrasts to the commonly held assumption that suspended sediment drives elevation gain in wetland, an assumption that underpins several modelling exercises (Coleman et al., 2022; Kirwan et al., 2010; Schuerch et al., 2018). A recent global-scale analysis of the relationship between suspended sediment concentration and accretion above feldspar horizons at tidal marsh SET stations has found this association to be weak ($r^2 < 0.10$: Saintilan et al., 2022). Our data suggest that higher accretion is being driven primarily by higher proportional pore space, a factor implicated in the consistently higher subsidence in high accretion settings (Rogers and Saintilan, 2021; Saintilan et al., 2022), also found in this study. Our sites with higher proportional inorganic sediment contributions to volume had lower rates of upper level subsidence. Living root material, sediment organic matter and inorganic sediment have markedly different bulk density, and their contributions to short- and long-term accretion and elevation gain are likely to be complex yet important considerations in determining marsh responses to sea-level rise.

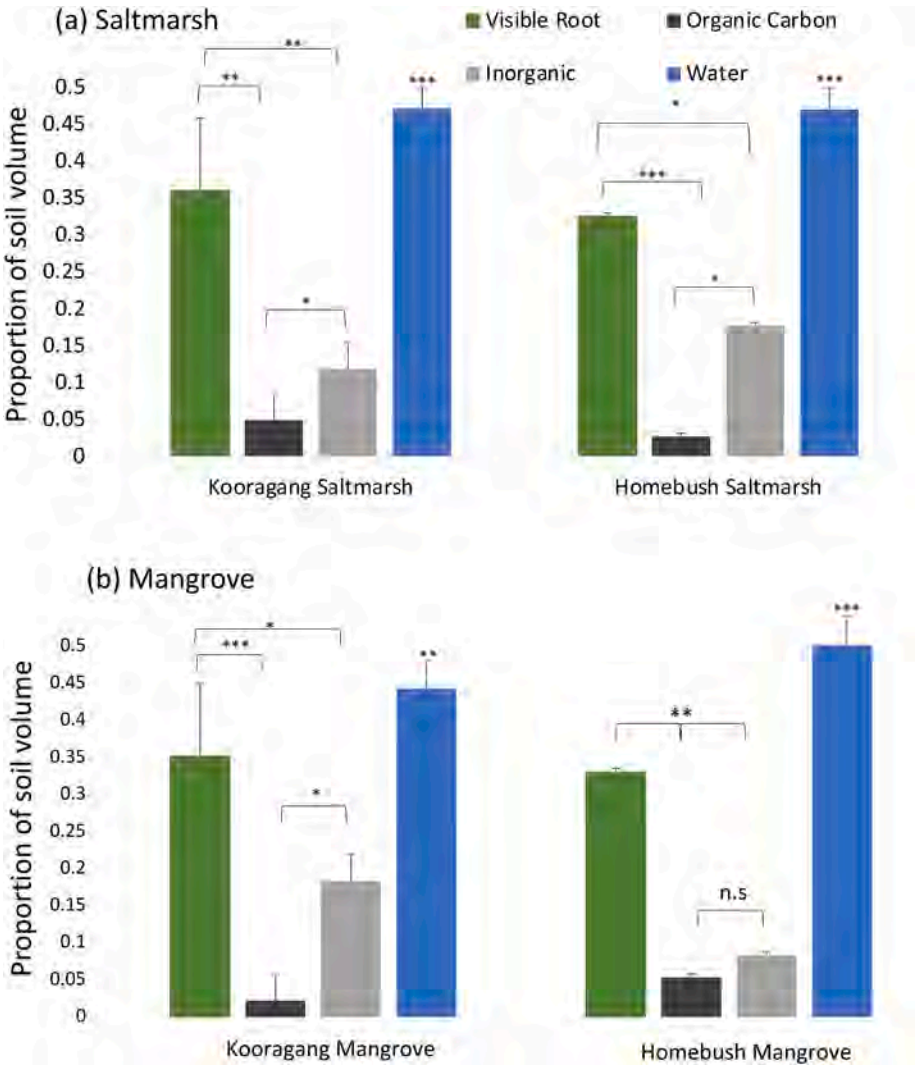


Fig. 3. The proportional volumetric contribution of living roots, other organic matter and inorganic matter to volume of accreted material above feldspar horizons. The remaining volume consisted of interstitial water and air. Asterisks denote statistical significance at *p < 0.05; **p < 0.01; ***p < 0.001.

The contribution of living root material to accretion and elevation gain is therefore a critically important process to be modelling marsh responses to sea-level rise. We found no difference between our mangrove and saltmarsh sites in the contribution of roots by volume to vertical accretion (consistently 30–40% of total volume), despite differences in root morphology between the mangrove *A. marina* (high density of cable roots and pneumatophores: Saintilan et al., 2013; Srikanth et al., 2016) and the *S. quinqueflora/S. virginicus* saltmarsh association, with far lower standing biomass, and a shallow root system supported by rhizomes (Saintilan et al., 2013). It may therefore be challenging to model root contributions to vertical elevation gain based on above-ground biomass estimates across the region. However, it should be emphasised that our measures only refer to root contributions above the feldspar horizons, and differences between mangrove and saltmarsh root contributions to elevation gain may become greater in deeper horizons (Adame et al., 2017; Lamont et al., 2020).

While organic matter (excluding roots) contributed little to vertical accretion (2%–7%), the contribution to the total mass of non-living organic matter equalled or exceeded that of living root material. This detrital organic matter comprised 20–50% of the accumulating non-root material (non-root organic matter + inorganic matter) for saltmarshes (32.2 ± 9.0%), and mangroves (37.1 ± 12.8%). This corresponds with the proportional loss on ignition for mud associated organic matter in Louisiana marshes (Mariotti et al., 2020) of 20–40%, which they argued was primarily allochthonous. In a previous study, stable isotopes were used to demonstrate that this detrital organic material was consistent with the incorporation of highly degraded mangrove leaf material, the importance of which declined with increasing sediment depth (Saintilan et al., 2013).

The contribution of inorganic material to accretion (by mass) was found to be dominant amongst the constituents measured (Fig. 2). The large differences in bulk density between living root material, non-root organic matter and inorganic matter need to be carefully considered when estimating the mass of soil components from soil volume. Ampuero Reyes and Chmura (2022) examined root and mass contributions of four marsh species in the St Lawrence Estuary, Canada and concluded that a mass to volume conversion factor of 8.2 reflected the contribution of living roots to soil volume (species they studied ranged from 5.6 to 8.9). Our estimated conversion factors of 6.7 for saltmarsh and 8.1 for mangrove falls within a similar range.

Geomorphic settings and sediment types also have significant implications in carbon storage and carbon preservation in SE Australian coastal wetlands (Saintilan et al., 2013; Kelleway et al., 2016b). The marine sand settings may prove to have lower root and organic matter contributions than those sampled. In a regional assessment of tidal wetland carbon stocks in SE Australia, (Kelleway et al., 2016b), fluvial settings appeared to have greater organic matter preservation than marine settings. Coarser sediments have longer oxygen exposure times,

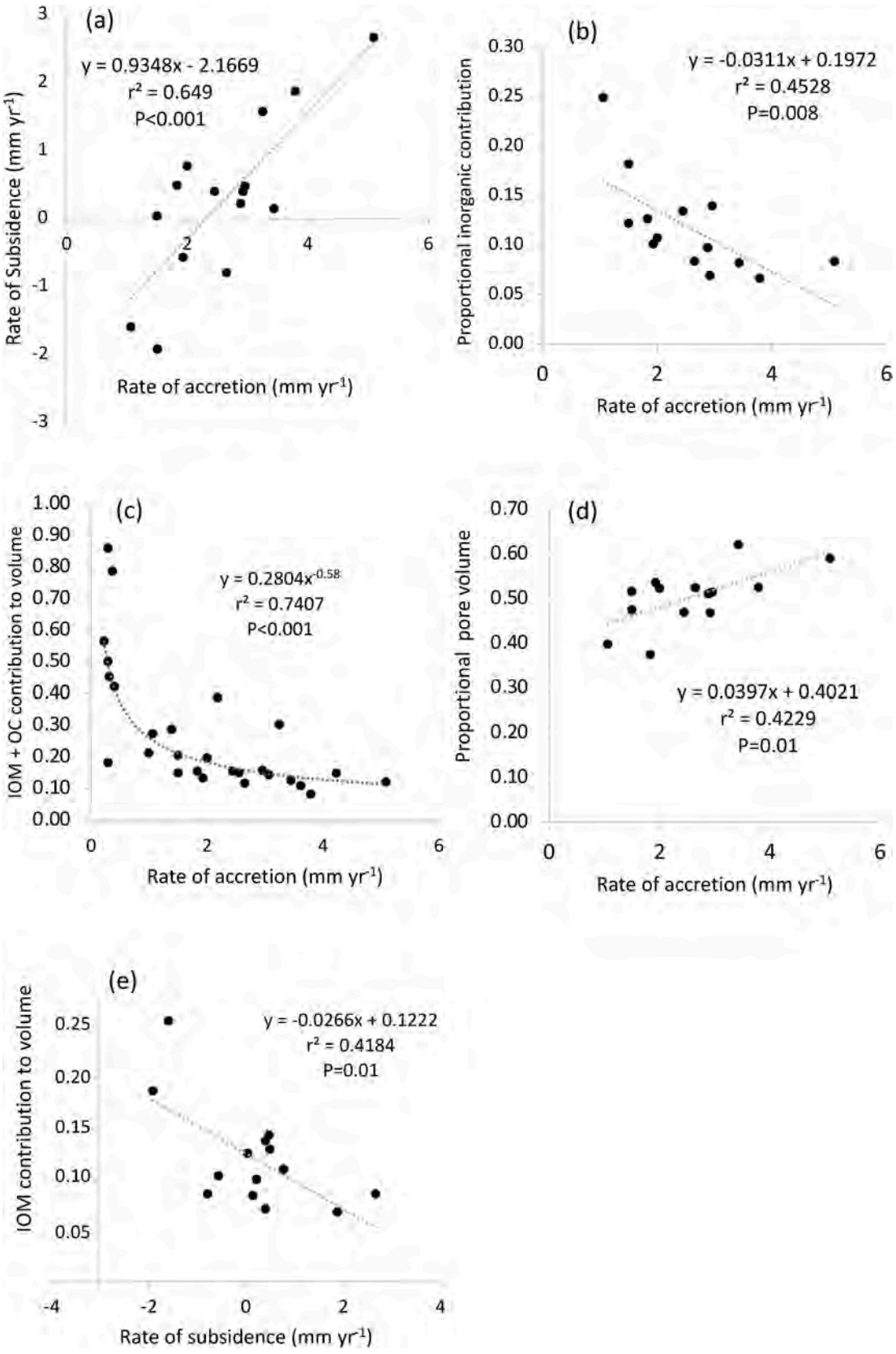


Fig. 4. The rate of upper-level subsidence increases with the rate of accretion (a). The rate of accretion is inversely related to proportional contributions of inorganic matter (IOM) to volume (b) and IOM and organic carbon (OC) contributions to volume (c), but positively associated with pore space contributions to volume (d). Higher proportional contributions of IOM are associated with lower rates of subsidence (e).

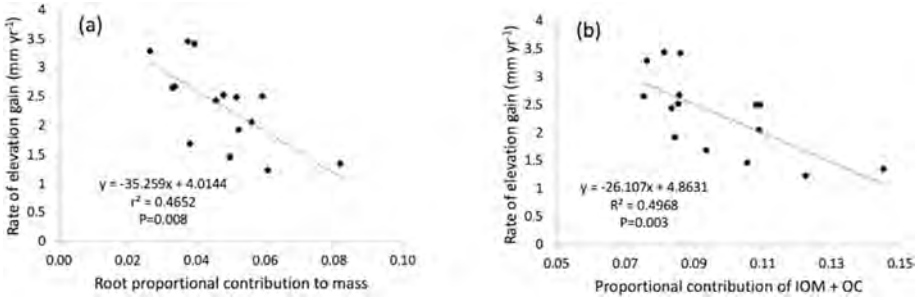


Fig. 5. Relationships between the mass contributions of roots (a), organic carbon (OC) and inorganic matter (IOM) combined (b) and the rate of elevation gain. Higher rates of elevation gain are associated with lower proportional solid mass contributions of roots, organic carbon and inorganic matter.

resulting in higher sediment redox potentials and accelerating remineralisation (Hedges and Keil, 1995; Kelleway et al., 2016b). Ultimately, wetland carbon storage capacity depends on the balance between organic matter inputs and its decay, comprising both autochthonous and allochthonous processes, and marsh C sequestration rate depends on sediment vertical accretion rate as well as soil C density (Mueller et al., 2016; Wang et al., 2019).

Our measures of root contributions were made above the feldspar horizon, and do not represent the zone for which upper subsidence is calculated (being the zone between the base of the SET benchmark rod and the feldspar horizon). Nearly all the SET-MH installations showed evidence of upper-level subsidence (that is, the rate of accretion was greater than the rate of elevation gain), consistent with tidal marshes globally (Saintilan et al., 2022). Of the four SET-MH showing upper-level soil expansion amongst the 15 SET-MH measured, three were the Homebush saltmarsh SET-MH, previously documented by Rogers et al. (2005a,b) as a site where subsurface root contributions increased resulting from mangrove regeneration. Subsidence is occurring despite a strong root contribution to accretion above the feldspar horizon, and a *prima facie* case that most root growth would be below this horizon (and as measured within the region by Lamont et al., 2020). This root volume expansion below the feldspar horizons must therefore be offset by greater losses due to sediment compaction, root collapse and organic decomposition. It may be that roots at depth are preferentially senesced as new root growth occurs at the marsh surface, given the higher respiratory demand associated with their retention.

This study is the first to look specifically at organic matter and root volume contributions to elevation gain above feldspar horizons within the SET-MH network. The widely adopted use of the SET-MH method allows the comparability of accretion and elevation change data across different sites, locations and vegetation types. The introduction of the feldspar marker horizon and repeat measurements over the observation years provide tight control on the age of sedimentation. The extensive global SET-MH network (Webb et al., 2013) provides the opportunity for consistent comparisons of living root and organic matter accumulation and their environmental drivers. Over 20 years, the living root volume drove accretion and elevation adjustment in spite of a proportionately low contribution to mass accumulation.

5. Conclusions

The SET-MH network in SE Australia installed in 2000–2002 provided the opportunity to examine the constituents contributing to vertical accretion above feldspar horizons laid down two decades ago. This period is sufficiently long to incorporate several phases of the El Nino Southern Oscillation, and important control on wetland accretion and groundwater recharge in the region (Rogers et al., 2005). We found living roots to be the dominant contributor to accretion (by volume) at all sites. Living root volume contributed more than double that of inorganic sediment and was an order of magnitude higher than the volumetric contributions of non-root organic matter.

While the importance of local factors, and organic contributions are recognised (Coleman et al., 2022), the widespread reporting of suspended sediment concentrations and accretion rates in tidal wetlands has invited the development of predictive models that may have under-represented the importance of plant autochthonous contributions to marsh elevation gain and survival, in spite of the significance of these factors in early models of marsh equilibrium responses (Morris et al., 2016; Morris et al., 2002), and observations from both sediment laden (Turner et al., 2000) and sediment deficient (McKee et al., 2007) environments.

CRediT authorship contribution statement

Yujie Sun: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Kerrylee Rogers:** Writing – review & editing, Investigation. **Kirti K. Lal:** Writing – review & editing, Data curation. **Neil Saintilan:** Investigation, Formal analysis, Conceptualization, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This work is funded by Macquarie University IMQRES MRES (Road to Research) Scholarship to YS. We thank Sean Murray and Kaushal Tewari for their assistance in laboratory work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108776.

References

Adame, M.F., Cherian, S., Reef, R., Stewart-Koster, B., 2017. Mangrove root biomass and the uncertainty of belowground carbon estimations. For. Ecol. Manag. 403, 52–60.
Adame, M.F., Connolly, R.M., Turschwell, M.P., Lovelock, C.E., Fatoyinbo, T., Lagomasino, D., Goldberg, L.A., Holdorf, J., Friess, D.A., Sasmito, S.D., Sanderman, J., Sievers, M., Buelow, C., Kauffman, J.B., Bryan-Brown, D., Brown, C. J., 2021. Future carbon emissions from global mangrove forest loss. Global Change Biol. 27, 2856–2866.
Allen, J.R., Cornwell, J.C., Baldwin, A.H., 2021. Contributions of organic and mineral matter to vertical accretion in tidal wetlands across a Chesapeake bay subestuary. J. Mar. Sci. Eng. 9, 751.

Alongi, D.M., 2020. Global significance of mangrove blue carbon in climate change mitigation. Science 2, 67.
Ampuero Reyes, W., Chmura, G.L., 2022. Contribution of belowground plant components to salt marsh soil volume. Estuar. Coast Shelf Sci. 275, 107974.
Arias, P., Bellouin, N., Coppola, E., Jones, R., Krinner, G., Marotzke, J., et al., 2021. Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. Tech. Summ. 150.
Atwood, T.B., Witt, A., Mayorga, J., Hammill, E., Sala, E., 2020. Global patterns in marine sediment carbon stocks. Front. Mar. Sci. 7, 165.
Bertram, C., Quaas, M., Reusch, T.B., Vafeidis, A.T., Wolff, C., Rickels, W., 2021. The blue carbon wealth of nations. Nat. Clim. Change 11 (8), 704–709.
Bolker, B.M., 2008. Ecological Models and Data in R. Princeton University Press.
Blum, L.K., Davey, E., 2013. Below the salt marsh surface: visualization of plant roots by computer-aided tomography. Oceanography 26 (3), 85–87.
Breithaupt, J.L., Smoak, J.M., Rivera-Monroy, V.H., Castañeda-Moya, E., Moyer, R.P., Simard, M., Sanders, C.J., 2017. Partitioning the relative contributions of organic matter and mineral sediment to accretion rates in carbonate platform mangrove soils. Mar. Geol. 390, 170–180.
Bricker-Urso, S., Nixon, S.W., Cochran, J.K., Hirschberg, D.J., Hunt, C., 1989. Accretion rates and sediment accumulation in Rhode Island salt marshes. Estuaries 12, 300.
Cahoon, D.R., Lynch, J.C., Perez, B.C., Segura, B., Holland, R.D., Stelly, C., et al., 2002. High-precision measurements of wetland sediment elevation: II. The rod surface elevation table. J. Sediment. Res. 72 (5), 734–739.
Cahoon, D.R., Hensel, P.F., Spencer, T., Reed, D.J., McKee, K.L., Saintilan, N., 2006. Coastal wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In: Verhoeven, J.T.A., Beltman, B., Bobbink, R., Whigham, D.F. (Eds.), Wetlands and Natural Resource Management, Ecological Studies. Springer, Berlin Heidelberg, pp. 271–292.
Cahoon, D.R., Reed, D.J., Day, J.W., Lynch, J.C., Swales, A., Lane, R.R., 2020. Applications and utility of the surface elevation table–marker horizon method for measuring wetland elevation and shallow soil subsidence-expansion: discussion/reply to: byrnes M., Britsch L., Berlinghoff J., Johnson R., and Khalil S. 2019. Recent subsidence rates for Barataria Basin, Louisiana. Geo-Marine Letters 39:265–278. Geo Mar. Lett. 40, 809–815.
Cahoon, D.R., McKee, K.L., Morris, J.T., 2021. How plants influence resilience of salt marsh and mangrove wetlands to seasea-level rise. Estuar. Coast 44, 883–898.
Coleman, D.J., Schuerch, M., Temmerman, S., Guntenspergen, G., Smith, C.G., Kirwan, M.L., 2022. Reconciling models and measurements of marsh vulnerability to sea level rise. Limnol. Oceanogr. Lett. lol2., 10230
Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S., Turner, R.K., 2014. Changes in the Global Value of Ecosystem Services.
Duarte, C.M., Middelburg, J.J., Caraco, N., 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2 (1), 1–8.
FitzGerald, D.M., Hughes, Z., 2019. Marsh processes and their response to climate change and sea-level rise. Annu. Rev. Earth. Planet Sci. 47, 481–517.
Friess, D.A., Rogers, K., Lovelock, C.E., Krauss, K.W., Hamilton, S.E., Lee, S.Y., et al., 2019. The state of the world's mangrove forests: past, present, and future. Annu. Rev. Environ. Resour. 44, 89–115.
Friess, D.A., Yando, E.S., Alemu, J.B., Wong, L.W., Soto, S.D., Bhatia, N., 2020. Ecosystem services and disservices of mangrove forests and salt marshes. Oceanogr. Mar. Biol.
French, J., 2006. Tidal marsh sedimentation and resilience to environmental change: exploratory modelling of tidal, sea-level and sediment supply forcing in predominantly allochthonous systems. Mar. Geol. 235 (1–4), 119–136.
Goldberg, L., Lagomasino, D., Thomas, N., Fatoyinbo, T., 2020. Global declines in human-driven mangrove loss. Global Change Biol. 26 (10), 5844–5855.
Hedges, J.I., Keil, R.G., 1995. Sedimentary organic matter preservation: an assessment and speculative synthesis. Mar. Chem. 49, 81–115.
Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. J. Paleolimnol. 25, 101–110.
Howard, R.J., From, A.S., Krauss, K.W., Andres, K.D., Cormier, N., Allain, L., Savarese, M., 2020. Soil surface elevation dynamics in a mangrove-to-marsh ecotone characterized by vegetation shifts. Hydrobiologia 847, 1087–1106.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Ralph, P.J., 2016a. Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes. Ecosystems 19, 865–880.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Skilbeck, C.G., Zawadzki, A., Ralph, P.J., 2016b. Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. Global Change Biol. 22, 1097–1109.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Baldock, J.A., Ralph, P.J., 2017. Sediment and carbon deposition vary among vegetation assemblages in a coastal salt marsh. Biogeosciences 14, 3763–3779.
Kirwan, M.L., Guntenspergen, G.R., D'Alpaos, A., Morris, J.T., Mudd, S.M., Temmerman, S., 2010. Limits on the adaptability of coastal marshes to rising sea level: ecogeomorphic limits to wetland survival. Geophys. Res. Lett. 37.
Kirwan, M.L., Temmerman, S., Skeehan, E.E., Guntenspergen, G.R., Fagherazzi, S., 2016. Overestimation of marsh vulnerability to sea level rise. Nat. Clim. Change 6, 253–260.
Lamont, K., Saintilan, N., Kelleway, J.J., Mazumder, D., Zawadzki, A., 2020. Thirty-year repeat measures of mangrove above-and below-ground biomass reveals unexpectedly high carbon sequestration. Ecosystems 23 (2), 370–382.
Lorenz, S.E., Hamon, R.E., McGRATH, S.P., 1994. Differences between soil solutions obtained from rhizosphere and non-rhizosphere soils by water displacement and soil centrifugation. Eur. J. Soil Sci. 45, 431–438.
Lovelock, C.E., Cahoon, D.R., Friess, D.A., Guntenspergen, G.R., Krauss, K.W., Reef, R., Rogers, K., Saunders, M.L., Sidik, F., Swales, A., Saintilan, N., Thuyen, L.X., Triet, T., 2015a. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. Nature 526, 559–563.
Lovelock, C.E., Adame, M.F., Bennion, V., Hayes, M., Reef, R., Santini, N., Cahoon, D.R., 2015b. Sea level and turbidity controls on mangrove soil surface elevation change. Estuar. Coast Shelf Sci. 153, 1–9.
Liu, Z., Fagherazzi, S., Cui, B., 2021. Success of coastal wetlands restoration is driven by sediment availability. Commun. Earth. Environ. 2 (1), 1–9.
Marx, S.K., Knight, J.M., Dwyer, P.G., Child, D.P., Hotchkis, M.A., Zawadzki, A., 2020. Examining the response of an eastern Australian mangrove forest to changes in hydro-period over the last century. Estuar. Coast Shelf Sci. 241, 106813.
Mariotti, Elsey-Quirk, T., Bruno, G., Valentine, K., 2020. Mud-associated organic matter and its direct and indirect role in marsh organic matter accumulation and vertical accretion. Limnol. Oceanogr.
McKee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Global Ecol. Biogeogr. 16, 545–556.
McKee, K.L., 2011. Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. Estuar. Coast Shelf Sci. 91, 475–483.
McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Front. Ecol. Environ. 9, 552–560.
Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., Cahoon, D.R., 2002. Response of coastal wetlands to rising sea. Ecology 83, 2869–2877.
Morris, J.T., Barber, D.C., Callaway, J.C., Chambers, R., Hagen, S.C., Hopkinson, C.S., Johnson, B.J., Megonigal, P., Neubauer, S.C., Troxler, T., Wigand, C., 2016. Contributions of organic and inorganic matter to sediment volume and accretion in tidal wetlands at steady state. Earth's Future 4, 110–121.
Mueller, P., Jensen, K., Megonigal, J.P., 2016. Plants mediate soil organic matter decomposition in response to sea level rise. Global Change Biol. 22, 404–414.
Nyman, J.A., Delaune, R.D., Patrick, W.H., 1990. Wetland soil formation in the rapidly subsiding Mississippi River Deltaic Plain: mineral and organic matter relationships. Estuar. Coast Shelf Sci. 31, 57–69.
Pang, W., Crow, W.T., Luc, J.E., McSorley, R., Giblin-Davis, R.M., Kenworthy, K.E., Kruse, J.K., 2011. Comparison of water displacement and WinRHIZO software for plant root parameter assessment. Plant Dis. 95 (10), 1308–1310.
Robert, U.W., Etuk, S.E., Agbasi, O.E., 2019. Bulk volume determination by modified water displacement method. Iraqi J. Sci. 1704–1710.
Rogers, K., Saintilan, N., Cahoon, D., 2005a. Surface elevation dynamics in a regenerating mangrove forest at Homebush bay, Australia. Wetl. Ecol. Manag. 13, 587–598.
Rogers, K., Saintilan, N., Heijnis, H., 2005b. Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence, and sea level rise. Estuaries 28, 551–559.
Rogers, K., Saintilan, N., Howe, A.J., Rodríguez, J.F., 2013. Sedimentation, elevation and marsh evolution in a southeastern Australian estuary during changing climatic conditions. Estuar. Coast Shelf Sci. 133, 172–181.
Rogers, K., Boon, P.I., Branigan, S., Duke, N.C., Field, C.D., Fitzsimons, J.A., Kirkman, H., Mackenzie, J.R., Saintilan, N., 2016. The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. Mar. Pol. 72, 139–155.
Rogers, K., Kelleway, J.J., Saintilan, N., Megonigal, J.P., Adams, J.B., Holmquist, J.R., Lu, M., Schile-Beers, L., Zawadzki, A., Mazumder, D., Woodroffe, C.D., 2019. Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. Nature 567, 91–95.
Rogers, K., Saintilan, N., 2021. Processes influencing autocompaction modulate coastal wetland surface elevation adjustment with sea-level rise. Front. Mar. Sci. 8, 694039.
Saintilan, N., Rogers, K., Mazumder, D., Woodroffe, C., 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuar. Coast Shelf Sci. 128, 84–92.
Saintilan, N., Kovalenko, K.E., Guntenspergen, G., Rogers, K., Lynch, J.C., Cahoon, D.R., et al., 2022. Constraints on the adjustment of tidal marshes to accelerating sea level rise. Science 377 (6605), 523–527.
Saintilan, N., Horton, B., Törnqvist, T.E., Ashe, E.L., Khan, N.S., Schuerch, M., et al., 2023. Widespread retreat of coastal habitat is likely at warming levels above 1.5° C. Nature 621 (7977), 112–119.
Sandi, S.G., Rodriguez, J.F., Saco, P.M., Saintilan, N., Riccardi, G., 2021. Accelerated Sea-Level rise limits vegetation capacity to sequester soil carbon in coastal wetlands: a study case in southeastern Australia. Earth's Future 9.
Sasmito, S.D., Kuzyakov, Y., Lubis, A.A., Murdiyarso, D., Hutley, L.B., Bachri, S., Friess, D.A., Martius, C., Borchard, N., 2020. Organic carbon burial and sources in soils of coastal mudflat and mangrove ecosystems. Catena 187, 104414.
Schuerch, M., Spencer, T., Temmerman, S., Kirwan, M.L., Wolff, C., Lincke, D., McOwen, C.J., Pickering, M.D., Reef, R., Vafeidis, A.T., Hinkel, J., Nicholls, R.J., Brown, S., 2018. Future response of global coastal wetlands to sea-level rise. Nature 561, 231–234.
Serrano, O., Lovelock, C.E., Atwood, T.B., Macreadie, P.I., Canto, R., Phinn, S., Arias-Ortiz, A., Bai, L., Baldock, J., Bedulli, C., Carnell, P., Connolly, R.M., Donaldson, P., Esteban, A., Ewers Lewis, C.J., Eyre, B.D., Hayes, M.A., Horwitz, P., Hutley, L.B., Kavazos, C.R.J., Kelleway, J.J., Kendrick, G.A., Kilminster, K., Lafratta, A., Lee, S., Lavery, P.S., Maher, D.T., Marbà, N., Masque, P., Mateo, M.A., Mount, R., Ralph, P.

J., Roelfsema, C., Rozaimi, M., Ruhon, R., Salinas, C., Samper-Villarreal, J., Sanderman, J., Sanders, C.J., Santos, I., Sharples, C., Steven, A.D.L., Cannard, T., Trevathan-Tackett, S.M., Duarte, C.M., 2019. Australian vegetated coastal ecosystems as global hotspots for climate change mitigation. Nat. Commun. 10, 4313.

Srikanth, S., Lum, S.K.Y., Chen, Z., 2016. Mangrove root: adaptations and ecological importance. Trees (Berl.) 30, 451–465.

Törnqvist, T.E., Cahoon, D.R., Morris, J.T., Day, J.W., 2021. Coastal wetland resilience, accelerated sea-level rise, and the importance of timescale. AGU Adv. 2.

Turner, R.E., Swenson, E.M., Milan, C.S., 2000. Organic and inorganic contributions to vertical accretion in salt marsh sediments. In: Weinstein, M.P., Kreeger, D.A. (Eds.), Concepts and Controversies in Tidal Marsh Ecology. Springer, Netherlands, Dordrecht, pp. 583–595.

Turner, R.E., Swenson, E.M., Milan, C.S., 2002. Organic and inorganic contributions to vertical accretion in salt marsh sediments. 5In. In: Weinstein, M.P., Kreeger, D.A. (Eds.), Concepts and Controversies in Tidal Marsh Ecology, pp. 583–595.

Wang, F., Lu, X., Sanders, C.J., Tang, J., 2019. Tidal wetland resilience to sea level rise increases their carbon sequestration capacity in United States. Nat. Commun. 10, 5434.

Wang, H., Steyer, G.D., Couvillion, B.R., Beck, H.J., Rybczyk, J.M., Rivera-Monroy, V.H., et al., 2017. Predicting landscape effects of Mississippi River diversions on soil organic carbon sequestration. Ecosphere 8 (11), e01984.

Watanabe, K., Seike, K., Kajihara, R., Montani, S., Kuwae, T., 2019. Relative sea-level change regulates organic carbon accumulation in coastal habitats. Global Change Biol. 25, 1063–1077.

Webb, E.L., Friess, D.A., Krauss, K.W., Cahoon, D.R., Guntenspergen, G.R., Phelps, J., 2013. A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. Nat. Clim. Change 3, 458–465.

COASTAL ECOLOGY

Constraints on the adjustment of tidal marshes to accelerating sea level rise

Neil Saintilan[1]*, Katya E. Kovalenko[2], Glenn Guntenspergen[3], Kerrylee Rogers[4], James C. Lynch[5], Donald R. Cahoon[3], Catherine E. Lovelock[6], Daniel A. Friess[7], Erica Ashe[8], Ken W. Krauss[9], Nicole Cormier[1], Tom Spencer[10], Janine Adams[11], Jacqueline Raw[11], Carles Ibanez[12], Francesco Scarton[13], Stijn Temmerman[14], Patrick Meire[15], Tom Maris[15], Karen Thorne[16], John Brazner[15], Gail L. Chmura[17], Tony Bowron[18], Vishmie P. Gamage[1], Kimberly Cressman[19], Charlie Endris[20], Christina Marconi[21], Pamela Marcum[22], Kari St. Laurent[23], William Reay[24], Kenneth B. Raposa[25], Jason A. Garwood[26], Nicole Khan[27]

Much uncertainty exists about the vulnerability of valuable tidal marsh ecosystems to relative sea level rise. Previous assessments of resilience to sea level rise, to which marshes can adjust by sediment accretion and elevation gain, revealed contrasting results, depending on contemporary or Holocene geological data. By analyzing globally distributed contemporary data, we found that marsh sediment accretion increases in parity with sea level rise, seemingly confirming previously claimed marsh resilience. However, subsidence of the substrate shows a nonlinear increase with accretion. As a result, marsh elevation gain is constrained in relation to sea level rise, and deficits emerge that are consistent with Holocene observations of tidal marsh vulnerability.

Tidal marshes are among the most vulnerable of the world's ecosystems. Throughout human civilization, tidal marshes have been reclaimed for agriculture and settlement, and the pace of loss has accelerated in concert with burgeoning coastal populations on all inhabited continents over the past century (*1*, *2*). To this pressure has been added the threat of accelerating sea level rise. Because tidal marshes occur within tightly defined elevation ranges relative to mean sea level, they are sentinel ecosystems at the forefront of coastal climate change impact. Potential tidal marsh loss with sea level rise threatens a range of ecosystem services valued at US ~$27 trillion per year (*3*), extending to fisheries production, recreation, cultural heritage, coastal protection, water quality enhancement, and carbon sequestration.

Sea level rise can lead to marsh loss through marsh edge erosion, conversion to mudflats, encroachment of mangrove forests where they occupy lower tidal position, and/or the expansion of internal ponds and channels, with all mechanisms enhanced by the loss of marsh surface elevation relative to mean tide level (*4*). The fate of tidal marshes under accelerating sea level rise will be determined not only by opportunities for landward marsh migration (*5*) but also by the capacity of tidal marshes to gain elevation through vertical accretion of mineral sediment and organic matter (*6*). Biophysical feedbacks between sea level rise and the vertical development of marsh substrates reduce the risk of loss occurring through conversion to unvegetated mudflats or open water (*7*).

Modeling based on observations from US East Coast organic marshes (*8*) and UK minerogenic marshes (*9*) has suggested that an equilibrium may emerge among the position of a marsh within the tidal frame, plant productivity, root mass development, sedimentation, and the elevation of the marsh in response to mean sea level (Fig. 1). This equilibrium may be sustained under low rates of relative sea level rise (RSLR), the combination of vertical land movement and sea level change. How widely these controls and their upper limits operate across marsh sites globally has been a crucial and disputed question in the regional- to global-scale modeling of tidal marsh responses to projected rates of RSLR under climate change (*5*, *7*, *10*). At present, observations of contemporary marsh accretion suggest that marshes can adjust to rates of RSLR of >10 mm $year^{-1}$ (*7*, *11*, *12*). However, the Holocene marsh record suggests that adjustment is highly unlikely (90% probability) at RSLR exceeding 7 mm $year^{-1}$ for UK tidal marshes (*13*) and tropical mangroves (*10*), and 3 to 5 mm $year^{-1}$ for marshes in the Gulf of Mexico (*14*). Here, we report on contemporary tidal marsh elevation gain in relation to RSLR, testing the importance of environmental conditions in mediating these responses.

Several factors may influence the efficacy of tidal marsh vertical adjustment to sea level rise, but their relative contributions to explaining observed regional to global variability in marsh responses remain poorly elucidated. Globally, tidal range in marshes can vary from a few centimeters to 16 m, and this variability will influence the susceptibility of marshes to drowning, particularly where the tidal range is low relative to the projected RSLR (*12*, *15*). The position within the tidal frame influences the depth and duration of inundation and the deposition of sediment, but it also influences mineral and organic accretion responses of the marsh vegetation occurring at these specific positions (*8*, *9*). Tidal hydrodynamics and river discharge contribute to sediment delivery and accumulation (*15*), and these may be modified by flow control structures (*16*). Plant productivity is influenced by climate (precipitation and temperature), salinity, nutrients (*17*), atmospheric CO_2, and vegetation composition, which in turn influence soil organic carbon accumulation and decomposition. The rate of RSLR varies between coastlines and continents, and millennial-scale variability in RSLR may also control soil organic content, which may increase with sea level rise when conditions are favorable (*18*). Sampling at regional to global scales across hydrogeomorphic settings and biogeographic regions can clarify the relative importance of these factors and determine the consistency of feedbacks facilitating marsh adjustment to RSLR.

Accurate measurements of tidal marsh vertical adjustment in relation to sea level require a fixed benchmark against which elevation gain or loss can be measured. To this end, the surface elevation table–marker horizon (SET-MH) method has been developed as a global standard (*19*) for monitoring tidal marsh responses to RSLR (Fig. 1). A rod is driven into the marsh to form a stable benchmark against which elevation change can be measured. Vertical accretion (the surface accumulation of inorganic sediment, organic sediment, and living roots) is also measured at most sites above an artificial marker horizon (typically white feldspar, clay, or sand) introduced at the time of the first measurements against the

[1]School of Natural Sciences, Macquarie University, Sydney, NSW, Australia. [2]Natural Resources Research Institute, University of Minnesota, Duluth, MN, USA. [3]US Geological Survey, Eastern Ecological Science Center, Beltsville, MD, USA. [4]School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW, Australia. [5]National Park Service, Washington, DC, USA. [6]School of Biological Sciences, University of Queensland, Brisbane, QLD, Australia. [7]Department of Geography, National University of Singapore, Singapore. [8]Department of Earth and Planetary Sciences, Rutgers University, Newark, NJ, USA. [9]US Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA, USA. [10]Cambridge Coastal Research Unit, Department of Geography, Cambridge University, Cambridge, UK. [11]Institute for Coastal and Marine Research and Department of Botany, Nelson Mandela University, Gqeberha, South Africa. [12]Eurecat, Unit of Climate Change, Centre Tecnològic de Catalunya, Catalonia, Spain. [13]SELC Societa Cooperativa, Venice, Italy. [14]Ecosphere Group, University of Antwerp, Antwerp, Belgium. [15]Nova Scotia Department of Natural Resources and Renewables, Nova Scotia, Canada. [16]US Geological Survey, Western Ecological Research Center, Davis, CA, USA. [17]Department of Geography, McGill University, Montreal, Canada. [18]Saint Mary's University, Halifax, Canada. [19]Mississippi State University, Starkville, MS, USA. [20]Moss Landing Marine Labs, California State University, Moss Landing, CA, USA. [21]Marine Science Institute, University of Texas, Austin, TX, USA. [22]Guana Tolomato Matanzas National Estuarine Research Reserve, Ponte Vedra Beach, FL, USA. [23]Delaware Department of Natural Resources and Environmental Control, Dover, DE, USA. [24]Virginia Institute of Marine Science, Gloucester Point, VA, USA. [25]Narragansett Bay National Estuarine Research Reserve, Prudence Island, RI, USA. [26]Apalachicola National Estuarine Research Reserve, Eastport, FL, USA. [27]Department of Earth Sciences, Swire Institute of Marine Science, University of Hong Kong, Hong Kong, China.
*Corresponding author. Email: neil.saintilan@mq.edu.au

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

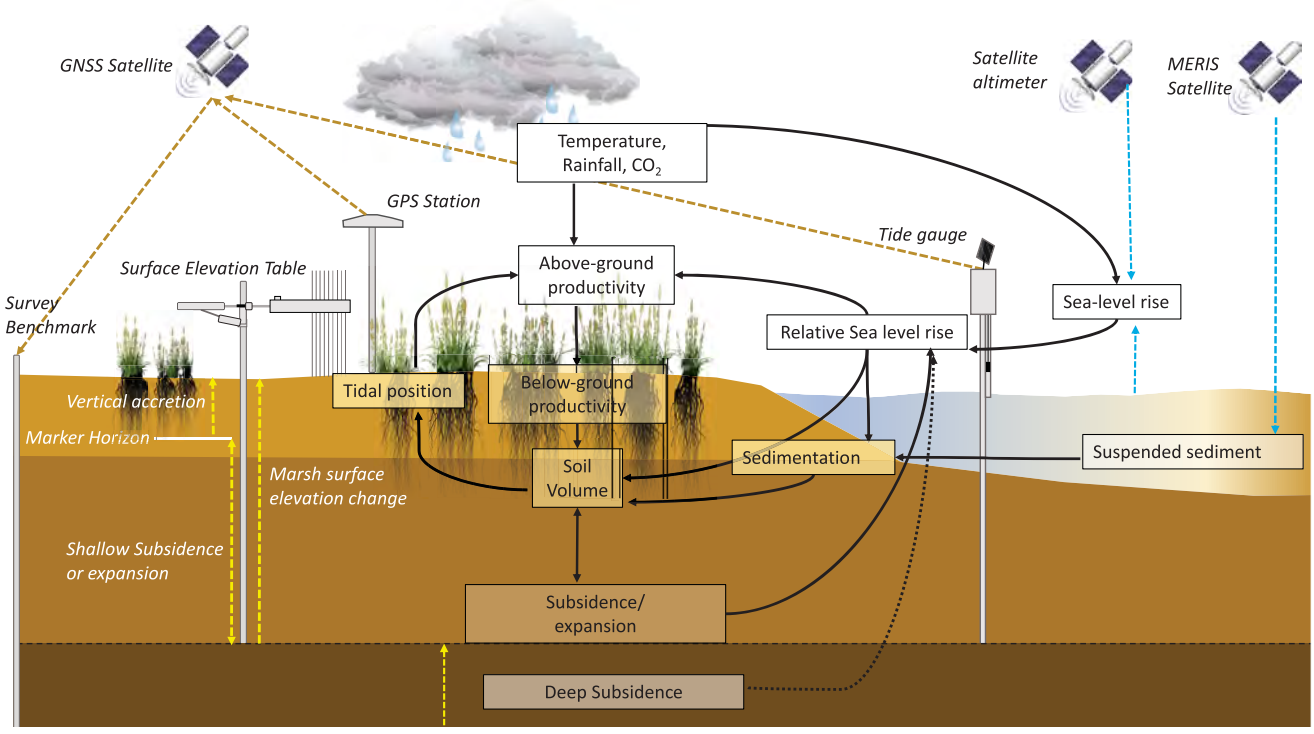


Fig. 1. Processes influencing marsh surface elevation and their measurement using the surface elevation table–marker horizon (SET-MH) monitoring station. Feedbacks among sea level rise, vertical accretion, and elevation gain are conceptualized as driving marsh substrates toward an equilibrium elevation within the tidal frame, facilitated by inputs of mineral and organic matter. The SET-MH method measures soil elevation relative to a benchmark (to which the portable component of the SET is attached), while a tide gauge records the combined effect of changes in sea level and land movement occurring below the survey benchmark rod, to which the gauge is routinely leveled. This combined recording of eustatic sea level (ocean volume) change and deep land movement is termed relative sea level rise (RSLR) and does not include processes measured by the SET-MH method. GNSS, Global Navigation Satellite System; MERIS, Medium Resolution Imaging Spectrometer.

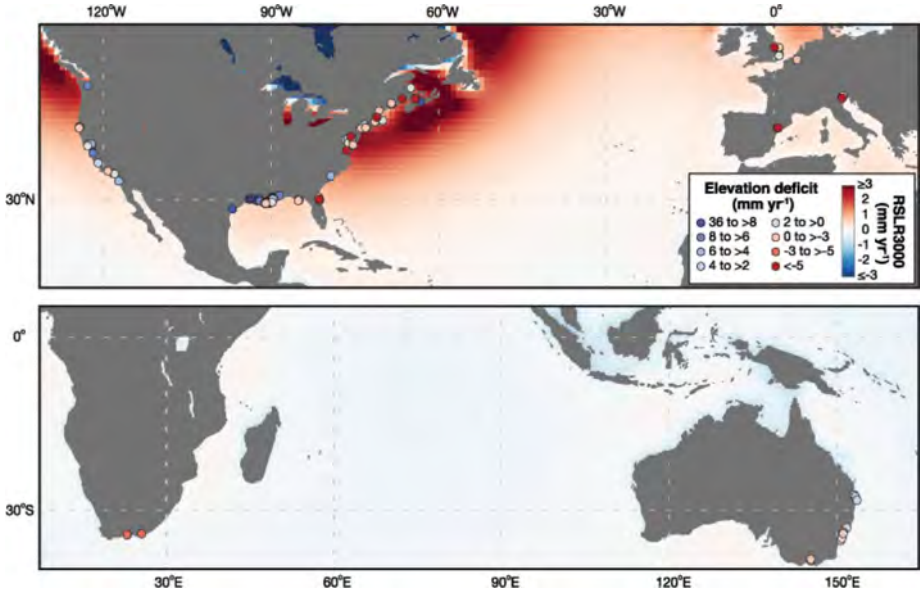


Fig. 2. Distribution of tidal marsh SET-MH monitoring stations used in the analyses, and deficit between elevation gain and contemporaneous local RSLR. Deficits are assigned positive numbers. The background of late Holocene (0 to 3000 years B.P.) RSLR is derived from glacio-isostatic modeling (*20*).

benchmark (*20*). Data from SET-MH stations have informed models of marsh resilience to RSLR (*7*, *12*), global projections of tidal marsh and mangrove change in the coming century (*5*, *21*, *22*), and the influence of vertical accretion on carbon sequestration (*23*, *24*).

We analyzed tidal marsh elevation adjustment in relation to RSLR from SET-MH monitoring stations that met our criteria of emergent tidal marsh vegetation, sufficient length of record (>3 years), and exclusion from hydrological or experimental manipulation. The resulting network of 477 tidal marsh SET-MH stations, across 97 sites, forms clusters in regions with distinct hydrogeomorphic histories and tidal and biogeographic characteristics thought to be important to marsh resilience (Fig. 2). In general, Southern Hemisphere stations (Australia and South Africa) are in estuaries subject to millennia of stable or falling sea levels, with micro- to mesotidal marshes on high, stable intertidal platforms typically low in percentage of soil organic carbon (table S1 and data S1). North Atlantic coastlines (Bay of Fundy, Canada; UK; Belgium) are predominantly macrotidal, have been subject until recently to relatively stable (< ±0.5 mm $year^{-1}$) or falling sea levels over the past few thousand years, have low soil organic carbon content, and are situated adjacent to waters with high total suspended matter. Coastlines in the network that are subject to low rates of sea level rise over the past few millennia include two large river deltas with a microtidal regime (the Mississippi, USA; the Ebro, Spain) and microtidal to mesotidal barrier estuaries and embayments (Venice Lagoon, Southern California; the US Gulf of Mexico chenier plains and estuaries).

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

The US Atlantic and North Pacific coastlines have been subject to relatively high rates of RSLR for several millennia, forming organic-rich marshes situated within barrier and embayment geomorphic settings. Contemporary RSLR varies between coastlines as a result of vertical land movement and climate variability (*25*), with relatively high rates of RSLR occurring in the Gulf of Mexico, the US North Atlantic, and parts of the North Pacific coasts and lower RSLR in most European and Southern Hemisphere sites (data S1).

This variability in RSLR allowed us to identify RSLR influences on marsh surface elevation change, and on mechanisms driving the latter, including vertical accretion and shallow subsidence. SET-MH stations were monitored for an average of 10.1 years (range: 3.5 to 20.0 years) over periods for which RSLR at nearest tide gauges (hereafter "contemporaneous" RSLR: $\bar{x}$ = 6.81 ± 6.41 mm year^{-1}) was significantly higher than both the 50-year average ($\bar{x}$ = 3.75 ± 2.73 mm year^{-1}; $P < 0.001$) and the 3000-year average derived from glacio-isostatic modeling (*20*) ($\bar{x}$ = 0.65 ± 0.72 mm year^{-1}; $P < 0.001$). This range of RSLR values encompassed rates associated with marsh retreat in the Holocene stratigraphic record (*10*, *13*, *14*). We therefore tested three hypotheses concerning the feedback among RSLR, vertical accretion, and elevation gain: (i) The rate of vertical accretion would increase with RSLR; (ii) the rate of vertical accretion would correspond to sediment availability; and (iii) vertical accretion would correspond to marsh elevation gain. We determined the extent to which these relationships are influenced by climatic, environmental, and edaphic conditions (table S2), including soil bulk density and organic carbon.

The most important predictor of the rate of vertical accretion at a global scale was the 50-year RSLR trend (r^2 = 0.48, $P < 0.0001$). The observation of vertical accretion parity with increased RSLR aligns with the predictions of feedback models suggesting marsh resilience to RSLR (*7*, *8*, *12*), although the relationship was stronger in organic than in minerogenic marshes (fig. S1). Marsh accretion across the network was higher at sites that are lower in the tidal frame [Fig. 3B; as measured by dimensionless D (*20*), an indicator of submergence (*26*), $P < 0.0001$]. Annual average suspended matter in adjacent waters explained less than 10% of global-scale variability in vertical accretion (fig. S2), and the incorporation of tidal range as an additional variable [as has recently been suggested (*12*)] did not improve the prediction of the rate of vertical accretion (linear regression r^2 = 0.03; n = 410) or the r^2 [typically <0.01 for low marshes (i.e., $D > 0$; n = 168)], contrary to model projections (*5*, *7*, *12*). Vertical accretion on marsh surfaces in settings of low total suspended matter suggests an important role for accretion of autochthonous sediment (i.e., organic and/or locally resuspended mineral matter). One caveat is that satellite-derived measures of suspended matter may not represent sediment concentrations at the point of deposition, particularly in channelized estuarine settings. However, hydrogeomorphic setting was also not strongly predictive of the rate of vertical accretion (fig. S2).

Although vertical accretion was the most important control on surface elevation gain at the global scale (r^2 = 0.3; fig. S2), shallow subsidence mediates the relationship between vertical accretion and surface elevation gain (*27*, *28*) (Fig. 1 and Fig. 3C). Shallow subsidence was greater under higher accretion rates (r^2 = 0.34, $P < 0.0001$; Fig. 3C and fig. S3) and higher contemporaneous and 50-year RSLR (r^2 = 0.16, $P < 0.0001$; fig. S3). As a result, on average less than half of the sediment accreted above marker horizons translated into surface elevation gain, and this proportion decreased between 5 mm year^{-1} and 10 mm year^{-1} of contemporaneous RSLR ($P < 0.0001$). The deficit between surface elevation gain and RSLR trend increased linearly with RSLR in all settings (Fig. 3, E and F), as did the proportion of SET-MH monitoring stations subject to an elevation deficit (Fig. 4).

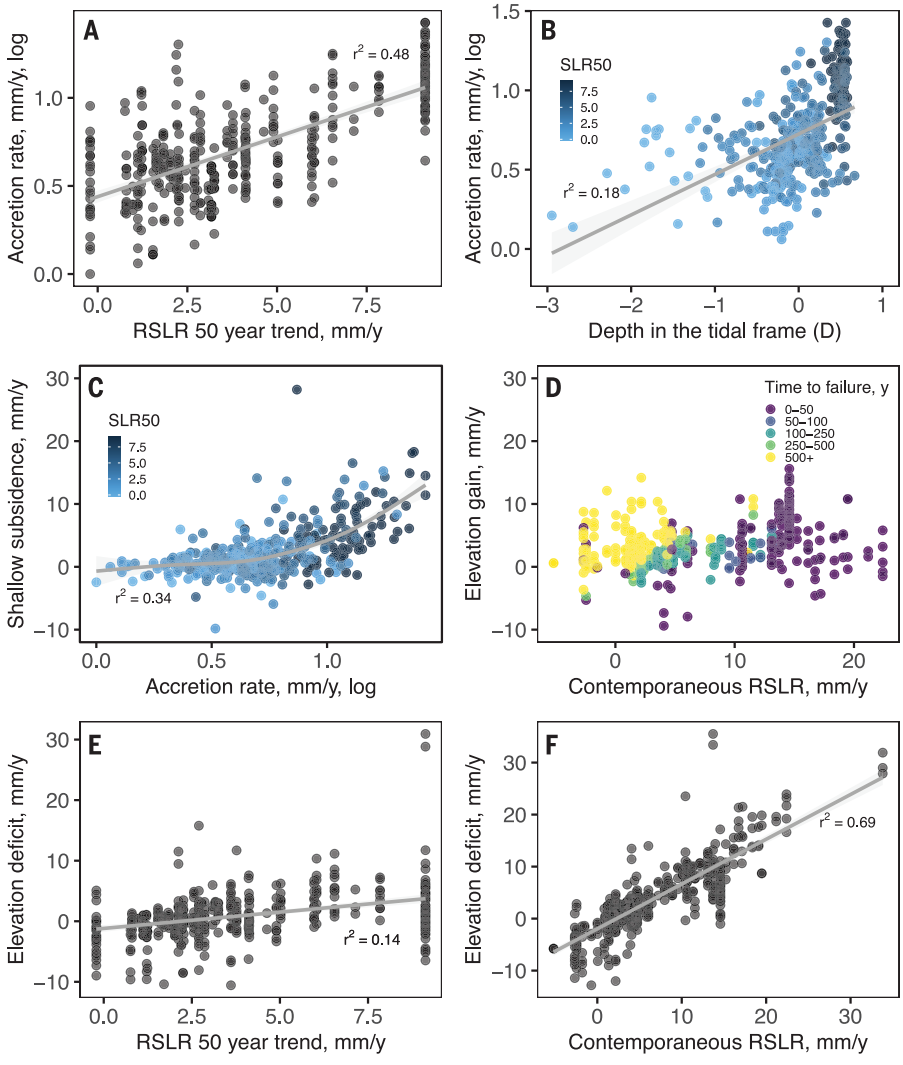


Fig. 3. The increasing vulnerability of tidal marshes to RSLR. (**A** and **B**) Accretion increases in parity with the 50-year RSLR trend (A) and with marshes lower in the tidal frame (B). (**C** and **D**) However, the rate of shallow marsh subsidence increases with the rate of vertical accretion, with an upward inflexion as RSLR increases between 5 and 10 mm year^{-1} (C), suppressing elevation adjustment to RSLR (D). (**E** and **F**) As a result, the deficit between elevation gain and RSLR increases with the 50-year RSLR trend (E) and the contemporaneous RSLR trend, the period over which individual SET-MH stations were measured (F). In (B) and (C), points are colored for the 50-year RSLR trend in mm year^{-1}, and in (D) for estimated time to failure (years) under the elevation deficit against the 50-year RSLR trend (*20*).

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

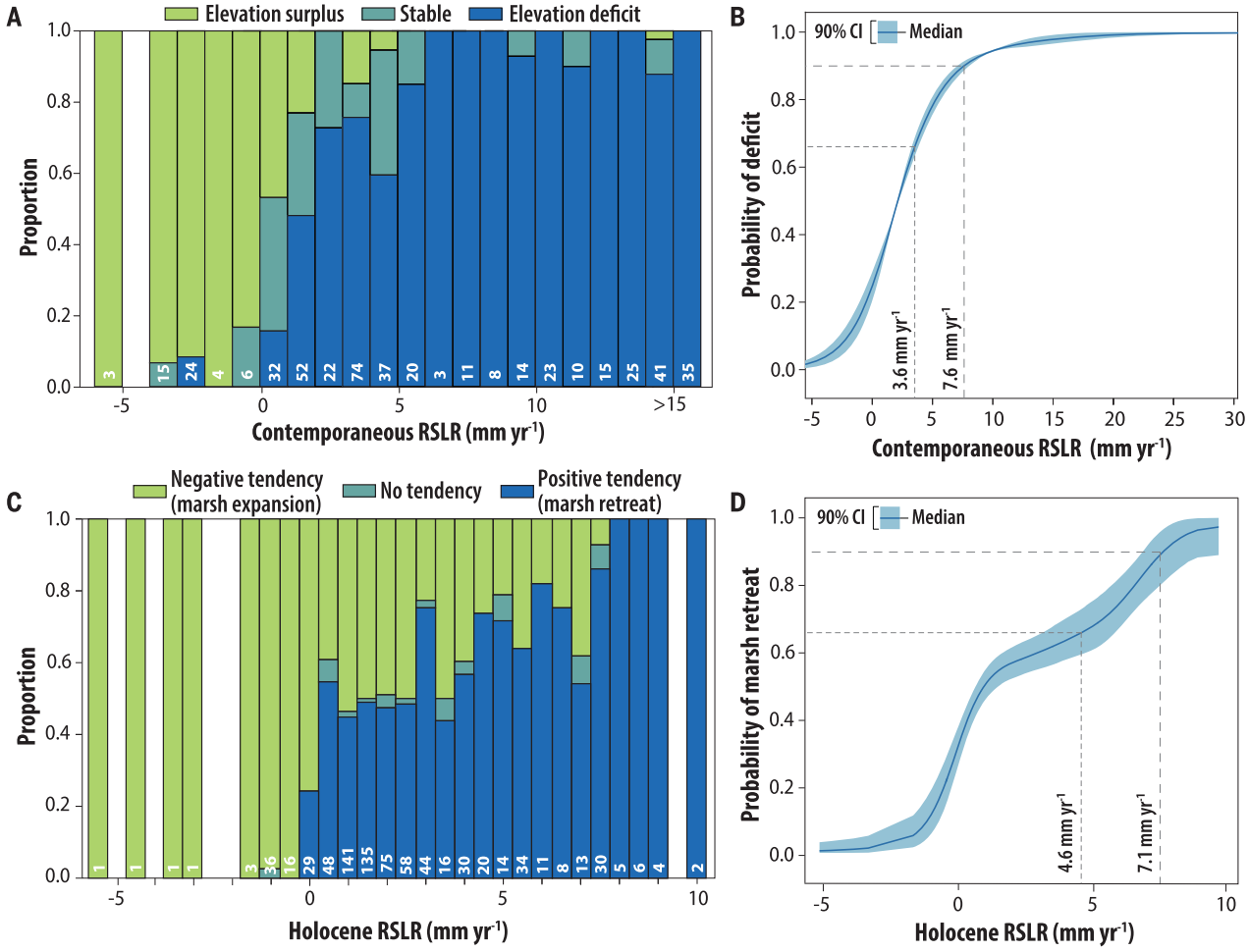


Fig. 4. Rates of relative sea level rise and marsh responses in the observational and paleo record. (**A**) Histogram of SET-MH monitoring stations showing elevation deficit, elevation surplus, and stability (parity) with contemporaneous RSLR. (**B**) Modeled probability of an elevation deficit with different rates of RSLR. (**C**) Histogram of paleo-marsh index points showing positive, negative, and no tendency in relation to RSLR in UK Holocene marshes (*13*). (**D**) Modeled probability of positive sea level tendency (i.e., sinking within the tidal frame) associated with different rates of Holocene RSLR. Numbers of observations for each RSLR increment are shown at the base of each column.

Marshes in the SET-MH network transition from a predominance of elevation surplus to elevation deficit over a similar range of RSLR, as has been historically observed in UK Holocene marshes (Fig. 4), which provide a record that is unique for the number of index points associated with a range of RSLR histories (*13*). Contemporary observations from the tidal marsh SET-MH network, which accounts for shallow subsidence, were therefore consistent with observations of tidal marsh and mangrove behavior during periods of relatively rapid sea level rise in the Holocene record (*10*, *13*, *14*, *22*). Cumulative probabilities based on Bayesian modeling using the SET-MH record suggest that a drowning trajectory is likely (66% probability) at 3.6 mm year^{-1} and 4.6 mm year^{-1} in UK Holocene marshes and very likely (90% probability) at 7.6 mm year^{-1} in the SET-MH record and 7.1 mm year^{-1} in UK Holocene marshes (*13*) (Fig. 4). Although several sites in the US Gulf and Atlantic coastlines had a contemporary rate of elevation gain exceeding 8 mm year^{-1}, these same sites had the lowest median projected time to open-water conversion, as estimated by the time to reach minimum survival elevation (*20*) (table S5). The elevation subsidy provided by their proximity to eroding shorelines (fig. S4) may represent laterally migrating levees (*29*), a precursor to marsh failure (table S4 and fig. S5).

In locations where sea level has been stable (<±0.5 mm year^{-1}) or falling over recent millennia (i.e., the macrotidal marshes of the North Atlantic and the Southern Hemisphere Australian and South African marshes), soil organic carbon concentrations were significantly lower (on average less than half) relative to marshes subject to millennial-scale RSLR (P < 0.0001; table S1 and fig. S6). Gradually rising sea levels can both promote and preserve highly organic marshes (*18*, *30*) by increasing plant productivity, increasing organic carbon burial, reducing oxidation, and slowing decomposition. At a global scale, the proportion of organic carbon in accreting sediments across our network was better explained by the 3000-year RSLR trend (r^2 = 0.23; P < 0.0001) than by contemporaneous RSLR (r^2 = 0.07; P < 0.0001; fig. S6). Sites with higher bulk density and lower percent organic carbon had lower rates of subsidence (table S1 and fig. S1) and a higher proportion of vertical accretion contributing to elevation gain, consistent with predictions (*9*). In these locations, shorelines were relatively stable and the proportion of vegetated to unvegetated marsh cover (*20*) was high (table S1).

The mechanisms promoting tidal marsh adjustment under low rates of sea level rise appear less effective under high rates of sea level rise. The substrates undergoing marsh elevation gain are increasingly subject to autocompaction and subsidence under increased accretion and inundation depth. The elevation response is nonlinear, and above a primary

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

breakpoint between 5 and 10 mm year^{-1} of vertical accretion, a higher proportional loss to subsidence constrains elevation adjustment in response to accelerating RSLR. This observation reconciles the instrumental record with probabilities of tidal marsh adjustment emerging from paleostratigraphic records during phases of high RSLR during the Holocene. Both datasets suggest a low likelihood (P < 0.1) that tidal marshes will be retained in situ under global average rates of RSLR attained by mid-century under high-emissions scenarios, and by the end of the century under midrange-emissions scenarios (*25*). These rates of RSLR are already reached in subsiding deltas occupied by tidal marshes. Under these circumstances, tidal marsh survival will increasingly depend on their upland migration.

REFERENCES AND NOTES

1. N. C. Davidson, *Mar. Freshw. Res.* **65**, 934–941 (2014).
2. N. J. Murray *et al*., *Science* **376**, 744–749 (2022).
3. R. Costanza *et al*., *Glob. Environ. Change* **26**, 152–158 (2014).
4. S. Fagherazzi *et al*., *J. Geophys. Res.* **125**, e2019JF005200 (2020).
5. M. Schuerch *et al*., *Nature* **561**, 231–234 (2018).
6. M. L. Kirwan, J. P. Megonigal, *Nature* **504**, 53–60 (2013).
7. M. L. Kirwan, S. Temmerman, E. E. Skeehan, G. R. Guntenspergen, S. Fagherazzi, *Nat. Clim. Change* **6**, 253–260 (2016).
8. J. T. Morris, P. Sundareshwar, C. T. Nietch, B. Kjerfve, D. R. Cahoon, *Ecology* **83**, 2869–2877 (2002).
9. J. French, *Mar. Geol.* **235**, 119–136 (2006).
10. N. Saintilan *et al*., *Science* **368**, 1118–1121 (2020).
11. M. L. Kirwan *et al*., *Geophys. Res. Lett.* **37**, L23401 (2010).
12. D. J. Coleman *et al*., *Limnol. Oceanogr. Lett.* **7**, 140–149 (2022).
13. B. P. Horton *et al*., *Nat. Commun.* **9**, 2687 (2018).
14. T. E. Törnqvist, K. L. Jankowski, Y.-X. Li, J. L. González, *Sci. Adv.* **6**, eaaz5512 (2020).
15. M. L. Kirwan, G. R. Guntenspergen, *J. Geophys. Res.* **115**, F02009 (2010).
16. J. P. Syvitski, A. Kettner, *Philos. Trans. R. Soc. A* **369**, 957–975 (2011).
17. L. A. Deegan *et al*., *Nature* **490**, 388–392 (2012).
18. K. Rogers *et al*., *Nature* **567**, 91–95 (2019).
19. E. L. Webb *et al*., *Nat. Clim. Change* **3**, 458–465 (2013).
20. See supplementary materials.
21. C. E. Lovelock *et al*., *Nature* **526**, 559–563 (2015).
22. K. L. Jankowski, T. E. Törnqvist, A. M. Fernandes, *Nat. Commun.* **8**, 14792 (2017).
23. C. E. Lovelock, R. Reef, *One Earth* **3**, 195–211 (2020).
24. F. Wang *et al*., *Natl. Sci. Rev.* **8**, nwaa296 (2020).
25. B. Fox-Kemper *et al*., in *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, V. Masson-Delmotte *et al*., Eds. (Cambridge Univ. Press, 2021), chap. 9.
26. J. T. Morris, *Estuar. Coast. Shelf Sci.* **69**, 395–402 (2006).
27. S. Nolte *et al*., *J. Coast. Conserv.* **17**, 301–325 (2013).
28. D. R. Cahoon, J. Day, D. Reed, *Curr. Top. Wetland Biogeochem.***3**, 72–88 (1999).
29. N. K. Ganju *et al*., *Nat. Commun.* **8**, 14156 (2017).
30. J. L. Breithaupt *et al*., *J. Geophys. Res.* **125**, e2019JG005349 (2020).

ACKNOWLEDGMENTS

A. Yeates contributed to data management. M. J. S. Casallas assisted with shoreline change detection. Data used in the paper are available as data S1. Original data for the Mississippi Delta and Mississippi Chenier sites were retrieved from the Coastal Information Management System (CIMS) database (http://cims.coastal.louisiana.gov). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government. **Funding:** NRF/SAEON Elwandle Node; the NRF/DSI Shallow Marine and Coastal Research Infrastructure (SMCRI); the SAEON Elwandle Coastal Biogeochemical Platform: UKRI NERC CBESS (NE/J015423/1); Australian Research Council FS100100024, FT130100532, and the Coasts and Clean Seas Initiative; National Environmental Science Program 2 Coastal and Marine Hub; the DSI/NRF Research Chair in Shallow Water Ecosystems (UID 84375); US Geological Survey Climate Research and Development Program and Ecosystems Mission Area; Research Foundation of Flanders, Belgium (FWO grants G.0600.18N and G.0316.20N); NSF grants OCE-1702587 and OCE-2002437; Coastal Protection and Restoration Authority (CPRA) of Louisiana, 2021, Coastwide Reference Monitoring System-Wetlands Monitoring Data; US Geological Survey Western Ecological Research Center; Ministero delle Infrastrutture e dei Trasporti – Provveditorato Interregionale alle OO. PP. del Veneto – Trentino Alto Adige – Friuli Venezia Giulia, through its concessionary Consorzio Venezia Nuova; Catalan Water Agency, Ebro Delta Monitoring Network Program. **Author contributions:** Conceptualization, N.S., T.S., D.R.C., G.G.; data curation, N.S., K.R., N.C., G.G., J.C.L., D.R.C., J.A., J.R., K.E.K., T.S., D.A.F., T.M., P.M., S.T., C.E.L., K.W.K., G.L.C., J.B., C.I., F.S., K.T., J.A.G., E.A., K.C., C.E., C.M., P.M., K.S.L., W.R., K.B.R., T.B.; formal analysis, N.S., K.E.K., E.A., N.K., D.A.F., V.P.G.; project administration, N.S.; supervision, N.S., G.G.; writing–original draft, N.S.; writing–review and editing, N.S., K.E.K., G.G., K.R., J.C.L., D.R.C., C.E.L., D.A.F., E.A., K.W.K., N.C., T.S., J.A., J.R., C.I., F.S., S.T., P.M., T.M., K.T., J.B., G.L.C., T.B., V.P.G., K.C., C.E., C.M., K.S.L., W.R., K.B.R., J.A.G. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data are available in the main text or the supplementary materials. Original SET-MH data held by the USGS are available at doi:10.5066/P9UZ4LQ2. **License information:** Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. www.science.org/about/science-licenses-journal-article-reuse

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abo7872
Materials and Methods
Figs. S1 to S6
Tables S1 to S5
References (*31*–*65*)
Data S1

Submitted 24 February 2022; accepted 27 June 2022
10.1126/science.abo7872

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

Chapter 4: Blue Carbon and Sea Level Rise

4.1 **Saintilan N**. 1997. Above and Below-ground Biomass of two species of Mangrove on the Hawkesbury River Estuary, New South Wales. *Marine and Freshwater Research.* 45 (1) 147-52

4.2 **Saintilan N.** 1997. Above and Below-ground Biomass of Mangroves in a Sub-tropical estuary. *Marine and Freshwater Research* 48 601-604.

4.3 Lamont, K., **Saintilan, N.,** Kelleway, J.J., Mazumder, D., & Zawadzki, A. (2020). Thirty-year repeat measures of mangrove above-and below-ground biomass reveals unexpectedly high carbon sequestration. *Ecosystems*, *23*(2), 370-382.

4.4 **Saintilan N.,** Rogers K., Mazumder D. and Woodroffe C.D., (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands *Estuarine Coastal and Shelf Science*. 128 84-92

4.5 Kelleway, J.J., **Saintilan, N**., Macreadie, P.I., Baldock, J.A., Heijnis, H., Zawadzki, A., Gadd, P., Jacobsen, G. & Ralph, P.J. 2017, 'Geochemical analyses reveal the importance of environmental history for blue carbon sequestration', Journal of Geophysical Research:Biogeosciences, vol. 122, no. 7, pp. 1789-1805

4.6 Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I., Baldock, J.A. & Ralph, P.J. 2017, 'Sediment and carbon deposition vary among vegetation assemblages in a coastal salt marsh', Biogeosciences, vol. 14, no. 16, pp. 3763-3779

4.7 Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I. & Ralph, P.J. 2016, 'Sedimentary Factors are Key Predictors of Carbon Storage in SE Australian Saltmarshes', Ecosystems, vol. 19, no. 5, pp. 865-880

4.8 Kelleway, J.J., **Saintilan, N.,** Macreadie, P.I., Skilbeck, C.G., Zawadzki, A. & Ralph, P.J. 2016, 'Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes', Global Change Biology, vol. 22, no. 3, pp. 1097-1109

4.9 Rogers K., **Saintilan N.,** Mazumder D. & Kelleway, J.J. 2019, 'Mangrove dynamics and blue carbon sequestration', Biology Letters, vol. 15, no. 3, pp. 1–5, doi:10.1098/rsbl.2018.0471

4.10 Rogers, K., Kelleway, J. J., **Saintilan, N**., Megonigal, J. P., Adams, J. B., Holmquist, J. R., ... & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature*, *567*(7746), 91-95.*

4.11 **Saintilan, N.,** Kelleway, J., & Rogers, K. (2021). Australian mangroves through the Holocene: interactions between sea level, mangrove extent, and carbon sequestration. In *Dynamic Sedimentary Environments of Mangrove Coasts* (pp. 217-234). Elsevier.

4.12 Karita Negandhi, Grant Edwards, Kelleway, Jeffrey J., Dean Howard, David Safari & **Neil Saintilan** 2019, 'Blue carbon potential of coastal wetland restoration varies with inundation and rainfall', Scientific Reports, vol. 9, no. 1, pp. 1–9, doi:10.1038/s41598-019-40763-8

CSIRO PUBLISHING

Marine & Freshwater Research

Volume 48, 1997
© CSIRO Australia 1997

A journal for the publication of original contributions
in physical oceanography, marine chemistry,
marine and estuarine biology and limnology

www.publish.csiro.au/journals/mfr

All enquiries and manuscripts should be directed to
Marine and Freshwater Research
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood Telephone: 61 3 9662 7618
Vic. 3066 Facsimile: 61 3 9662 7611
Australia Email: ann.grant@publish.csiro.au

Published by **CSIRO** PUBLISHING
for CSIRO Australia and
the Australian Academy of Science

Mar. Freshwater Res., 1997, **48**, 147–52

Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales

Neil Saintilan

Australian Catholic University, PO Box 201, Castle Hill, NSW 2154, Australia.

Abstract. Above- and below-ground biomasses of two species of mangrove, *Avicennia marina* and *Aegiceras corniculatum*, were estimated in a range of intertidal environments along the Hawkesbury River. Estimates of biomass of *Avicennia* communities in freshly accreted brackish substrata were in the order of 40 kg m^{-2}, the highest figure ever recorded for temperate mangrove communities. The above-ground biomass communities of each species declined with increasing substratum salinity, whereas root/shoot ratios increased with increasing substratum salinity.

Introduction

The intertidal environments of the Hawkesbury River are dominated by two sympatric mangrove species, *Avicennia marina* (Forssk.) Vierh. subsp. *australasica* J.Everett and *Aegiceras corniculatum* (L.) Blanco. *Avicennia marina* in particular has been the subject of extensive research on the physiology of seedlings (Ball 1981, 1988; Downton 1982; Burchett *et al.* 1984*a*), demography (Clarke 1993) and biomass (Clough and Attiwill 1975; Briggs 1977; Goulter and Allaway 1979; Woodroffe 1985; Mackay 1993). Little, however, is known of the variation in growth of either species over the range of environments within any given estuary. The extensive array of environments occupied by both species on the Hawkesbury River provides an opportunity to examine biomass patterns in environments of contrasting soil water conditions.

Given the degree of control that mangrove seedlings exert over biomass partitioning, and the water-use efficiency of both seedlings (Ball 1988) and mature trees (Clough and Sim 1989), it would be surprising if mangroves did not closely control biomass partitioning under field conditions. A central purpose of this paper is to determine whether the patterns in root/shoot ratio detected by Ball (1988) for seedlings in the laboratory correspond to patterns in root/shoot ratios of mature trees of *Aegiceras corniculatum* and *Avicennia marina* on the Hawkesbury River.

Materials and methods

Site description

The Hawkesbury River estuary (33°30′S,151°30′E), immediately to the north of Sydney, is one of the largest drowned river valleys on the Australian east coast (Fig. 1). The tidal limit is 110 km from the mouth and the river supports an extensive array of mangrove environments ranging from the sandy flood-tide and tributary deltas of the marine zone to the channel-fringing mud substrata of the brackish reaches. Wide intertidal flats of prograding fluvial muds and silts occur in the central reaches and are hypersaline at supratidal elevations.

Sampling procedure

Above-ground and below-ground biomasses were estimated for 56 quadrats (each 16 m^2) on the Hawkesbury River (Fig. 2). The sampling strategy recognized four community types suitable for sampling (mixed communities were not included), with a distinction being drawn between tall communities (top of canopy greater than 3 m in height, all individuals with a measurable diameter at breast height, or DBH) and low communities (top of canopy less than 3 m in height). Sampling extended across the range of estuarine environments in which each community was found, with sites being duplicated at each locality. Two random quadrats were laid at each site and four 14-cm-diameter cores were sunk in each quadrat for the estimation of below-ground biomass. The height and DBH of all individuals were recorded for each quadrat. Soil samples were extracted at a depth of between 30 and 50 cm and placed in a sealed container for the determination of soil water salinity.

Estimation of above-ground biomass

Estimates of total above-ground biomass from measurements of stem diameter were found by Clough and Scott (1989) to correlate strongly with harvested samples of Rhizophoraceae in tropical Queensland mangrove forests. However, harvested individuals of *Avicennia marina* and *Aegiceras corniculatum* in temperate localities differed significantly in dry mass from predictions of allometric equations of this type, particularly as DBH increased above 10 cm. Apparently, mangroves of wide girth in tropical estuaries grow taller than their subtropical counterparts, which may show substantial variation in girth once maximum height is reached.

Briggs (1977) used a volumetric equation from Rochow (1974) to estimate the biomass of *Avicennia marina* in temperate environments, although the Rochow equation yielded values of less than 50% of the dry biomass of felled trees weighed by Cole *et al.* (personal communication). Cole *et al.* found the relationship between dry weight (W, in g) and stem girth (G, in cm) to be

$$W = (0{\cdot}214G - 0{\cdot}113)^2, \quad (1)$$

and this procedure was followed in the present study.

An extrapolation was then made by using tree height (h, in m) and DBH (D_{BH}, in cm) to estimate above-ground biomass:

$$W = \frac{h[0{\cdot}214(D_{BH} \times \prod) - 0{\cdot}113]^2}{10}, \quad (2)$$

where W is now in kilograms.

10.1071/MF96079 1323-1650/97/020147$05.00

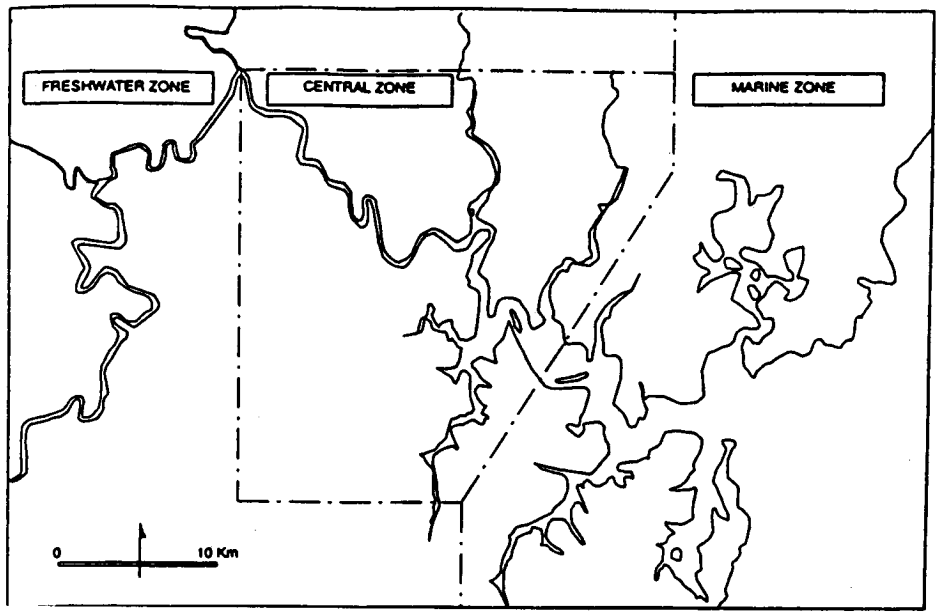


Fig. 1. Zones of the Hawkesbury River estuary.

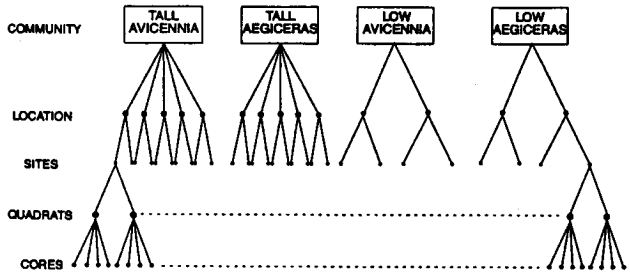


Fig. 2. Biomass sampling strategy.

Table 1. Biomass estimates for height classes of *Avicennia marina* and *Aegiceras corniculatum*

Avicennia marina		*Aegiceras corniculatum*	
Height (m)	Dry weight (kg)	Height (m)	Dry weight (kg)
1·5–2·0	5·0	1·5–2·0	5·0
1·0–1·5	4·0	1·0–1·5	2·0
0·5–1·0	2·0	0·5–1·0	1·0

Smaller trees and shrubs of *Avicennia marina* and *Aegiceras corniculatum* have numerous stems, often not reaching breast height. In such cases, height was used to estimate tree weight (Table 1).

Estimation of below-ground biomass

The relatively even distribution of roots in mangrove forests was noted by Clough and Attiwill (1975) and Gill and Tomlinson (1977) and has prompted many studies on mangrove root biomass through random coring (Clough and Attiwill 1975; Lichacz *et al.* 1984) or systematic coring along a transect (Briggs 1977; Komiyama *et al.* 1987). Komiyama *et al.* (1987) found an even distribution of finer roots through the soil and a higher proportion of coarser roots around the base of the trees. This indicates that although random coring is valid for the sampling of finer roots, coarser roots ought to be sampled as a separate population by the random selection of cores at the base of the trees. A stratified sampling procedure was therefore used to sample biomass directly beneath trees (representing a 'clustering' of roots), and biomass between trees, which was considered homogeneous.

For root mass beneath trees, the basal area of trees (t, in m^2) within the 16-m^2 quadrats used was determined from

$$t = \frac{\Sigma[(D_{BH}/2)^2 \Pi]}{10000}, \quad (3)$$

summed over all trees within each quadrat.

The area occupied by a single core is 0·0154 m^2. The biomass in the core must therefore be multiplied by the factor $F = t/0{\cdot}0154$ to gain a figure for the total biomass beneath trees within each quadrat.

For roots between trees, the area between trees (A, in m^2) may be given by the equation $A = 16 - t$. And so, to estimate between-tree biomass, we may multiply the core sample by F_2, where

$$F_2 = 16 - t/(0{\cdot}0154 \times 16). \quad (4)$$

The estimates for beneath- and between-tree root mass were added to produce an estimate of total root biomass for each quadrat.

Estimation of soil water salinity

Five grams of wet soil were weighed and added to 25 mL of distilled water and the vial sealed. The entire sample was shaken on a rotation wheel for 40 min. The electrical conductivity of the resulting extract was then measured with a calibrated Metrohm 660 conductivity meter and is expressed according to the Practical Salinity Scale of 1978.

Results

Above- and below-ground biomasses

The above- and below-ground biomasses of each species were highly variable at the scale of sampling. Nevertheless, significant correlations were found between above-ground biomass and salinity (Fig. 3) and between below-ground biomass and salinity (Fig. 4) for each species.

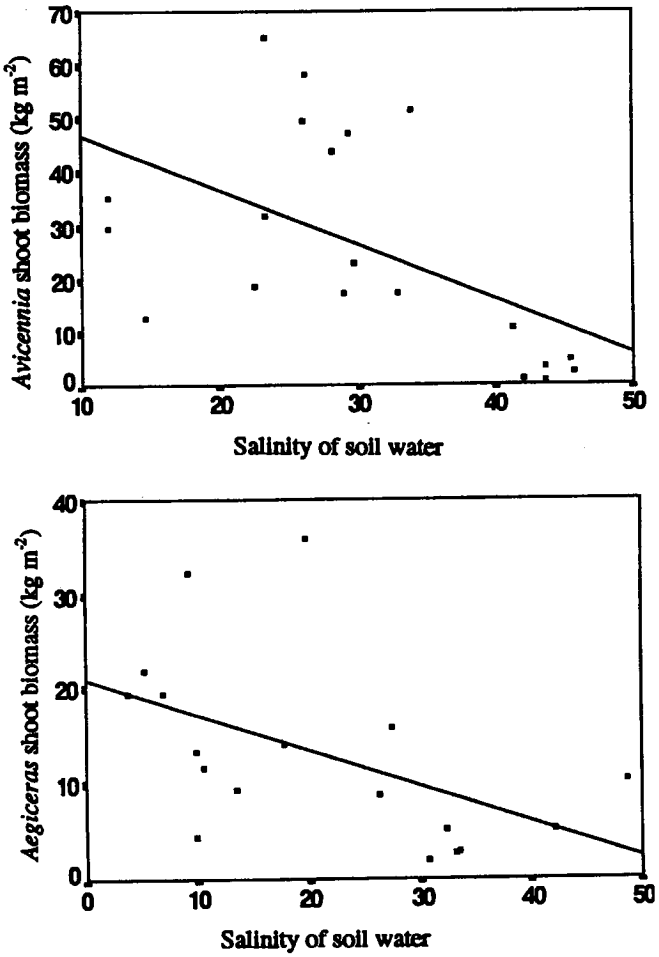


Fig. 3. Estimated above-ground biomass in individual 16-m^2 quadrats in communities of (top) *Avicennia marina* and (bottom) *Aegiceras corniculatum*, plotted against soil water salinity. The regression equation for *Avicennia marina* ($y = -1{\cdot}023x + 57{\cdot}25$) is significant at $P = 0{\cdot}015$ ($r^2 = 0{\cdot}289$) and the regression equation for *Aegiceras corniculatum* ($y = -0{\cdot}371x + 20{\cdot}92$) is significant at $P = 0{\cdot}025$ ($r^2 = 0{\cdot}263$).

Biomass partitioning

The root/shoot ratios of *Avicennia marina* and *Aegiceras corniculatum* remained consistently below 1 at sites where salinity did not exceed sea-water concentrations. Root/shoot ratio was significantly higher in hypersaline environments (Fig. 5).

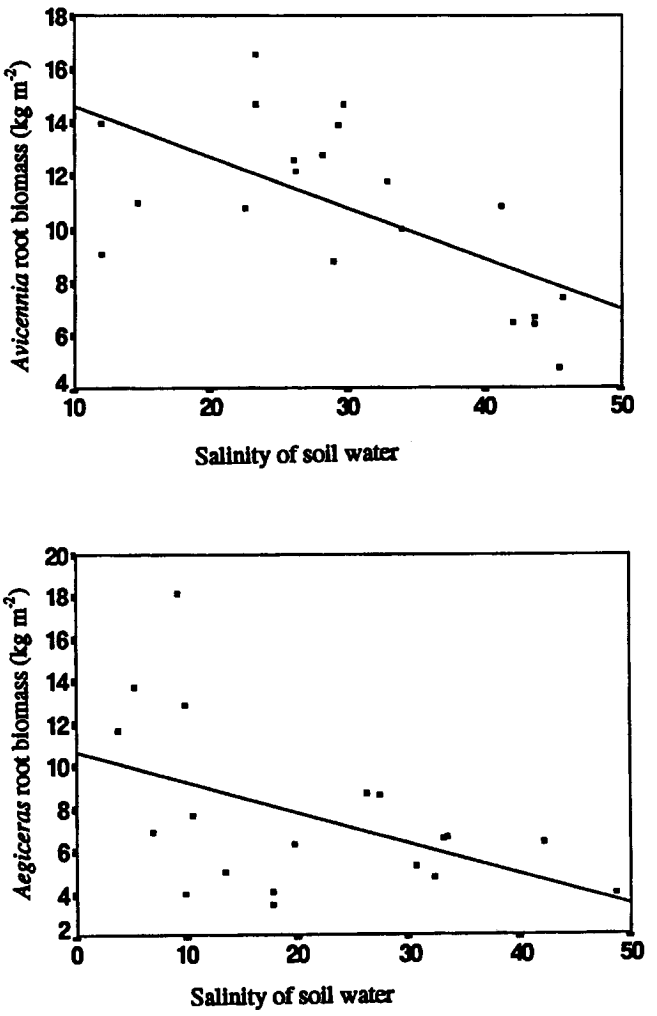


Fig. 4. Estimated below-ground biomass in individual 16-m^2 quadrats in communities of (top) *Avicennia marina* and (bottom) *Aegiceras corniculatum*, plotted against soil water salinity. The regression equation for *Avicennia marina* ($y = -0{\cdot}192x + 16{\cdot}59$) is significant at $P = 0{\cdot}003$ ($r^2 = 0{\cdot}402$) and the regression equation for *Aegiceras corniculatum* ($y = -0{\cdot}143x + 10{\cdot}63$) is significant at $P = 0{\cdot}037$ ($r^2 = 0{\cdot}231$).

There was no significant correlation between root/shoot ratio and distance from the mouth of the estuary. Root/shoot ratios for both species were greatest on supratidal flats 27 km from the mouth of the estuary (Fig. 5).

Discussion

Biomasses of Avicennia marina and Aegiceras corniculatum

Both *Avicennia marina* and *Aegiceras corniculatum* show consistent differences in biomass between environments along the Hawkesbury River. Stunted communities on the hypersaline point bars and the marine sand environments are comparable in biomass for both species, with *Avicennia* communities having a mean estimated biomass of 5·21

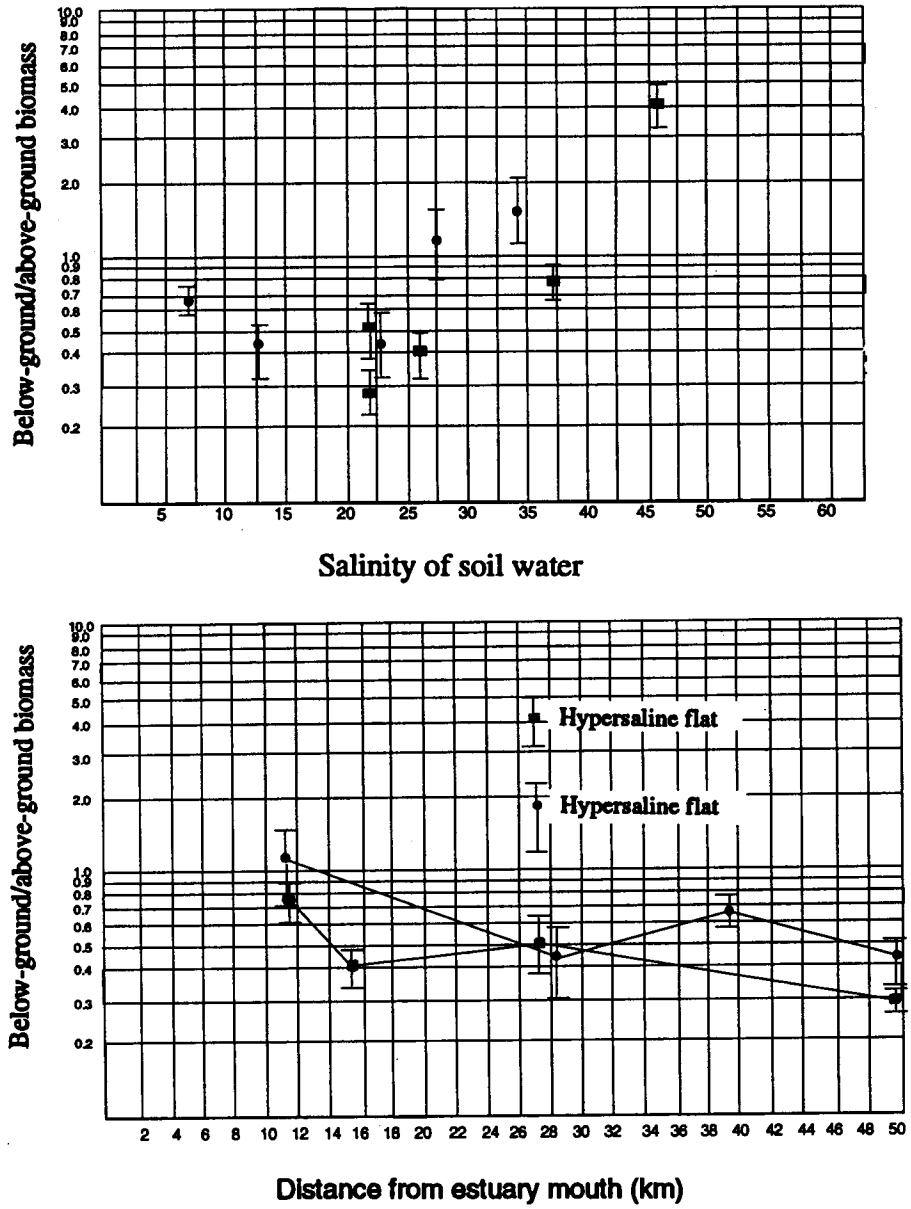


Fig. 5. Variation in root/shoot ratio of communities of (■) *Avicennia marina* and (●) *Aegiceras corniculatum* with (top) increasing soil water salinity and (bottom) increasing distance from the mouth of the estuary. Each point represents the mean and standard error for three sites of equal distance from the estuary mouth.

kg m^{-2} and 6·01 kg m^{-2} on the hypersaline point bars and marine environments, respectively, and *Aegiceras* communities having a mean estimated biomass of 5·49 kg m^{-2} and 5·25 kg m^{-2} in the same environments.

It is on the freshly accreted riverine flats of the Hawkesbury that the biomass of communities of both species becomes particularly high. An average biomass of 40 kg m^{-2} for communities in these environments is well in excess of an estimated biomass for *Avicennia marina* in other temperate localities such as the Lane Cove River (11–12 kg m^{-2}; Briggs 1977; Cole, personal communication) and Salt Pan Creek (13·3 kg m^{-2}; Burchett *et al.* 1984*b*) and is consistent with subtropical values (Mackay 1993).

Comparison with the data of Briggs (1977) from the Lane Cove River reveals a higher individual *Avicennia* tree mass for the Hawkesbury (176·4 kg compared with 122·8 kg) and a greater density (1 tree per 5 m^2 compared with 1 tree per 9·5 m^2), when mature forests are compared. *Avicennia* density on

Table 2. Observed root/shoot ratios for *Avicennia marina* in temperate environments
Marine environment refers to the deltaic environments at the estuary mouth. The central environment is situated headward of the marine environment, where sea water is diluted with freshwater discharge

Locality	Author	Environment	Root/shoot ratio
Pelican Island	Lichacz *et al.* (1984)	Marine	4·72
Hawkesbury River	Present study	Central–lower	4·10
Westernport Bay	Clough and Attiwill (1975)	Marine	1·64
Lane Cove River	Briggs (1977) (recalculated by Cole, unpublished)	Central–lower	0·90 (0·64)
Lane Cove River	Cole (personal communication)	Central–lower	0·88
Hawkesbury River	Present study	Central–lower	0·77
Koorang Island	Lichacz *et al.* (1984)	Central	0·71
Hawkesbury River	Present study	Central–upper	0·50
Boggy Creek	Mackay (1993)	Central	0·28

the Hawkesbury approximates that of a younger stand on the Lane Cove River (Site B of Briggs 1977), and it may well be that the very high nutrient contents of these Hawkesbury substrata (Gardiner 1993) allow mature stands of *Avicennia marina* to grow at densities unsustainable in other temperate localities.

Root/shoot ratios

Root/shoot ratios of both species varied considerably between environments along the Hawkesbury River estuary. In the brackish riverine environments, root/shoot ratios of both species varied around 0·5 and increased toward the mouth of the estuary, reaching 1·0 or above in the marine-dominated estuary mouth. By far the highest root/shoot ratios were recorded on the wide hypersaline point bars midway along the estuary, where mangroves occupy fluvial deltaic flats at upper tidal elevations. Here, root/shoot ratios reached 1·9 for *Aegiceras corniculatum* and 4·1 for *Avicennia marina*.

The results correspond with published root/shoot ratios of *Avicennia marina* (Table 2), which vary from 0·28 (Mackay 1993) to 4·72 (Lichacz *et al.* 1984), with a number of authors indicating 0·7–0·8 as being common for the lower-central estuary where plants experience marine waters (Briggs 1977 as recalculated by Cole *et al.*, personal communication; Lichacz *et al.* 1984). These figures are high compared with other terrestrial forests, though desert shrubs have yielded higher values (Caldwell *et al.* 1977).

The high root/shoot ratios of both *Avicennia marina* and *Aegiceras corniculatum* may well be part of the adaptive mechanism of mangroves to a saline, physiologically dry environment (Ball 1988). In experiments on seedlings, Ball (1988) found that root/shoot ratios of both species increased from brackish to saline conditions, *Avicennia* more so than *Aegiceras*. Ball (1988) attributed the higher growth rate of *Aegiceras* in brackish conditions to a higher relative shoot mass and suggested that the more conservative water-use strategy of *Avicennia* facilitated a higher photosynthetic rate than that of *Aegiceras* in saline conditions. The present study supports the contention that mangroves increase root/shoot ratio with increasing salinity, though no significant differences could be identified between species in environments were they coexisted.

Acknowledgments

I thank Professor B. G. Thom and Dr Peter Myerscough for helpful comments through the course of this research and in the writing of this paper. The project was partially funded through an Australian Postgraduate Research Award.

References

Ball, M. C. (1981). Physiology and photosynthesis in two mangrove species: responses to salinity and other environmental factors. Ph.D. Thesis, Australian National University, Canberra.

Ball, M. C. (1988). Salinity tolerance in mangroves *Aegiceras corniculatum* and *Avicennia marina*. I. Water use in relation to growth, carbon partitioning, and salt balance. *Australian Journal of Plant Physiology* **15**, 447–64.

Briggs, S. V. (1977). Estimates of biomass in a temperate mangrove community. *Australian Journal of Ecology* **2**, 369–73.

Burchett, M. D., Field, C. D., and Pulkownik, A. (1984*a*). Salinity, growth and root respiration in the grey mangrove, *Avicennia marina*. *Physiologia Plantarum* **60**, 113–18.

Burchett, M. D., Meredith, S., Pulkownik, A., and Walsh, S. (1984*b*). Short term influences affecting growth and distribution of mangrove communities in the Sydney region. *Wetlands (Australia)* **4**, 63–72.

Caldwell, M. M., White, R. S., Moore, R. T., and Camp, L. B. (1977). Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. *Oecologia (Berlin)* **29**, 275–300.

Clarke, P. J. (1993). Population ecology of the grey mangrove *Avicennia marina*. Ph.D. Thesis, University of Sydney, Sydney.

Clough, B. F., and Attiwill, P. M. (1975). Nutrient cycling in a community of *Avicennia marina* in a temperate region of Australia. In 'Proceedings of the International Symposium on Biology and Management of Mangroves'. (Eds G. E. Walsh, S. C. Snedaker and H. J. Teas.) Vol. 1, pp. 137–46. (University of Florida Press: Gainesville.)

Clough, B. F., and Scott, K. (1989). Allometric relationships for estimating above-ground biomass in six mangrove species. *Forest Ecology and Management* **27**, 117–27.

Clough, B. F., and Sim, R. G. (1989). Changes in gas exchange characteristics and water use efficiency of mangroves in response to salinity and vapour pressure deficit. *Oecologia* **79**, 38–44.

Downton, W. J. S. (1982). Growth and osmotic relations of the mangrove *Avicennia marina*, as influenced by salinity. *Australian Journal of Plant Physiology* **9**, 519–28.

Gardiner, B. (1993). Hawkesbury–Nepean River sediment dynamics study: sediment accumulation and sediment cycling in two estuarine depositional environments in the Foul Weather Reach and Spencer areas. Australian Water Technologies Science and Environment Division Report No. 93/133.

Gill, A. M., and Tomlinson, P. B. (1977). Studies on the growth of the red mangrove (*Rhizophora mangle* L.). 4. The adult root system. *Biotropica* **9**, 145–55.

Goulter, P. F. E., and Allaway, W. G. (1979). Litter fall and decomposition in a mangrove stand (*Avicennia marina* Forsk. (Vierh.)) in Middle Harbour, Sydney. *Australian Journal of Marine and Freshwater Research* **30**, 541–6.

Komiyama, A., Ogino, K., Aksornkoae, S., and Sabhasri, S. (1987). Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. *Journal of Tropical Ecology* **3**, 97–108.

Lichacz, W., Hardiman, S., and Buckney, R. T. (1984). Below-ground biomass in some intertidal wetlands in New South Wales. *Wetlands (Australia)* **4**(2), 56–62.

Mackey, A. P. (1993). Biomass of the mangrove *Avicennia marina* (Forsk.) Vierh. near Brisbane, south-eastern Queensland. *Australian Journal of Marine and Freshwater Research* **44**, 721–5.

Rochow, J. J. (1974). Estimates of above-ground biomass and primary production in a Missouri forest. *Journal of Ecology* **62**, 567–77.

Woodroffe, C. D. (1985). Studies of a mangrove basin, Tuff Crater, New Zealand. I. Mangrove biomass and production of detritus. *Estuarine, Coastal and Shelf Science* **20**, 265–80.

Manuscript received 29 July 1996; revised and accepted 24 October 1996

CSIRO PUBLISHING

Marine & Freshwater Research

Volume 48, 1997
© CSIRO Australia 1997

A journal for the publication of original contributions
in physical oceanography, marine chemistry,
marine and estuarine biology and limnology

www.publish.csiro.au/journals/mfr

All enquiries and manuscripts should be directed to
Marine and Freshwater Research
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood Telephone: 61 3 9662 7618
Vic. 3066 Facsimile: 61 3 9662 7611
Australia Email: ann.grant@publish.csiro.au

Published by **CSIRO** PUBLISHING
for CSIRO Australia and
the Australian Academy of Science

© CSIRO Australia 1997 *Mar. Freshwater Res.,* 1997, **48**, 601–604

Above- and below-ground biomass of mangroves in a sub-tropical estuary

N. Saintilan

Australian Catholic University, PO Box 201, Castle Hill, NSW 2154, Australia

Abstract. Above- and below-ground biomass of five species of mangroves was estimated for the Mary River, south-eastern Queensland. Below-ground : above-ground biomass ratios of species in the upstream reaches (*Avicennia marina, Aegiceras corniculatum* and *Excoecaria agallocha*) averaged <0.5, and those of species in the saline conditions of the mouth (*Avicennia marina, Rhizophora stylosa*) ranged between 0.9 and 1.5. Within the estuary mouth, above-ground biomass of *Avicennia marina* and *Ceriops tagal* decreased between frontal saline and upper-intertidal hypersaline environments, and this was reflected in the below-ground : above-ground biomass ratios, which increased to approximately 3.5 for both species.

Extra keywords: Salinity, intertidal, root mass, shoot mass.

Introduction

The growth characteristics of a plant are determined by the allocation of photosynthetic products to leaves, stems, roots and reproductive parts. Environmental conditions strongly influence this allocation, with root:shoot ratios increasing with aridity, infertility, light intensity, grazing and fire (Mooney 1972; Aung 1974; Russell 1977; Iwasa and Roughgarden 1984). Competitive interactions may also influence allocation of mass (Kozlowski *et al.* 1991).

Mangroves have higher relative root mass than other forest types (Saenger 1982), with root:shoot ratios closer to those of arctic, desert and grassland communities (Mooney 1972). High root:shoot ratios in mangroves have been attributed to unstable substratum conditions (Hutchings and Saenger 1987) but they could equally be due to low water potential in the substratum or nutrient deficiency, for root:shoot ratios of seedlings decline with decreasing salinity in laboratory conditions (Ball 1988) and with the addition of nutrients in brackish but not in saline soil cultures (Naidoo 1987).

Few data are available for mangrove root:shoot ratios under field conditions, partly because of difficulties of sampling. Clough (1992) and Snedaker (1995) provide useful summaries, although none of the studies cited compares root:shoot ratios of different species occupying the same environment or the same species over a range of environments on a single river. This information is important not only in understanding mangrove responses to environmental stress, but also in modelling the capacity of mangrove ecosystems to keep pace with a rise in the sea-level as carbon fixed in the leaves is transported to the roots (Snedaker 1995). Saintilan (1997) recorded above-ground and below-ground biomass of mangroves in the Hawkesbury River estuary, New South Wales, where *Avicennia marina* (Forssk.) Vierh. and *Aegiceras corniculatum* (L.) Blanco form a sympatric association. The present paper records above-ground and below-ground biomass for communities in a river of intermediate diversity of mangrove species, where five species form monospecific stands over widely ranging conditions of soil-water salinity.

Materials and methods

Study site

The Mary River, south-eastern Queensland (Fig. 1), has a mesotidal estuary showing the characteristics of tide dominance as described in the model of Dalrymple *et al.* (1992). The wide, funnel-shaped mouth is protected from wave attack by Fraser Island, and the intertidal flats fringing

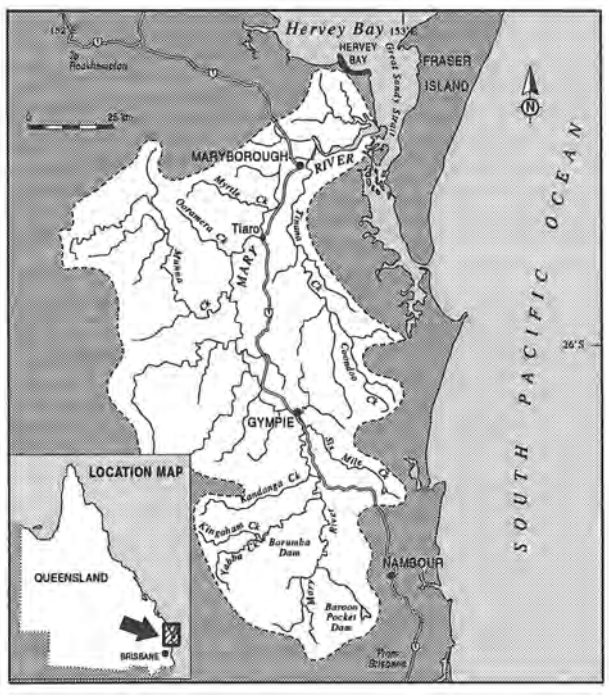


Fig. 1. Location of the Mary River, south-eastern Queensland.

10.1071/MF97009 1323-1650/97/070601$05.00

the mouth support extensive mangrove forest and shrubland on Holocene fluvial sand deposits. The substratum increases in soil-water salinity from saline to hypersaline from the frontal to the upper intertidal sections of these flats (Saintilan 1996). The meandering upstream reaches of the estuary are fringed by highly dynamic fluvial mud and sand deposits where salinity of the intertidal substratum is freshened by fluvial discharge (Saintilan 1996).

The climate is subtropical, and ten species of mangrove fringe the estuary: *Rhizophora stylosa* Griff.; *Ceriops tagal* (Perr.) C.B. Rob, var. *australis* C.T. White; *Avicennia marina* (Forssk.) Vierh.; *Aegiceras corniculatum* (L.) Blanco; *Excoecaria agallocha* L.; *Bruguiera gymnorhiza* (L.) Lamk.; *Osbornia octodonta* F. Muell.; *Lumnitzera racemosa* Willd.; *Aegialitis annulata* R. Br.; and *Xylocarpus granatum* Koen. Of these species, five form pure stands and occur as dominants over significant areas: *R. stylosa, C. tagal, A. marina, A. corniculatum* and *E. agallocha. R. stylosa* and *C. tagal* are restricted to the funnel-mouth of the estuary, with *R. stylosa* occurring as a frontal stand. *C. tagal* tolerates hypersalinity in the landward high intertidal environments. *A. marina* is found throughout the estuary, whereas *A. corniculatum* and *E. agallocha* are found predominantly in the upstream reaches, being rare in the funnel mouth.

Sampling procedure

Quadrats were placed at equal distances along the range of the river occupied by each of the five species forming extensive monospecific stands; 150 quadrats were used in the estimation of above-ground biomass. At each site, two 4 × 4 m^2 quadrats were laid, and height and diameter at breast height (DBH) of all individuals were measured. Soil was sampled at 30–50 cm depth for the determination of soil-water conductivity.

Estimation of above-ground biomass

Two individuals of each of the five species were harvested for comparison with published allometric equations for mangrove biomass. Species within the Mary River departed significantly from the equations of Clough and Scott (1989) for DBH > 10 cm, reflecting differences between the growth habits of subtropical mangroves and those of the tropical forests harvested by Clough and Scott (1989). For these individuals, an extrapolation based on the general volumetric equation of Rochow (1974) was used to estimate above-ground biomass on the basis of diameter at breast height and tree height (Saintilan 1997), such that

$$\text{dry wt (kg)} = \frac{h(0.214(D\times\pi) - 0.113)^2}{10}, \quad (1)$$

where h is tree height (m) and D represents DBH (cm).

Estimation of below-ground biomass

In a subsample of 56 quadrats, coring for below-ground biomass entailed four cores of 14 cm diameter in each quadrat, dug to the depth of root penetration. Samples were washed through a 599-µm sieve, and sandy material was separated from organic material by flotation. Because dead mangrove roots are well preserved in the anoxic soil medium, separation of live and dead roots following sampling is problematic. Previous studies have used microscopic inspection of root colour and branching (Lichacz *et al.* 1984) or buoyancy in a medium of colloidal silica (Robertson and Dixon 1993). In the present study a subsample of ten larger roots were dissected and analysed for turgidity and colour. The proportion of live roots identified on this basis was multiplied through the whole core sample for an estimation of live root mass, following drying to constant weight. These weights were converted to dry mass (Saintilan 1997).

Estimation of soil-water salinity

A sealed vial containing 5 g wet soil and 25 mL distilled water was shaken for 40 min. The electrical conductivity was then measured with a calibrated Metrohm 660 conductivity meter.

Statistical methods

Linear regression analysis was used to determine the nature and strength of relationships between biomass and soil-water conditions. Correlation coefficients were calculated and tested for significance by calculating the two-tailed t-statistic. Single-factor analysis of variance was used to assess the significance of differences between estuarine zones in the variables selected.

Results

Above- and below-ground biomass

Estimates of above- and below-ground biomass were highly variable in relation to both salinity and distance from the estuary mouth. Of all species sampled, only *R. stylosa* showed a consistent change in biomass with distance from the mouth of the estuary, decreasing with distance upstream. Above- and below-ground biomass of *A. marina* and *C. tagal* decreased significantly with distance upslope from the seaward edge of the wide intertidal flats at the estuary mouth as salinities increased from saline to hypersaline. There was little variation in biomass of *A. corniculatum* and *E. agallocha*.

Below-ground : above-ground biomass ratios

Below-gound : above-ground biomass ratios of *A. marina* and *C. tagal* were >3.0 in the landward portions of the wide intertidal flats of the channel mouth, where salinities were hypersaline (Fig. 2), but were significantly lower in less-saline environments at the seaward edge of these flats.

In the upstream reaches of the estuary, the below-ground: above-ground biomass ratios of *A. marina* and *A. corniculatum* were lower than in the channel mouth and were comparable with that of *E. agallocha*. The ratio in *E. agallocha* and *R. stylosa* did not differ significantly over their range.

When mangrove communities were grouped together (Fig. 3) the ratios decreased significantly with distance from the mouth (R = 0.443, n = 56, P < 0.005) and increased with increasing soil-water salinity (R = 0.338, n = 56, P <0.005).

Discussion

The below-ground : above-ground biomass ratios of species were found to vary in relation to distance from the mouth of the estuary and distance from the seaward edge of the wide intertidal flats of the channel mouth. The lowest ratios were found in communities of *A. marina*, *E. agallocha* and *A. corniculatum* in the upstream, meandering segment of the estuary. Downstream, the ratios in *A. marina* and *R. stylosa* attain unity in the frequently inundated seaward edges of the wide intertidal flats of the channel mouth, a value camparable to those found in saline field conditions for *Kandella candel, Bruguiera sexangula, Rhizophora stylosa* (Lin *et al.* 1990), *Rhizophora mangle* (Golley *et al.*

1962; Golley *et al.* 1974), and *Avicennia marina* (Briggs 1977; Clough and Attiwill 1982; Lichaz *et al*. 1984; Saintilan 1997), although Gong and Ong (1990) reported lower relative root mass for *Rhizophora apiculata* in Malaysia. The increase in the below-ground : above-ground biomass ratio of *A. marina* toward the estuary mouth is effected primarily by a decrease in shoot mass, which declines to a value compable to estimates for the same species in marine environments in temperate regions (Briggs 1977; Saintilan 1997).

The shoot biomass of *A. marina* and *C. tagal* decreases landwards on these flats to <1 kg m^{-2}, a value lower than

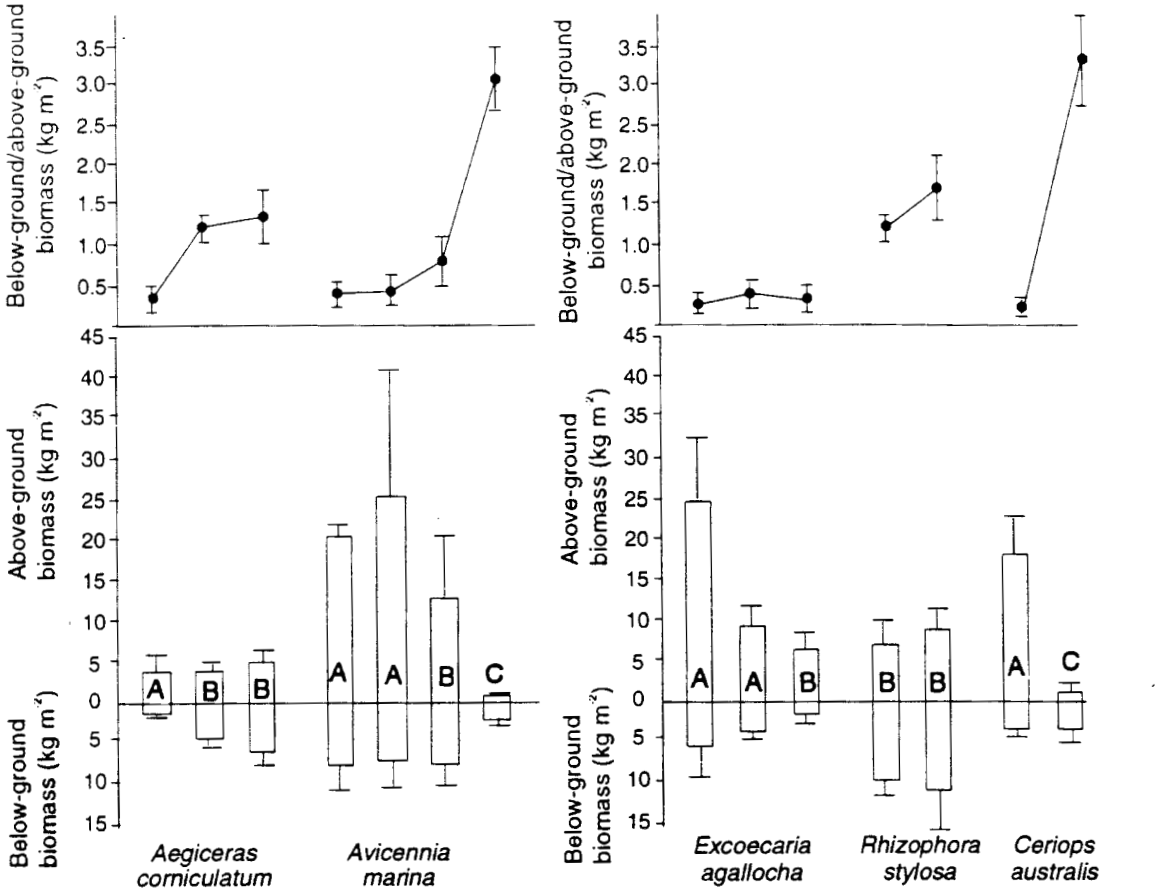


Fig. 2. Above- and below-ground biomass of five mangrove species on the Mary River (mean ± s.e.). A, upstream meandering reaches; B, seaward edge of wide intertidal flats in the channel mouth; C, landward segment of wide intertidal flats of the channel mouth.

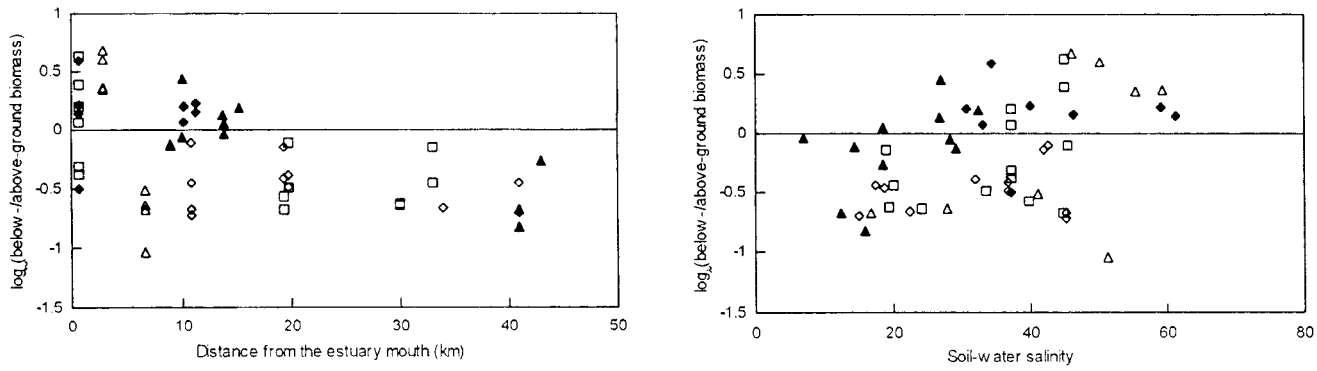


Fig 3. Above-ground : below-ground biomass ratios (log_{10}) of five species with *(a)* distance from the mouth of the Mary River and *(b)* variation in soil-water salinity. (▲) *Aegiceras corniculatum*, (◇) *Excoecaria agallocha*, (□) *Avicennia marina*, (△) *Ceriops tagal*, (◆) *Rhizophora stylosa*.

that found in comparable environments in temperate localities (Woodroffe 1985; Saintilan 1997); this possibly reflects the seasonally lower rainfall of the region which contributes to hypersaline conditions in less-frequently inundated sites. In these environments, below-ground : above-ground biomass ratios of *A. marina* and *C. tagal* increase to ~3.5, a figure similar to that attained by *A. marina* in a comparable bay-head deltaic environment on the Hawkesbury River (Saintilan 1997). Again, the increase in the ratio is effected primarily by a decrease in shoot mass.

Increases in the ratio with increasing salinity have been observed in laboratory studies of seedlings of *A. marina* (Burchett *et al.* 1984; Naidoo 1987; Ball 1988) and *A. corniculatum* (Ball 1988). Ball (1988) and Ball and Passioura (1995) have argued that an increase in root:shoot ratio with salinity is a response to water stress, and is linked to a conservative water-use strategy, particularly in *A. marina*.

Estimates from this study suggest that below-ground : above-ground biomass ratio increases logarithmically with a linear increase in substratum salinity. Perhaps in the arid upslope environments of the river mouth a point is reached where the respiratory demand of an extensive root system exceeds the carbon fixing ability of a smaller shoot system. This may be one factor delimiting the upslope distribution of mangroves.

Acknowledgments

The author thanks Professor B. G. Thom and Dr Peter Myerscough for helpful comments through the course of this research and in the writing of this paper. The project was partially funded through an Australian Postgraduate Research Award.

References

Aung, L. H. (1974). Root–shoot relationships. In 'The Plant Root and Its Environment'. (Ed. E. W. Carson.) pp. 29–61. (University Press of Virginia: Charlottesville.)

Ball, M. C. (1988). Salinity tolerance in mangroves *Aegiceras corniculatum* and *Avicennia marina* I. Water use in relation to growth, carbon partitioning, and salt balance. *Australian Journal of Plant Physiology* **15**, 447–64.

Ball, M. C., and Passioura, J. B. (1995). Carbon gain in relation to water use: photosynthesis in mangroves. In 'Ecophysiology of Photosynthesis'. (Eds E. D. Schulze and M. M. Caldwell.) pp. 247–59. (Springer: Berlin.)

Burchett, M. D., Meredith, S., Pulkownik, A., and Walsh, S. (1984). Short-term influences affecting growth and distribution of mangrove communities in the Sydney Region. *Wetlands (Australia)* **4**, 63–72.

Briggs, S. V. (1977). Estimates of biomass in a temperate mangrove community. *Australian Journal of Ecology* **2**, 369–73.

Clough, B. F. (1992). Primary productivity and growth of mangrove forests. In 'Tropical Mangrove Ecosystems'. Coastal and Estuarine Studies 41. (Eds A. I. Robertson and D. M. Alongi.) pp. 225–92. (American Geophysical Union: Washington, DC.)

Clough, B. F., and Attiwill, P. M. (1982). Primary productivity of mangroves. In 'Mangrove Ecosystems in Australia — Structure, Function and Management'. (Ed. B. F. Clough.) pp. 213–23. (Australian National University Press: Canberra.)

Clough, B. F., and Scott, K. (1989). Allometric relationships for estimating above-ground biomass in six mangrove species. *Forest Ecology and Management* **27**, 117–27.

Dalrymple, R. W., Zaitlin, B. A., and Boyd, R. (1992). Estuarine facies models: conceptual basis and stratigraphic implications. *Journal of Sedimentary Petrology* **62**, 1130–46.

Golley, F., Odum, H. T., and Wilson, R. F. (1962). The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology* **43**, 9–19.

Golley, F. B., McGinnis, J. T., Clements, R. G., Child, G. I., and Duever, M. J. (1974). 'Mineral Cycling in a Tropical Moist Forest Ecosystem.' (University of Georgia Press: Athens.) 248 pp.

Gong, W. K., and Ong, J. E. (1990). Plant biomass and nutrient flux in a managed mangrove forest in Malaysia. *Estuarine, Coastal and Shelf Science* **31**, 519–30.

Hutchings, P., and Saenger, P. (1987). 'Ecology of Mangroves.' p. 388. (University of Queensland Press: Brisbane.)

Iwasa, Y., and Roughgarden, J. (1984). Shoot/root balance of plants: optimal growth of a system with many vegetative organs. *Theoretical Population Biology* **25**, 78–105.

Kozlowski, T. T., Kramer, P. J., and Pallardy, S. G. (1991). 'The Physiological Ecology of Woody Plants.' (Academic Press: San Diego.) 657 pp.

Lichacz, W., Hardiman, S., and Buckney, R. T. (1984). Below-ground biomass in some intertidal wetlands in New South Wales. *Wetlands (Aust.)* **4**, 56–62.

Lin, P., Lu, C., Wang, G., and Chen, H. (1990). Biomass and productivity of a *Bruguiera sexangula* mangrove forest in Hainan Island, China. *Journal of Xiamen University of Natural Science* **29**, 209–213.

Mooney, H. A. (1972). The carbon balance of plants. *Annual Reviews of Ecology and Systematics* **3**, 315–43.

Naidoo, G. (1987). Effects of salinity and nitrogen on growth and water relations in the mangrove *Avicennia marina* (Forsk.) Vierh. *New Phytologist* **107**, 317–25.

Robertson A. I., and Dixon P. (1993). Separating live and dead fine roots using colloidal silica: an example from mangrove forests. *Plant–Soil* **157**, 151–4.

Rochow, J. J. (1974). Estimates of above-ground biomass and primary production in a Missouri forest. *Journal of Ecology* **62**, 567–77.

Russell, R. S. (1977). 'Plant Root Systems: their Function and Interaction with the Soil.' (McGraw–Hill: London/ New York.)

Saenger, P. (1982). Morphological, anatomical and reproductive adaptations of Australian mangroves, In 'Mangrove Ecosystems in Australia'. (Ed. B. F. Clough.) pp. 153–91. (Australian National University Press: Canberra.)

Saintilan, N. (1996). Mangrove environments of the Mary River. *Wetlands(Australia)* **15**, 31–8.

Saintilan, N. (1997). Above- and below-ground biomass of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Marine and Freshwater Research* **48**, 147–52.

Snedaker, S. C. (1995). Mangroves and climate change in the Florida and Caribbean region: scenarios and hypotheses. *Hydrobiologia* **295**, 43–9.

Woodroffe, C. D. (1985). Studies of a mangrove basin, Tuff Crater, New Zealand. I. Mangrove biomass and production of detritus. *Estuarine, Coastal and Shelf Science* **20**, 265–80.

Manuscript received 17 January 1997; revised 23 June, 5 August and 18 September; accepted 18 September 1997

Ecosystems (2020) 23: 370–382
https://doi.org/10.1007/s10021-019-00408-3

ECOSYSTEMS

© 2019 Springer Science+Business Media, LLC, part of Springer Nature

Thirty-Year Repeat Measures of Mangrove Above- and Below-Ground Biomass Reveals Unexpectedly High Carbon Sequestration

Karen Lamont,[1] Neil Saintilan,[1]* Jeffrey J. Kelleway,[2] Debashish Mazumder,[3] and Atun Zawadzki[3]

[1]*Department of Environmental Sciences, Macquarie University, North Ryde, Sydney, New South Wales 2109, Australia;* [2]*Department of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia;* [3]*Australian Nuclear Science and Technology Organization (ANSTO), Lucas Heights 2234, Australia*

Abstract

Mangrove ecosystems store large quantities of organic carbon for long periods of time. This study explores organic carbon stock change through the first comparative study of radiometric analysis and repeat field measures over a multi-decadal period in a mangrove system. Examining one tall gallery forest of *Avicennia marina*, and an adjacent interior scrub mangrove of mixed *Avicennia marina* and *Aegiceras corniculatum*, radiometric analysis estimated a soil organic carbon accumulation rate of 4.3 ± 0.6 Mg C ha^{-1} y^{-1} in the tall gallery forest and 2.2 ± 0.5 Mg C ha^{-1} y^{-1} in a stunted mangrove. Repeat measures of root carbon separated by 30 years estimated an increase of 5.06 Mg C ha^{-1} y^{-1} in the tall forest and 6.63 Mg C ha^{-1} y^{-1} in the stunted forest—suggesting an underestimate of carbon accumulation by radiometric dating of 15% and 67% in the tall and stunted forest, respectively. A higher carbon stock in the interior forest was attributed to root mass increase, associated with landward mangrove encroachment. Extrapolated to the entire region of NSW we estimate that mangrove encroachment has contributed at least about 1.8 Tg C sequestration over the 70 years for which this has been observed in New South Wales, Australia.

Key words: blue carbon; mangrove; stock change; organic carbon.

Highlights

- Mangrove above- and below-ground forest biomass re-surveyed after 30 years.
- Additional carbon estimated by direct, repeat measures is substantially higher than estimates using radiometric dating of carbon accumulation.

Received 11 December 2018; accepted 22 May 2019;
published online 13 June 2019

Author's Contribution KL led field and laboratory analysis, and drafted the manuscript. NS further developed the manuscript and figures. JJK contributed to field and laboratory analysis and the preparation of the manuscript. DM conducted the stable isotope and elemental analysis. AZ conducted the radiometric analysis.

**Corresponding author; e-mail:* neil.saintilan@mq.edu.au

- Mangrove landward encroachment and poleward expansion is facilitating large increases in carbon sequestration.

Introduction

The burial of carbon in sediments of intertidal wetlands creates some of the oldest and largest carbon sinks in the world (Grimsditch and others 2013; Howard and others 2014; Mcleod and others 2011). Waterlogged soils suppress the oxidation and remineralisation of carbon, and thereby suppressing release of CO_2 into the atmosphere (Chmura 2013; Howard and others 2014; Mcleod and others 2011). Saline tidal wetlands generally have low CH_4 emissions as sulphates from tidal flows encourage the dominance of sulphur-reducing microorganisms and the anaerobic oxidation of methane (Kroeger and others 2017), furthering these ecosystem's efficiency in mitigating greenhouse gas emissions. Coastal ecosystems therefore play a potentially important role in carbon cycling and climate change mitigation, as they possess a natural mechanism of sequestering carbon over time (Bouillon and others 2008; Chmura and others 2003; Duarte and others 2005). Despite their evident importance, coastal ecosystems are currently facing extensive loss, attributable to the threat of sea-level rise, as well as land use conversion for agricultural, industrial and urban development (Lovelock and others 2015; Rogers and others 2016). It is therefore important to improve our understanding of how tidal carbon sinks naturally change over time, and how they will respond to climate change and human activities.

Increasingly, investors in the carbon market are seeking projects that can provide strong evidence of long-term additions to the carbon store, and the degree of certainty in the measurement of additional carbon sequestration directly influences the carbon price (Marland and others 2001). Despite this, few carbon sequestration projects in tidal wetlands are of sufficient duration to allow for a meaningful time-series of carbon store change detection (Thomas 2014). Further, elevated CO_2, temperature and sea level are altering competitive interactions between mangrove and saltmarsh, facilitating the conversion of saltmarsh to mangrove in latitudes where the two coastal wetland communities grow in sympatric association (Saintilan and others 2019). Understanding the implications of this global trend for carbon sequestration is an important guide to local and regional management responses (Kelleway and others 2017a, b).

Three broad approaches have been adopted to the quantification of rates of carbon accumulation in wetlands over inter-annual and inter-decadal timelines: radiometric dating, space-for-time substitution, and repeat measures. Radiometric dating has long been applied to reconstruct sedimentation chronologies, and by implication the rate of carbon accumulation in tidal wetland settings (Pethick 1981; Crosby and others 2016). The most commonly used isotope is ^{210}Pb, given the continuous decay series extending over the inter-decadal timeframe relevant to carbon accumulation. Although ^{14}C has been used to date old mangrove and shell material and derive accumulation rates (Saintilan and Wilton 2001; Saintilan and Hashimoto 1999), the deep penetration of modern root material compromises the application of this technique in many settings (Kelleway and others 2017a, b). Mangrove roots may proliferate in channels formed by the refractory remains of old roots (McKee 2002), and incorporation of modern root material at depth in mangrove forests ($\sim$ 1 m) also challenges the assumptions of ^{210}Pb as a means of dating autochthonous carbon accumulation in these settings.

Space-for-time substitution utilises chrono-sequences of wetland establishment or restoration to deduce the rate of carbon addition to the soil, commonly in relation to reference or ''target'' wetlands. For example, Osland and others (2012) examined restored wetlands in Florida ranging in age from 2 to 20 years, comparing vegetation composition and soil carbon to nine reference forests. Marchand (2017) quantified soil carbon stock across a mudbank in French Guiana, along a chrono-sequence from 3 to 48 years, whereas Salmo and others (2013) compared soil organic carbon in restored *Rhizophora mucronata* forests in the Philippines ranging in age from 6 to 50 years. Both Osland and others (2012) and Marchand (2017) stress length of time (20 + years) required for the accumulation of soil carbon to levels approaching mature target forests, though Salmo and others (2013) suggest soil organic carbon approached their reference conditions after 17 years. Kelleway and others (2016a, b) found that increases in soil carbon following mangrove encroachment of saltmarsh on the Georges River in New South Wales, Australia, were significant only after about 30 years or more.

The space-for-time approach is a commonly pursued experimental design in the literature and is a useful method of extrapolating long-term information without waiting the impractical length of time required to document long-term trends.

However, this experimental design only ever gives an indication of what long-term change might be, and the potential for systematic bias in the location and characteristics of old and young sites precludes certainty in the reconstruction of temporal trends. Without direct repeat measures through time, we cannot accurately quantify how much carbon has accumulated in situ over time.

There are very few published studies using repeat measures of organic carbon in wetlands over the time period required to demonstrate stock change. Lunstrum and Chen, (2014) examined the effect of mangrove afforestation in southeast China with repeat measures annually at two afforested mangroves for 6 years from the time of planting. Their repeat measures of below-ground carbon consisted in 10-cm-deep soil cores, from which they demonstrated an increase in organic carbon over time. Rogers and others (2019) estimated carbon accumulation rates in surface soils over an 18-y period, utilising the surface elevation table-marker horizon (SET-MH) method. This study, along with the spatial chrono-sequence studies cited above, suggests decadal time periods may be required to demonstrate significant changes to organic carbon in vegetated habitats, and such studies are understandably rare.

We assess carbon storage and accumulation across a 30-y timeframe, utilising a unique set of measures taken within the study sites in the late 1980s in a stretch of the Hawkesbury River subject to seaward and landward development of mangrove since the earliest aerial photography in the mid 1940s. The specific objectives are to quantify above- and below-ground biomass change over a 30-y period at two localities: a tall gallery forest adjacent to the river channel which colonised a freshly accreted mudflat in the 1970s, and an upper-intertidal mixed saltmarsh-mangrove site subject to mangrove encroachment over the past 60 years. The encroachment of mangrove into formerly saltmarsh intertidal environments in subtropical and temperate regions has been documented as a global trend (Saintilan and others 2014), and there is considerable interest on the carbon sequestration implications (Kelleway and others 2017a, b). We sought to quantify bulk carbon accumulation rates for these sites using radiometric dating and determine the provenance of carbon accumulating in the wetland, whether autochthonous (mangrove leaf/root) or allochthonous. In doing so, we will test the assumption that radiometric (^{210}Pb) dating of sediment accretion will provide reliable estimates of carbon accumulation, while testing the hypothesis that mangrove encroachment and development enhances carbon sequestration.

Methods

Site Description

The study was conducted in a mangrove flat adjacent to the town of Spencer on the Hawkesbury River, New South Wales, Australia, to replicate the above and below-ground biomass estimate of Saintilan (1997) conducted in 1989. Two adjacent sites were compared: a tall gallery forest of *Avicennia marina* (Site 1), and an interior, higher elevation, stunted mixed community of *A. marina* and *Aegiceras corniculatum*. Early aerial photography of the site shows that Site 1 became vegetated between 1947 (Figure 1) and 1982, possibly following flood deposition. The survey of Saintilan (1997) was of a forest at most 30 years old, though represented at this time a tall forest of relatively high above-ground biomass. In 1947, Site 2 was an upper-intertidal mudflat, relatively free of mangrove and likely to have been dominated by saltmarsh (Figure 1). Aerial photography in following decades demonstrates a pattern of mangrove encroachment and thickening (increased density), and was one of the sites referenced by Saintilan and Williams (1999) in making the case for a widespread regional trend of mangrove encroachment into saltmarsh. The Site 2 (stunted interior forest), occurring higher in the tidal frame, was inundated less frequently and to lower depth than the tall forest (Figure 2).

Soil Organic Carbon and Radiometric Dating

All sampling was conducted in the same 20 × 50 m plots used in the 1989 survey of Saintilan (1997). Soil coring for soil organic carbon and radiometric dating was undertaken in March 2018 with a Russian D-Core to allow for easy trapping of wet material without compaction, capturing depths of 0–100 cm. Five cores were taken at each of the two sites, one in each of the five randomly located above-ground biomass plots (detailed below). All cores were placed in cool storage and transported to the laboratory. Cores were then sectioned and dried in the oven at 60°C until constant mass was achieved. Samples were prepared for ^{210}Pb and stable isotope analysis (δ^{13}C) and elemental analysis (%C) at the Australian Nuclear Science and Technology Organisation (ANSTO) facilities, and Loss-on-Ignition (LOI) at Macquarie University.

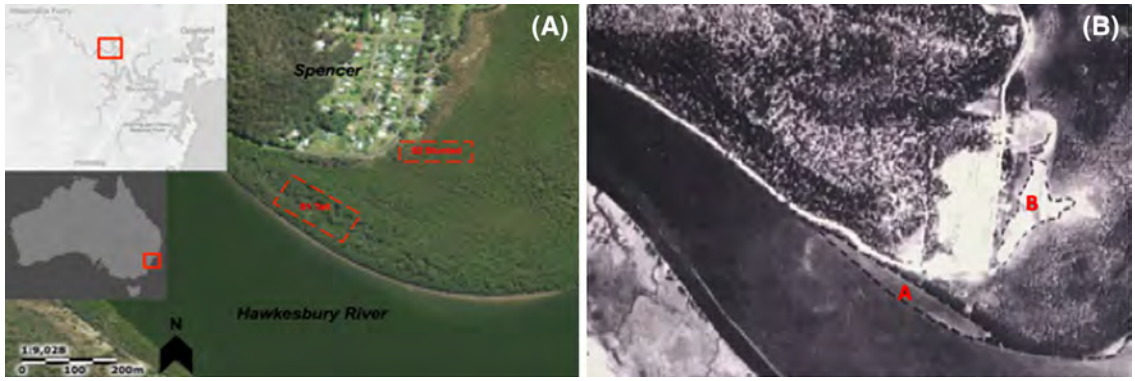


Figure 1. (**a**) Location of the Spencer tall (Site 1) and low (Site 2) mangrove sampling plots (2018 photography), and (**b**) the location in 1947 showing open water at Site 1 **(A)** and saltmarsh at Site 2 (**B**).

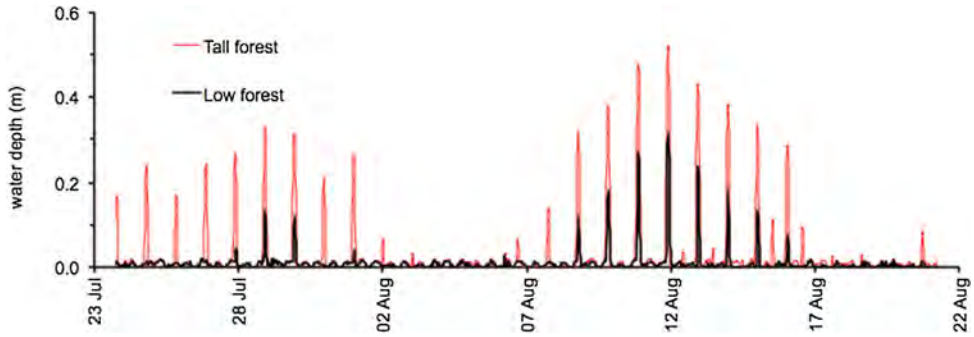


Figure 2. Depth of inundation above the wetland surface derived from HOBO pressure sensors for the period 23 July–22 August 2018.

Cores were split, with ^{210}Pb samples sectioned at 0.5-cm intervals for precision, to a depth of 20.5 cm, a depth considered sufficient to identify the 1989 horizon. Stable isotope, elemental analysis and LOI samples were sectioned at 1-cm intervals to a depth of 10 cm, 2-cm intervals to a depth of 30 cm, and 5-cm intervals to a depth of 100 cm. All samples were analysed for LOI, and every second sample was analysed for %C and δ^{13}C. Bulk soil samples were then homogenised with a mortar and pestle prior to stable isotope and elemental analysis. Following Schlacher and Connolly, (2014), the champagne test was used for each sample to reveal whether material contained inorganic carbon. All tests returned an absence of carbonates; thus, %C is equal to %organic carbon and hitherto referred to as %C. Samples subject only to LOI had %C estimated based upon the relationship determined between %C (elemental analysis) and % organic matter (LOI) for sub-samples subjected to both methods.

Soil profile dating using ^{210}Pb was specifically selected to (1) allow for an estimation of carbon accumulation using a standard method and (2) identify the depth at which Saintilan was sampling in 1989, to identify below-ground compartments above and below this horizon. Soil ^{210}Pb samples were processed to determine polonium-210 (^{210}Po) and radium-226 (^{226}Ra) activities by alpha spectrometry (Atahan and others 2015). Unsupported ^{210}Pb activities were estimated as the difference between total ^{210}Pb activity (measured from ^{210}Po) and supported ^{210}Pb activity (measured from ^{226}Ra) (Appleby and Oldfield 1978). Sediment chronology was determined using a constant initial concentration (CIC) model (Appleby and Oldfield 1978). Percent C assessed using both LOI and elemental analysis was multiplied by soil accumulation rates (determined through ^{210}Pb analysis) to generate surface carbon accumulation rates.

Above- and Below-Ground Biomass

Saintilan (1997) established 20 m by 50 m plots in Site 1 (tall forest) and Site 2 (stunted forest). Within these, five randomly placed 16 m^2 quadrats were used to measure above-ground plant dimension. For tall trees (> 3 m), height and diameter at breast height (DBH) were measured. For stunted

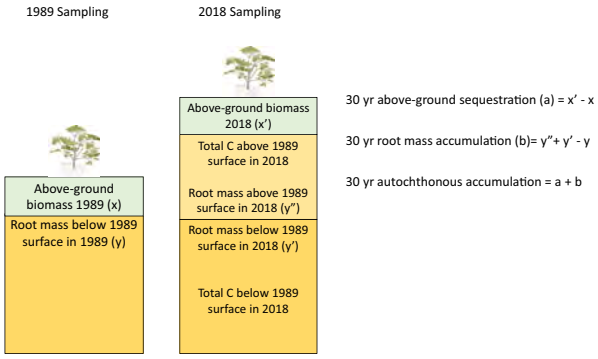


Figure 3. Schematic of the major components of biomass being compared between the 1989 and 2018 surveys. Comparisons are made in 2018 between stocks above and below the 1989 horizon determined by radiometric dating.

trees, which included shrub trees (1.3–3 m) and dwarf trees (< 1.3 m), a similar approach was used where height, DBH, diameter at 30 cm (D30), diameter at 5 cm (D5) and crown area were measured. We replicated this sampling strategy, to allow a comparison of biomass stocks (Figure 3). We therefore used the same plot locations and above-ground measures, though larger quadrats of 100 m^2 were used in Site 1 and 25 m^2 in Site 2, to allow for potential decreases in density and maintain consistency with contemporary biomass estimates in the region (for example, Kelleway and others 2016a, b). The allometric equations of Owers and others (2018) were applied to both our 2018 data and the original data of Saintilan (1997) to calculate above-ground biomass and estimate above-ground carbon stock. Our elemental analysis of root carbon (described below) suggested a conversion to per cent carbon of 0.35. For conversion of above-ground plant mass to above-ground C, we used the figure of 0.48, midway in the range of 0.46–0.5 suggested by Howard and others (2014) for mangrove trees and shrubs.

Root material was excavated with a trenching shovel, with dimensions of 15 cm by 15 cm, following the methods of Saintilan (1997). Radiometric analysis (Figure 4) indicated that the contemporary surface was 12 cm above the 1989 surface in Site 1 and 13 cm above the 1989 surface in Site 2. Four samples were taken at each site, at a depth of 62 cm in Site 1 and 63 cm in Site 2, to sample to 50 cm below the 1989 horizon at each site, corresponding to the depth of the 1989 sampling. Prior to transport, we separated the upper 12 cm at Site 1 and 13 cm at Site 2. Samples were placed in cool storage and transported to the laboratory. Once returned to the laboratory, the samples, both shallow (0–12/13 cm), and deep (12/13–62/63 cm) were washed through a sieve to drain bulk sediment and collect all root biomass. The root material was dried in the oven at 60°C until constant mass was achieved. Samples were then weighed for their mass to compare to Saintilan (1997). No attempt was made to distinguish live from dead roots, and for this reason we do not seek to interpret plant root/shoot ratios.

It has been demonstrated that *Avicennia marina* roots have a $\delta^{13}C$ signature distinct from that of their leaves, enabling $\delta^{13}C$ to be used as a proxy for the contribution of leaf and root carbon to below-

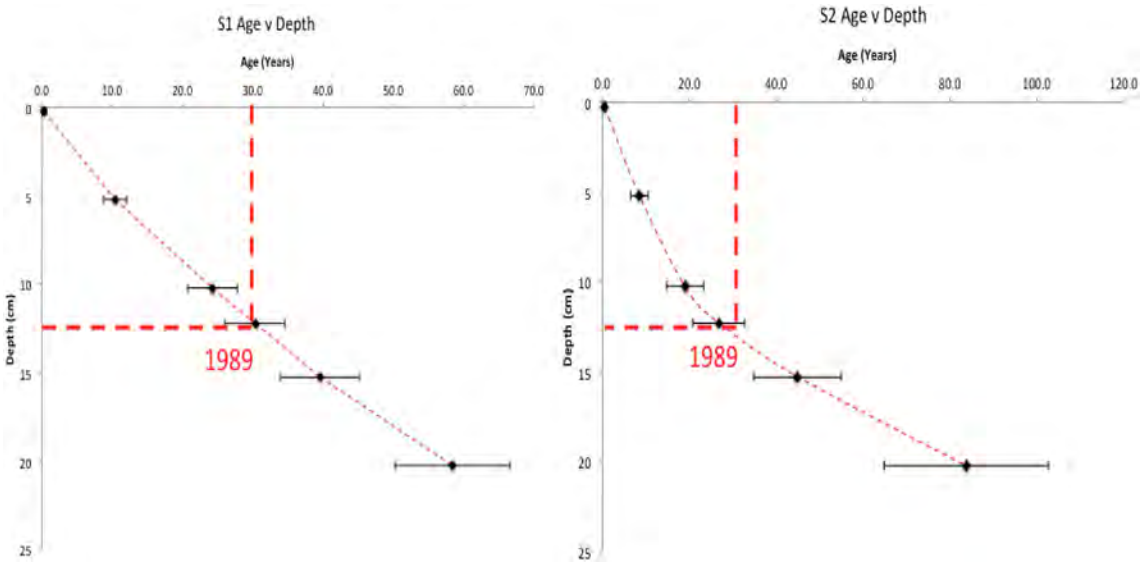


Figure 4. Sedimentary radiometric age plotted against depth in Site 1 (tall forest) and Site 2 (stunted community).

ground carbon stores (Kelleway and others 2018). A subset of ten root sub-samples, five from each site, were prepared for stable isotope analysis to determine root %C and δ^{13}C by elemental analysis and isotope ratio mass spectrometry (IRMS), respectively. Sub-samples were homogenised through the mortar and pestle approach and analysed at ANSTO.

For %C and δ^{13}C analysis, 0.15 mg of each powdered sample was loaded into tin capsules and compacted manually to remove air spaces. Analysis was conducted at ANSTO in Sydney, Australia, using a continuous-flow isotope ratio mass spectrometer (CF-IRMS) model Delta V Plus (Thermo Scientific Corporation, USA), interfaced with an elemental analyser (Thermo Fisher Flash 2000 HT EA, Thermo Electron Corporation, USA). All data were reported relative to IAEA (International Atomic Energy Agency) secondary standards, and were certified relative to Vienna PeeDee Belemnite (VPDB) for carbon. A two-point calibration was used to normalise the data, using standards (Chitin and Casein Sodium Salt from Bovine Milk) which bracket the analysed samples. Both of these standards were used as quality control references and were included in every sample run. All results were accurate to 1% for C% and ± 0.3 parts per thousand (‰) for δ^{13}C; they were reported in delta (δ) units in parts per thousand (‰) determined by the formula:

$$X(\%) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000$$

Statistical Analyses

A two-way ANOVA was employed to test differences in below-ground biomass estimates amongst the factors of time (1989; 2018) and site (tall; stunted) and the time × site interaction. Separate analyses were conducted for two dependent variables: (1) biomass across the entire root range (2018 surface to 1989 root base); and (2) biomass across the 1989 root zone only (1989 surface to 1989 root base). Above-ground biomass data did not meet the equal variances requirements for the two-way ANOVA, so are reported as a series of independent sample *t* tests with statistics reported according to whether equal variances were or were not assumed. All analyses were conducted in SPSS v24 (IBM Corp., Armonk, New York, USA).

Results

Radiometric Dating of Sediment Accretion

The age and depth of sample material were plotted showing gradual accretion at both sites, with a slight accelerating trend at Site 2 (Figure 4). On this basis the ^{210}Pb profile was considered a reliable guide in determining the depths at which Saintilan (1997) would have been sampling, calculated to be 12 cm below the contemporary surface in Site 1, and 13 cm below the contemporary surface in Site 2, referred hitherto as the 1989 horizon.

Above- and Below-Ground Plant Mass

Above-ground biomass was substantially higher in Site 1 relative to Site 2 in both 1989 (t = 8.96; P = 0.001) and 2018 (t = 3.82; P = 0.02) (Figure 5). For Site 2, there was a greater than sevenfold increase in mean above-ground biomass (t = 3.35; P = 0.03). For Site 1 no significant difference was detected (t = 1.729; P = 0.14) due in part to high variability in 2018 estimates. Increased biomass at Site 2 was driven by a substantial increase in density of both species in the stunted community of mixed *Avicennia marina* and *Aegiceras corniculatum* (Table 1).

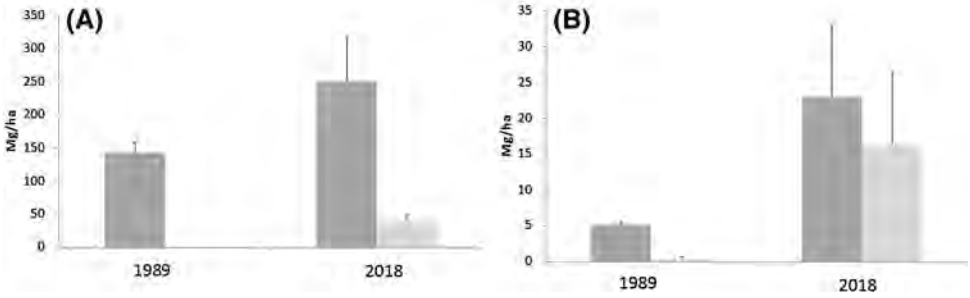


Figure 5. Mean above-ground biomass (Mg ha^{-1}) of *Avicennia marina* (dark shading) and *Aegiceras corniculatum* (light shading) at Site 1 (**A**) and Site 2 (**B**) between 1989 (Saintilan 1997 data) and 2018 (present study). Error bars represent 1 standard error.

Table 1. Comparison of Above-ground Vegetation Metrics 1989–2018

	Density *A. marina* (/100 m^2)	Density *Ae. corniculatum* (/100 m^2)	Height *A. marina* (*m*)	Height *Ae. corniculatum* (*m*)	DBH *A. marina* (*cm*)	DBH *Ae. corniculatum* (*cm*)
S1 1989	18.75 ± 10.8	–	8.5 ± 0.3	–	58.6 ± 3.1	–
S1 2018	9.8 ± 4.4	2.6 ± 2.0	10.4 ± 0.4	3.9 ± 0.4	61.9 ± 4.4	8.6 ± 0.8
S2 1989	54 ± 31.9	2.1 ± 3.6	2.1 ± 0.1	1.5 (n = 1)	8.8 ± 0.5	1.3 (n = 1)
S2 2018	44.8 ± 40.6	76 ± 12.3	1.9 ± 0.1	1.2 ± 0.04	9.6 ± 0.9	10.6 ± 1.0

Values represent mean ± 1 standard deviation, where appropriate.

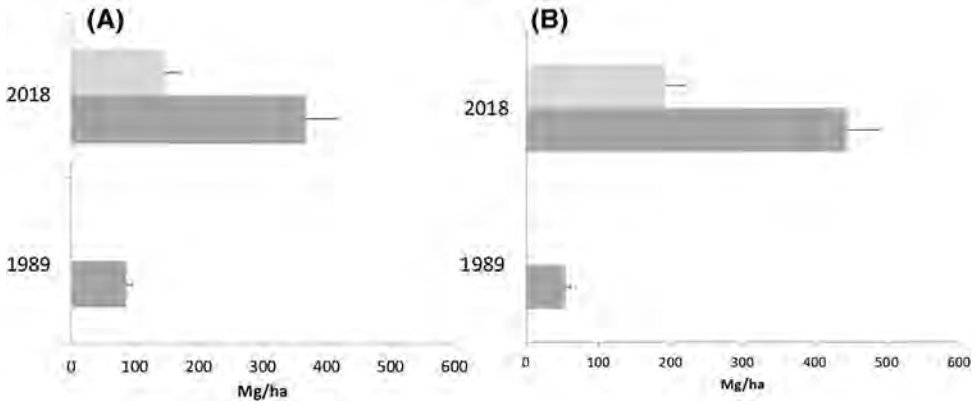


Figure 6. Mean dry root mass (Mg ha^{-1}) at Site 1 (**A**) and Site 2 (**B**) above (light shading) and below (dark shading) the 1989 horizon. Error bars represent 1 standard error.

Total below-ground root mass increased substantially over the period (F = 109; $P < 0.001$), outweighing increases in above-ground biomass, with a sixfold and 12-fold increase at Site 1 and Site 2, respectively (Figure 6). Although considerable new root material was introduced above the 1989 horizon at both sites, there was a significant increase in root mass below this horizon (F = 91; $P < 0.001$). That is, there were fourfold and eightfold increases in mean root biomass below this horizon at Site 1 and Site 2, respectively (Figure 6). There was no difference in root biomass between the two sites across either depth range ($P > 0.3$), nor were there significant time × site interactions ($P > 0.1$).

Bulk Organic Carbon

Approximately half of the below-ground carbon is stored root material. The ratio of root carbon to bulk carbon in Site 1 is 0.615 above the 1989 horizon, and 0.434 below the 1989 horizon. The ratio of root carbon to bulk carbon in Site 2 is 0.57 above the 1989 horizon, and 0.435 below the 1989 horizon—a remarkable consistency between sites. Bulk sediment $\delta^{13}C$ corresponded to root mass $\delta^{13}C$ at both Site 1 (mean − 26.9‰ and − 27.0‰, respectively) and at Site 2 (mean − 26.4‰ and − 26.7‰, respectively). Leaves of both species are depleted compared to the roots (− 27.3ppt *A. marina*, − 28.6 *Ae. corniculatum*).

Carbon accumulation as estimated by ^{210}Pb (Figure 7) shows a consistently higher rate of accumulation at Site 1, with an accelerating trend at both sites over the past decade. When integrated over the entire period of ^{210}Pb dating, overall surface soil carbon accumulation rates are 4.3 ± 0.6 Mg C ha^{-1} y^{-1} for S1 and 2.2 ± 0.5 Mg C ha^{-1} y^{-1} for S2.

Overall Stock Change

Our estimates of stock and stock change in the tall and stunted forests are presented in Figure 8. The above- and below-ground pools presented in Figures 5 and 6 were converted into Mg C ha^{-1} using the conversion factors 0.48 for above ground and 0.35 for below-ground carbon. The additional carbon estimates are the difference between the 1989 and 2018 stocks. These consist of above-ground stock changes, accumulation of carbon above the 1989 horizon, and the difference in root carbon

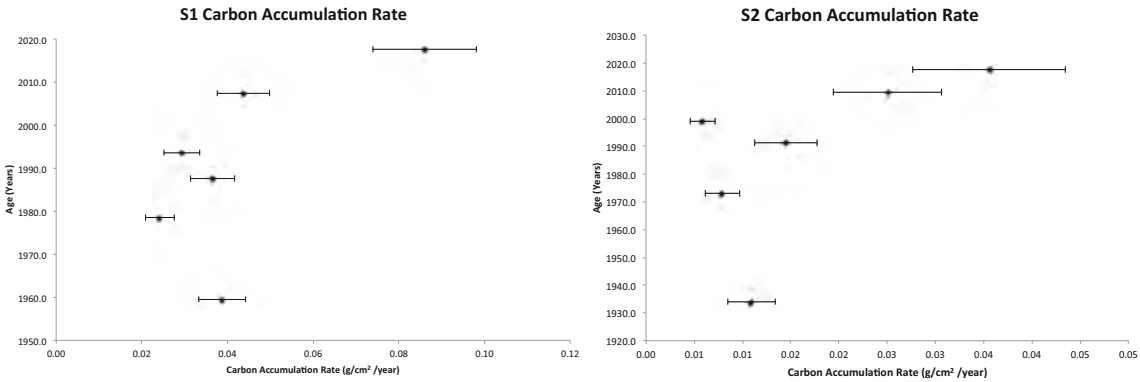


Figure 7. Down-core variations in bulk soil carbon accumulation rate estimated by multiplying the soil carbon content (%C) at each depth interval by bulk accumulation rates determined through ^{210}Pb dating.

below the 1989 horizon between the contemporary and Saintilan (1997) survey in 1989. We assume all allochthonous input post-1989 is above the 1989 ^{210}Pb horizon, and the volume of this input is therefore less than the difference between root carbon and Bulk C above the 1989 horizon.

Discussion

Mangroves are an increasingly important contributor to carbon mitigation strategies, given the significant carbon stocks held in above- and below-ground stores. Below-ground measures of organic carbon in mangroves are most commonly derived from bulk soil analysis, with studies of the specific contribution of root mass relatively scarce (Adame and others 2017), due to the labour intensive, difficult nature of the sampling. This is an important gap in the literature, given the significance of autochthonous contributions in making the case for ecosystem-based carbon management in intertidal settings.

Our estimate of mangrove root stock in the 2018 survey (mean ± 1SE = 511 ± 66 Mg ha^{-1} in the tall forest and 638 ± 70 Mg ha^{-1} in the encroachment zone) is amongst the highest recorded, matched only by *Rhizophora* forests in Thailand (Komiyama and others 1987) and Puerto Rico (Golley and others 1962) amongst 25 studies reviewed by Adame and others (2017). However, studies utilising fixed cores rarely represent mangrove root mass as greater than 100 Mg ha^{-1}, whereas trenches rarely return values less than 100 Mg ha^{-1}(Adame and others 2017). The high variability introduced by forest age and hydrology may contribute to the poor predictive power of allometric equations (Adame and others 2017). The equations of Comley and Mcguinness (2005) developed for *Avicennia* of northern Australia underestimate our below-ground root mass by an order of magnitude. Allometric equations incorporating DBH and location-specific variables explained less than 16 per cent of below-ground root and carbon variability in *Avicennia* forests in New Zealand (Bulmer and others 2016). The result brings into question estimates of *Avicennia* below-ground root mass and carbon derived from allometric equations.

Our estimates of organic carbon accumulation derived from radiometric analysis (4.3 ± 0.6 Mg C ha^{-1} y^{-1} in the tall forest and 2.2 ± 0.5 Mg C ha^{-1} y^{-1} in the encroachment zone) are at the upper end of mangrove estimates derived from radiometric dating in Australia (mean = 1.26; range = 0.17 to 3.4 Mg C ha^{-1} y^{-1}; Kelleway and others 2017a, b), and substantially higher than estimates based on surficial carbon burial rates (1.74 Mg C ha^{-1} y^{-1}) reported by Alongi (2014). Elsewhere, Osland and others, (2012) estimated a rate of 2.18 Mg C ha^{-1} y^{-1} in a mangrove-encroached salt marsh in Florida, USA, Lunstrum and Chen (2014) estimated 1.55 Mg C ha^{-1} y^{-1} in a mangrove forest in China, and Marchand (2017) estimated 2.3 Mg C ha^{-1} y^{-1} in a mangrove forest in French Guiana. For southeast Australia, Saintilan and others (2013) estimated short-term accumulation rates above feldspar marker horizons of 2.50 Mg C ha^{-1} y^{-1}, though this is likely to be an overestimate relative to longer-term radiometric approaches. The root carbon accumulation rate determined by repeat measures of below-ground root mass, of 5.06 Mg C ha^{-1} y^{-1} in the tall *A. marina* forest, and 6.63 Mg C ha^{-1} y^{-1} in the mixed *A. marina*/*Ae. corniculatum* encroachment zone, is substantially greater than the estimate of bulk carbon accumulation determined by radiometric analysis of bulk soil carbon.

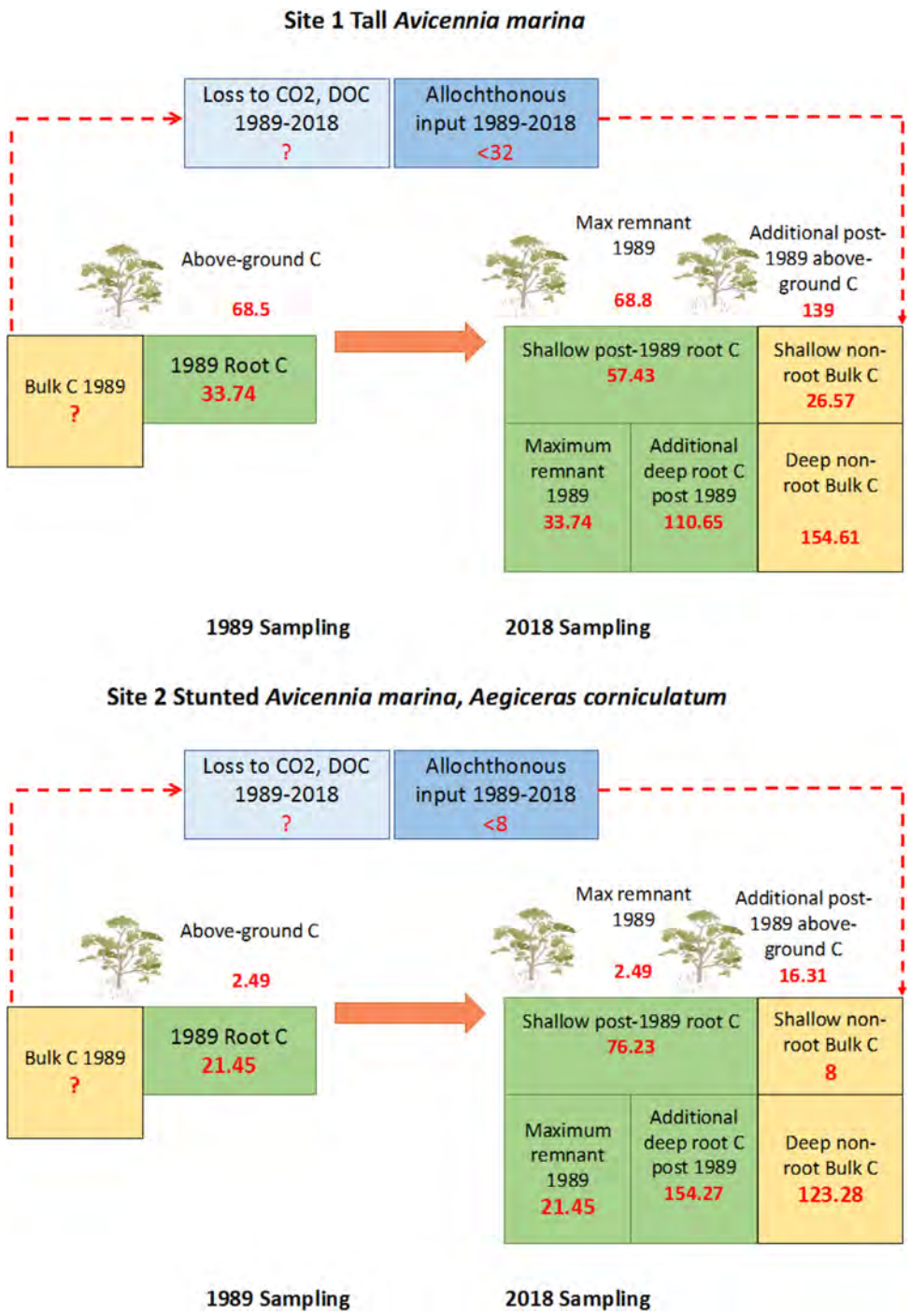


Figure 8. Changes in carbon stocks between below-ground compartments, 1989–2018. Bulk C was not measured in 1989. Minimum additional carbon is deduced as the difference between contemporary carbon and 1989 stocks, assuming all is preserved (maximum remnant 1989). Shallow root and Bulk C in 2018 is defined as that accreted above the 1989 horizon. All data in Mg C ha^{-1}.

There are two primary reasons why radiometric dating of soil horizons might underestimate below-ground carbon accumulation. First, sediment is commonly retrieved using narrow (5–10 cm diameter) corers, which tend to exclude larger roots, and/or laterally displace roots during insertion. Adame and others (2017) note that below-ground root carbon estimates derived from trenching are consistently higher than those derived from fixed diameter coring devices. Second,

the radiometric dating approach only quantifies new carbon that has been contributed only above the dated horizons. Our study demonstrated that most additional, new root carbon may be contributed at depths where the mineral sediment is decades old, and this may dominate soil carbon stocks. This is supported by our soil organic carbon $\delta^{13}C$ values which were consistently in the range of contemporary mangrove root material—as measured in this study and elsewhere (Kelleway and others 2018). In total, accumulation of below-ground root mass over the past 30 years contributed to more than half of the measured contemporary below-ground carbon.

Changes in vegetation composition and density are a likely dominant influence on changes in the quantity and depth distribution of below-ground root mass (Kelleway and others 2017a, b). Adame and others (2017) in a review found highest root biomass in densely populated forests, with trees that have small DBH measures. This may explain why Site 2 has a higher mass of below-ground root material. Similar findings of correlation between high tree density above-ground and high root density below-ground in other areas of the world have been reported (Komiyama and others 1987; Lang'at and others 2013; Tamooh and others 2008). Mangroves may respond to less frequent tidal inundation and higher salinity by increasing the proportion of carbon allocated to root systems (Saintilan 1997). Species mix and richness of above-ground biomass may also be having an influence. Lang'at and others (2013) found that forests with mixed species developed denser root networks below-ground at faster rates compared to homogenous forests, and within 3 to 4 years, below-ground biomass had exceeded above-ground biomass. The colonisation of Site 2 by *Aegiceras corniculatum*, without noticeable decrease in the density of *Avicennia marina,* significantly increased above-ground biomass stocks and may have facilitated the mixed forest accumulating root biomass at a significantly fast pace.

The encroachment of mangroves into saltmarsh environments has been commonly observed in recent decades on several continents (Saintilan and others 2014). The underlying causes have been investigated in the Gulf Coast USA, where expansion follows periodic frost-induced die-back (Cavanaugh and others 2014), tropical Queensland where phases of higher rainfall may facilitate mangrove colonisation (Eslami-Andargoli and others 2009), and SE Australia where higher sea levels appear to be driving landward encroachment (Rogers and others 2006). Mangrove encroachment of saltmarsh has a range of implications for ecosystem services (Kelleway and others 2017a, 2017b) including carbon sequestration. Doughty and others (2016) found that mangrove encroachment of saltmarsh in Florida led to increases in carbon stock, although primarily in above-ground biomass rather than below-ground biomass. Yando and others (2016) compared mangrove and saltmarsh soil carbon across three Gulf of Mexico sites along an aridity gradient. They found that in only the driest site did mangrove support a significantly higher carbon store. However, the accumulation of soil carbon in mangrove encroachment zones may take time. Kelleway and others (2016a, b) working in the Sydney region, Australia, found that 70 years of mangrove encroachment onto saltmarsh habitats had increased carbon stocks in tidal wetland ecosystems, but that statistically significant changes in below-ground carbon store could not be detected until after 30 years of colonisation by mangrove. The decadal timeframe required to demonstrate a significant change in soil carbon following mangrove recruitment is confirmed by recent estimates using the surface elevation table method in the same region (Rogers and others 2019), whereas Osland and others (2012) found soil carbon in restored mangroves equilibrating with natural mangroves after 20 years in southern USA, but only in the upper 10 cm. Frequent frosts on the US Gulf Coast may truncate the development of soil carbon in mangroves periodically subject to mass mortality. Our Site 2 is an active encroachment zone, with mangroves initially colonising between 1945 and the first biomass survey by Saintilan in 1989, but substantial encroachment and thickening has occurred since then. Our results suggest that this has led to substantial increases in carbon above- and below-ground, driven by strong increases in shoot and root biomass well below the upper 10 cm.

This finding is of regional significance, given that Saintilan and Williams (1999) found that significant losses of saltmarsh were evident in Queensland, New South Wales, Victoria and South Australia over a 50-y period, and mangrove forests were colonising landward and replacing these ecosystems. The results reported here suggest that the encroaching mangrove replaced the relatively bare mudflat, with a dense, mixed-species forest, capable of storing large quantities of carbon. Saintilan and others (2014) estimated that 30% of saltmarsh was lost to mangrove encroachment in Southeast Australia. Kelleway and others (2016a, b) estimated that below-ground carbon stocks increased at 2.3 Mg C ha^{-1} y^{-1} as mangroves colo-

nised salt marsh habitats, which was extrapolated to a total below-ground carbon stock of 7155 Mg C y^{-1} along the coastline of New South Wales, approximating an overall increase of 500 864 Mg C over 70 years. Our estimated rate of below-ground carbon stock change in the mangrove encroachment zone annualized over 30 years from the data in Figure 7 found additional root addition above the 1989 horizon to be similar (2.3 Mg C ha^{-1} y^{-1}). However, to this can be added additional root material below the 1989 horizon (5.3 Mg C ha^{-1} y^{-1}), and additional above-ground biomass (0.56 Mg C ha^{-1} y^{-1}). Following Kelleway and others (2016a, b), this was extrapolated to the entire region of mangrove encroachment forests in New South Wales. We refine this estimate and suggest that encroachment has contributed increases of about 1.8 Tg C over the 70 years for which mangrove encroachment has been observed in the state, not including the substantial increase in above-ground carbon stocks. These estimates do not include the contribution of above-ground biomass change, or the effect of lateral export of dissolved inorganic carbon, which may represent a substantial additional carbon sink (Maher and others 2018).

Over the 30 years of observation, root production has provided an important subsidy to the elevation of the marsh in relation to sea level. Regional tide gauges have recorded an increase of about 3 mm y^{-1} since the early 1990s (White and others 2014), or a rise of approximately 8 cm between surveys. The rate of accretion in the encroachment zone (13 cm as indicated by our ^{210}Pb dating) is several times larger than in saltmarshes growing at comparable positions in the tidal frame across the region (Rogers and others 2006). The addition of root mass by colonising mangrove appears to be making an important contribution to the increase in elevation of the marsh. Of the total bulk soil accumulation over the past 30 years, estimated to be 1110 ± 156 Mg ha^{-1} in the tall forest, and 753 ± 168 Mg ha^{-1} in the encroachment zone, mangrove root material contributed more than half by weight, with additions of root material at depth likely offsetting subsidence.

This elevation subsidy provided by mangrove root productivity has been noted in scrub mangrove settings in Florida (Castaneda-Moya and others 2011) and the Caribbean (McKee and others 2007). Root accumulation in scrub mangroves, typical of mangrove encroachment zones, is potentially aided by slow decomposition rates in lower nutrient environments (Cormier and others 2015), and soil water conditions encouraging higher root density (Reef and others 2015). Elevated atmospheric CO_2 may also increase the proportional allocation of carbon to root systems (Nie and others 2013). The pattern of mangrove expansion into saltmarsh documented across five continents (Saintilan and others 2014) is therefore likely to promote both carbon sequestration and adaptation to sea-level rise.

ACKNOWLEDGEMENTS

We thank Jennifer Van Holsten and Sabika Maizma at the Australian Nuclear Science and Technology Organisation (ANSTO) for their assistance with the radiometric analysis. Nicole Cormier made valuable comments on an earlier draft of the manuscript. The analysis was funded by an ANSTO research grant and AINSE Honours award to KL. Figure 8 incorporates content from Christine Thurbur IAN Image Library (ian.umces.edu), used with permission.

REFERENCES

Adame MF, Cherian S, Reef R, Stewart-Koster B. 2017. Mangrove root biomass and the uncertainty of below-ground carbon estimations. For Ecol Manag 403:52–60.

Alongi DM. 2008. Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. Estuar Coast Shelf Sci 76:1–13.

Appleby P, Oldfield F. 1978. The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210 Pb to the sediment. Catena 5:1–8.

Atahan P, Heijnis H, Dodson J, Grice K, Le Metayer P, Taffs K, Hembrow S, Woltering M, Zawadzki A. 2015. Pollen, biomarker and stable isotope evidence of late Quaternary environmental change at Lake McKenzie, southeast Queensland. J Paleolimnol 53:139–56.

Bouillon S, Borges AV, Castañeda-Moya E, Diele K, Dittmar T, Duke NC, Kristensen E, Lee SY, Marchand C, Middelburg JJ, Rivera-Monroy VH, Smith TJ, Twilley RR. 2008. Mangrove production and carbon sinks: A revision of global budget estimates. Global Biogeochemical Cycles 22:1–12.

Bulmer RH, Schwendenmann L, Lundquist CJ. 2016. Carbon and nitrogen stocks and below-ground allometry in temperate mangroves. Frontiers in Marine Science 3:150.

Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W, Feller IC. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proceedings of the National Academy of Sciences 111:723–7.

Chmura GL. 2013. What do we need to assess the sustainability of the tidal salt marsh carbon sink? Ocean and Coastal Management 83:25–31.

Cormier N, Twilley RR, Ewel KC, Krauss KW. 2015. Fine root productivity varies along nitrogen and phosphorus gradients in high-rainfall mangrove forests of Micronesia. Hydrobiologia 750:69–87.

Crosby SC, Sax DF, Palmer ME, Booth HS, Deegan LA, Bertness MD, Leslie HM. 2016. Salt marsh persistence is threatened by predicted sea-level rise. Estuarine, Coastal and Shelf Science 181:93–9.

Doughty CL, Langley JA, Walker WS, Feller IC, Schaub R, Chapman SK. 2016. Mangrove range expansion rapidly increases coastal wetland carbon storage. Estuaries and Coasts 39:385–96.

Duarte CM, Middelburg JJ, Caraco N. 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2:1–8.

Eslami-Andargoli L, Dale PER, Sipe N, Chaseling J. 2009. Mangrove expansion and rainfall patterns in Moreton Bay, southeast Queensland, Australia. Estuarine, Coastal and Shelf Science 85:292–8.

Fink D, Hotchkis M, Hua Q, Jacobsen G, Smith AM, Zoppi U, Child D, Mifsud C, Van Der Gaast H, Williams A, Williams M. 2004. The ANTARES AMS facility at ANSTO. Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms 223–224:109–15.

Golley FB, Odum HT, Wilson RF. 1962. The structure and metabolism of a Puerto Rico red mangrove forest in May. Ecology 43:9–19.

Grimsditch G, Alder J, Nakamura T, Kenchington R, Tamelander J. 2013. The blue carbon special edition—introduction and overview. Ocean and Coastal Management 83:1–4.

Howard J, Hoyt S, Isensee K, Pidgeon E, Telszewski M. 2014. Coastal Blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrass meadows. Intergov. Oceanogr. Comm. UNESCO, Int. Union Conserv. Nature. Arlington, Virginia, USA.

Howe AJ, Rodríguez JF, Saco PM. 2009. Surface evolution and carbon sequestration in disturbed and undisturbed wetland soils of the Hunter estuary, southeast Australia. Estuarine Coastal and Shelf Science 84:75–83.

Hua Q, Jacobsen GE, Zoppi U, Lawson EM, Williams AA, Smith AM, McGann MJ. 2001. Progress in radiocarbon target preparation at the ANTARES AMS centre. Radiocarbon 43:275–82.

Kelleway JJ, Saintilan N, Macreadie PI, Ralph PJ. 2016a. Sedimentary factors are key predictors of carbon storage in SE Australian Saltmarshes. Ecosystems 19:865–80.

Kelleway JJ, Saintilan N, Macreadie PI, Skilbeck CG, Zawadzki A, Ralph PJ. 2016b. Seventy years of continuous encroachment substantially increases ''blue carbon'' capacity as mangroves replace intertidal salt marshes. Global Change Biology 22:1097–109.

Kelleway JJ, Cavanaugh K, Rogers K, Feller IC, Ens E, Doughty C, Saintilan N. 2017a. Review of the ecosystem service implications of mangrove encroachment into salt marshes. Global Change Biology 23:3967–83.

Kelleway JJ, Serrano O, Baldock J, Cannard T, Lavery P, Lovelock CE, Macreadie PI, Masqué P, Saintilan N, Steven AD. 2017b. Technical review of opportunities for including blue carbon in the Australian Government's Emissions Reduction Fund. Canberra, ACT: CSIRO.

Kelleway JJ, Mazumder D, Baldock JA, Saintilan N. 2018. Carbon isotope fractionation in the mangrove Avicennia marina has implications for food web and blue carbon research. Estuarine Coastal and Shelf Science 205:68–74.

Komiyama A, Ogino K, Aksornkoae S, Sabhasri S. 1987. Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. Journal of Tropical Ecology 3:97–108.

Kroeger KD, Crooks S, Moseman-Valtierra S, Tang J. 2017. Restoring tides to reduce methane emissions in impounded wetlands: a new and potent Blue Carbon climate change intervention. Scientific reports 7:11914.

Lang'at JKS, Kirui BKY, Skov MW, Kairo JG, Mencuccini M, Huxham M. 2013. Species mixing boosts root yield in mangrove trees. Oecologia 172:271–8.

Lovelock CE, Cahoon DR, Friess DA, Guntenspergen GR, Krauss KW, Reef R, Rogers K, Saunders ML, Sidik F, Swales A, Saintilan N, Thuyen LX, Triet T. 2015. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. Nature 526:559-U217.

Lunstrum A, Chen L. 2014. Soil carbon stocks and accumulation in young mangrove forests. Soil Biol. Biochem. 75:223–32.

Maher DT, Call M, Santos IR, Sanders CJ. 2018. Beyond burial: lateral exchange is a significant atmospheric carbon sink in mangrove forests. Biology Letters 14:20180200.

Marchand C. 2017. Soil carbon stocks and burial rates along a mangrove forest chronosequence (French Guiana). Forest Ecology and Management 384:92–9.

Marland G, McCarl BA, Schneider UWE. 2001. Soil carbon: policy and economics. Climate Change 51:101–17.

McKee KL. 2001. Root proliferation in decaying roots and old root channels: a nutrient conservation mechanism in oligotrophic mangrove forests? Journal of Ecology: 876–887.

McKee KL, Cahoon DR, Feller IC. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Global Ecology and Biogeography 16:545–56.

Mcleod E, Chmura GL, Bouillon S, Salm R, Björk M, Duarte CM, Lovelock CE, Schlesinger WH, Silliman BR. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Frontiers in Ecology and the Environment 9:552–60.

Nie M, Lu M, Bell J, Raut S, Pendall E. 2013. Altered root traits due to elevated CO2: a meta-analysis. Global Ecology and Biogeography 22:1095–105.

Osland MJ, Spivak AC, Nestlerode JA, Lessmann JM, Almario AE, Heitmuller PT, Russell MJ, Krauss KW, Alvarez F, Dantin DD, Harvey JE, From AS, Cormier N, Stagg CL. 2012. Ecosystem development after mangrove wetland creation: plant-soil change across a 20-year chronosequence. Ecosystems 15:848–66.

Owers CJ, Rogers K, Woodroffe CD. 2018. Spatial variation of above-ground carbon storage in temperate coastal wetlands Estuarine. Coastal and Shelf Science 210:55–67.

Pethick JS. 1981. Long-term accretion rates on tidal salt marshes. Journal of Sedimentary Research 51:571–7.

Reef R, Winter K, Morales J, Adame M, Reef DL. 2015. The effect of atmospheric carbon dioxide concentrations on the performance of the mangrove Avicennia germinans over a range of salinities. Physiolgia Plantarum 154:358–68.

Rogers K, Boon PI, Branigan S, Duke NC, Field CD, Fitzsimons JA, Kirkman H, Mackenzie JR, Saintilan N. 2016. The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. Marine Policy 72:139–55.

Rogers K, Saintilan N, Mazumder D, Kelleway JJ. 2019. Vegetation Shift and Blue Carbon: an 18-year field measurement record of transition from saltmarsh to mangrove. Biological Letters 15(3):20180471.

Rogers K, Wilton KM, Saintilan N. 2006. Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. Estuarine, Coastal and Shelf Science 66:559–69.

Saintilan N. 1997. Above and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. Marine and Freshwater Research 48:147–52.

Saintilan N, Hashimoto TR. 1999. Mangrove-saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia. Hydrobiologia 413:95–102.

Saintilan N, Rogers K, Mazumder D, Woodroffe C. 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuarine Coastal and Shelf Science 128:84–92.

Saintilan N, Williams R. 1999. Mangrove transgression into saltmarsh environments in south-east Australia. Global Ecology and Biogeography 8:117–24.

Saintilan N, Wilton K. 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetlands Ecology and Management 9:409–20.

Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW. 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Global Change Biology 20:147–57.

Saintilan N, Rogers K, McKee KL. 2019. The shifting saltmarsh-mangrove ecotone in Australasia and the Americas. In *Coastal Wetlands* (pp. 915–945). Elsevier.

Salmo SGIII, Lovelock C, Duke NC. 2013. Vegetation and soil characteristics as indicators of restoration trajectories in restored mangroves. Hydrobiologia 720:1–18.

Schlacher TA, Connolly RM. 2014. Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: a review and synthesis. Methods in Ecology and Evolution 5:541–50.

Serrano O, Lovelock C, Atwood T, Macreadie P, Canto R, Phinn S, Arias-Ortiz A, Bai L, Baldock J, Bedulli C, Carnell P, Connolly R, Donaldson P, Esteban A, Ewers CJ, Eyre BD, Hayes M, Horwitz P, Hutley L, Kavazos C, Kelleway JJ, Kendrick GA, Kilminster K, Lafratta A, Lee J, Lavery PS, Maher D, Marbà N, Masque P, Mateo MA, Mount R, Ralph PJ, Roelfsema C, Rozaimi M, Ruhon R, Salinas C, Samper-Villarreal J, Sanderman J, Sanders C, Santos I, Sharples C, Steven A, Trevathan-Tackett SM, Duarte CM, In Prep. The potential of Australian blue carbon ecosystems for climate change mitigation.

Tamooh F, Huxham M, Karachi M, Mencuccini M, Kairo JG, Kirui B. 2008. Below-ground root yield and distribution in natural and replanted mangrove forests at Gazi bay, Kenya. Forest Ecology and Management 256:1290–7.

Thomas S. 2014. Blue carbon: knowledge gaps, critical issues, and novel approaches. Ecological Economics 107:22–38.

Walcker R, Gandois L, Proisy C, Corenblit D, Christophe M, Raghab L, Franc R. 2018. Control of ''blue carbon'' storage by mangrove ageing: evidence from a 66-year chronosequence in French Guiana. Global Change Biology 24:2325–38.

White NJ, Haigh ID, Church JA, Koen T, Watson CS, Pritchard TR, Watson PJ, Burgette RH, McInnes KL, You ZJ, Zhang X. 2014. Australian sea levels—trends, regional variability and influencing factors. Earth-Science Reviews 136:155–74.

Yando ES, Osland MJ, Willis JM, Day RH, Krauss KW, Hester MW. 2016. Salt marsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. Journal of Ecology 104:1020–31.

Estuarine, Coastal and Shelf Science 128 (2013) 84–92

Contents lists available at SciVerse ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands

N. Saintilan [a,*], K. Rogers [b], D. Mazumder [c], C. Woodroffe [b]

[a] Science Division, NSW Office of Environment and Heritage, PO Box A290, Sydney South, NSW 1232, Australia
[b] School of Earth and Environmental Science, University of Wollongong, Australia
[c] Australian Nuclear Science and Technology Organisation (ANSTO), Australia

ARTICLE INFO

Article history:
Received 15 February 2013
Accepted 11 May 2013
Available online 21 May 2013

Keywords:
carbon sequestration
mangrove
saltmarsh
stable isotope
geomorphology
in-situ
tidal

ABSTRACT

Estimates of carbon store and carbon accumulation rate in mangrove and saltmarsh are beset by issues of scale and provenance. Estimates at a site do not allow scaling to regional estimates if the drivers of variability are not known. Also, carbon accumulation within soils provides a net offset only if carbon is derived in-situ, or would not otherwise be sequestered. We use a network of observation sites extending across 2000 km of southeastern Australian coastline to determine the influence of geomorphic setting and coastal wetland vegetation type on rates of carbon accumulation, carbon store and probable sources. Carbon accumulation above feldspar marker horizons over a 10-year period was driven primarily by tidal range and position in the tidal frame, and was higher for mangrove and saltmarsh dominated by *Juncus kraussii* than for other saltmarsh communities. The rate of carbon loss with depth varied between geomorphic settings and was the primary determinant of carbon store. A down-core enrichment in $\delta^{13}C$ was consistent with an increased relative contribution of mangrove root material to soil carbon, as mangrove roots were found to be consistently enriched compared to leaves. We conclude that while surface carbon accumulation is driven primarily by tidal transport of allocthonous sediment, in-situ carbon sequestration is the dominant source of recalcitrant carbon, and that mangrove and saltmarsh carbon accumulation and store is high in temperate settings, particularly in mesotidal and fluvial geomorphic settings.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Mangrove and saltmarsh are among the most efficient ecosystems in the world at sequestering carbon (Pidgeon, 2009; Donato et al., 2011), a capacity that places these wetlands at the forefront of scientific and policy interest. This is because methane emissions are dramatically reduced in environments where methanogenic bacteria are inhibited by salt (Poffenbarger et al., 2011), and because the biogeochemical conditions in tidal wetlands are conducive to long-term carbon retention (DeLaune et al., 1990; Choi and Wang, 2004). Reviews by Duarte et al. (2005) and Bouillon et al. (2008) report a mean organic carbon burial rate of 1.51 Mg ha y^{-1} for saltmarsh (maximum 17.2 Mg ha y^{-1}) and 1.39 Mg ha y^{-1} for mangrove (maximum 6.54 Mg ha y^{-1}), exceeding by 10 and 6 times respectively the maximum burial rate of undisturbed Amazonian forest (1.02 Mg ha y^{-1}) (Grace et al., 1993; Nellemann et al., 2009).

Considerable progress has been made in developing standard methodologies for carbon benefits associated with terrestrial forests. Programs and incentives under the REDD + framework (Reduced Emission from Deforestation and Degradation) provide a mechanism for compensating countries for the avoidance of carbon losses to the atmosphere resulting from deforestation and degradation (Anglesen, 2009). However, REDD + has not to date been extended to coastal wetlands, even though the carbon store of coastal mangrove and saltmarshes are potentially large, and their rate of decline in extent at a global scale has been rapid in modern times. Improved estimates of coastal mangrove and saltmarsh carbon stores and fluxes are required to meet obligations to monitor, report and verify sequestration needed for carbon financing programs such as REDD+ and emission trading schemes (Alongi, 2011).

The inclusion of coastal wetlands in carbon accounting, trading and incentive schemes will be contingent upon improved estimates of the carbon store and rates of flux in coastal wetlands, and an

* Corresponding author.
E-mail address: neil.saintilan@environment.nsw.gov.au (N. Saintilan).

0272-7714/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.ecss.2013.05.010

improved understanding of drivers of variability in carbon sequestration potential. There are *a priori* reasons for supposing mangrove and saltmarsh below-ground biomass and carbon stores vary between geomorphic and geographic settings, given differences in productivity forced by temperature and nutrient levels (Saenger et al., 1993). For example, Chmura et al. (2003) compiled data on mangrove and saltmarsh carbon accumulation rates for 154 sites, predominantly in North America, but including some Oceanic, Indian, and European locations. They found evidence that soil carbon density declines with increasing air temperature for *Spartina*, but otherwise variation in sequestration rate was associated with variability in sedimentation rates.

Understanding factors relating to variation in sequestration rates at regional scales will be important for national carbon accounting, as well as targeting the application of incentive and wetland restoration schemes. Coastal wetlands of southeast Australia provide a natural testing ground to investigate drivers of variability as they occupy a range of geomorphic types and span subtropical to cool temperate climates. Mangrove and saltmarsh co-exist across the entire region, with mangroves generally occupying the lower, more frequently inundated position within the tidal prism. Prior studies in the region indicate that the estuaries of Westernport Bay (Livesley and Andrusiak, 2012) and Hunter River (Howe et al., 2009) both show higher carbon store in saltmarsh than mangrove. Howe et al. (2009) used feldspar marker horizons to estimate the rate of carbon accumulation in the Hunter intertidal wetlands, with estimates low by global standards, though higher in a restoration site compared to an undisturbed site.

Howe et al. (2009) proposed a carbon store for coastal wetlands of 3900–5600 GgC for New South Wales. However, there are three important caveats in accepting this estimate. First, the estimate of soil carbon store was based on sampling of the upper 20 cm of soil, which may be insufficient to account for losses of carbon down profile encountered in other studies (Wang et al., 2011; Livesley and Andrusiak, 2012). Second, it is unclear whether the accumulation rates derived from feldspar horizons, as described by Howe et al. (2009) and Chmura et al. (2003), consist of allochthonous or autochthonous carbon, a potentially important consideration in the context of carbon emission offsets. Third, the estimate does not incorporate potential variability between geomorphic and habitat settings encountered across the region.

In this study we assess carbon sequestration for mangrove and saltmarsh where they co-exist across 2000 km of coastline in southeastern Australia, incorporating measures from a greater range of vegetation communities and geomorphic settings than any previously published account. Geomorphic setting integrates a range of geochemical conditions relevant to growth of vegetation and carbon accumulation and efflux, as well as geomorphic history as an influence on down-core changes in carbon density and source, while vegetation community composition is an important potential driver of carbon accumulation. Our aim is to determine the relative importance of vegetation communities, frequency of inundation, tidal range and temperature in forecasting carbon store in the upper metre of sediment and surficial carbon sequestration rates for mangrove and saltmarsh at regional scales.

We also seek to identify, through field studies and isotopic analysis, the likely sources of carbon being accumulated, specifically, whether it is autochthonous or allocthonous, as this is an important consideration in carbon sequestration benefit of restored or protected wetlands. Stable isotopes have been used to clarify the sources of carbon, utilising differences in isotopic composition of C_3 and C_4 plants, and aquatic submerged plants (seagrasses) that derive carbon from the water column. Studies in forest and coastal wetland systems have noted down-core enrichment in the heavier isotope (Garten et al., 2007). In terrestrial studies this has been associated with the loss of carbon resulting from microbial activity and decomposition, and hence providing a potential indicator of the rate of decay of organic carbon and the depth at which carbon store is stable (Ehleringer et al., 2000; Garten, 2006). However, previous studies in coastal wetlands have emphasised the importance of vegetation change in interpreting down-core $\delta^{13}C$ (Choi et al., 2001; Wang et al., 2011) with $\delta^{13}C$ enrichment associated with communities dominated by C_4 photosynthesising plants.

Our study samples carbon accumulation and below-ground carbon store across a range of geomorphic settings and vegetated habitats in southeastern Australia. We test the following hypotheses:

- the rate of surface carbon accumulation is related to vegetation type and geomorphic setting; specifically that where mangrove and saltmarsh will show consistent differences in the rate of carbon accumulation. We use a 10-year record of surface accumulation across 10 sites to test this hypothesis.
- carbon store, as defined by carbon density in the upper metre of sediment, varies predictably between habitat types and geomorphic settings, with higher store in mangrove than saltmarsh.
- carbon density decreases down-core, reflecting the loss of carbon from the profile over time.
- changes in carbon isotope ratios within the core are consistent with carbon derived primarily from local plant material.

2. Methods

2.1. Study sites

The estuaries of southeastern Australia, in particular, have been described by Roy (1984), who recognised three types: drowned river valleys; barrier estuaries; and saline coastal lakes, which have more recently been termed: tide-dominated; wave-dominated; and intermittently closed (Roy et al., 2001). The classification, and subsequent conceptual models of ecological functioning and geomorphic development of these systems, was based on a detailed program of coring and radiometric dating which enabled the identification of successive evolutionary stages.

The larger wave-dominated estuaries can be broadly divided into three zones (Dalrymple et al., 1992). The size and shape of the features in each of the three zones is controlled by the form of the paleo-valley and the degree to which the estuary has infilled. The head of the estuary is characterised by a fluvial, or bay-head, delta in which the river (or creek) channel is flanked by a floodplain and may contain channel bars. The fluvial delta is built from alluvial sediment and protrudes into the estuary, developing a birds-foot, lobate or cuspate morphology depending on the relative magnitude of wave and tidal processes at this landward margin of the central basin. The central regions of the estuary form a mud basin, comprising a low-energy environment where silt and clay transported from the land accumulates. This central basin fills in progressively and may be fringed by subtidal to intertidal deposits with mangroves and saltmarshes. The mouth of a barrier estuary comprises a sand barrier which separates the estuary from the open ocean. This generally contains a sandy barrier/spit, beach ridges, and an entrance channel with ebb and/or flood tidal deltas, which protrude seaward or landward of the inlet, respectively. These environments are typically comprised of sandy sediments, derived from the nearshore, because of the relatively high wave energy at the mouth and tide energy in the inlet, and contrast with the more lithic, less angular sands that are delivered from the catchment by the river.

Individual estuaries progress through successive stages of infill, from open basins, to shallower waterways with cut-off embayments and fringing coastal wetlands, to largely infilled floodplains, termed mature riverine estuaries by Roy et al. (2001). At this final stage, the river is channelised and flows through the former estuarine reaches, generally between sandy levees to deliver fluvial sands directly to the nearshore, and mangroves and related wetlands are restricted to tributaries and incompletely filled cut-off embayments (Heap et al., 2004). Estuary type and phase of infill places important controls on estuarine hydrology which in turn influences a range of soil chemical properties relevant to the distribution of wetland species and their growth, most notably soil water content, nutrient status and salinity (Saintilan, 1998; Roy et al., 2001).

The sites chosen for an assessment of rates of carbon accumulation are distributed from the southern limit of mangrove distribution in Australia (Westernport Bay, Victoria), to the Tweed River on the NSW/Queensland border (Fig. 1, Table 1). Geomorphic settings sampled included a coastal embayment (Westernport Bay) with approximately 3 m maximum tidal range; drowned river valleys (Parramatta River, Hawkesbury River) with approximately 2 m maximum tidal range; barrier estuaries with full tidal exchange (Hunter River, Tweed River) and tidal range of approximately 2 m; and barrier estuaries with restricted tidal exchange (Cararma Inlet, Currambene Creek, Minnamurra estuary), and microtidal range.

We sampled within the dominant intertidal vegetation communities at each location. For the purposes of this study we defined three vegetation communities common across settings, these being mangrove, saltmarsh rushes dominated by *Juncus kraussii*, and saltmarsh herbfields dominated by *Sporobolus virginicus* and *Sarcocornia quinqueflora*.

2.2. Field sampling methods: sediment accumulation carbon store and carbon source

Feldspar marker horizons were installed in 0.25 m^2 plots at nine replicate locations within each vegetation community surveyed at each site (46 locations, 414 plots). We installed the feldspar marker horizons in 2000–2001 and followed the rate of sediment accumulation for 10 years, by periodically extracting small shallow cores from each plot, and measuring accretion above the feldspar layer using a ruler (following techniques of Cahoon et al., 2002). As some marker horizons dispersed due to bioturbation, results were pooled to establish accretion trajectories and identify rates of vertical accretion for each vegetation community at each site.

Three larger surface cores (0.2 m) were extracted from the vicinity of the feldspar plots, and used for the measurement of carbon density in support of the surface carbon accumulation estimates. Data from Livesley and Andrusiak (2012) were used for this purpose in Westernport Bay. In addition, deep (1.0 m) core samples were collected in replicates of three from mangrove and saltmarsh at a subset of sites covering the contrasting geomorphic settings of fluvial muds and marine sands: the Hunter River; Hawkesbury River (Berowra Creek and Marramarra Creek); and Jervis Bay (Currambene Creek and Cararma Inlet) (i.e., 5 sites, 10 locations, 3 cores per location: Fig. 2). Cores were sectioned in the field at depths of 0–10 cm, 20–30 cm, 50–60 cm and 80–90 cm. Sections were capped and frozen until further analysis. In preparation for laboratory analysis of samples, core samples were carefully removed from tubes; they were then defrosted and free water was allowed to drain away over a 12 hour period. Core length and wet sample weight was recorded.

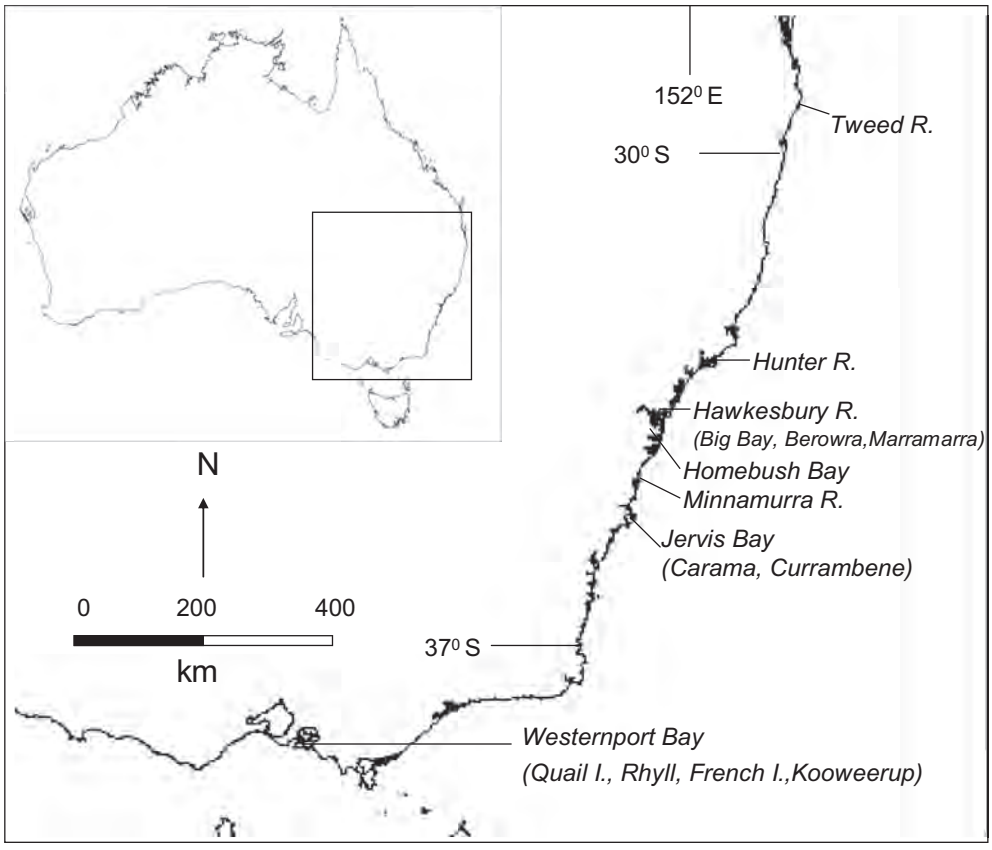


Fig. 1. Location of estuaries within which sampling sites were established.

Table 1
Characteristics of study sites (See Fig. 1 for location).

Site	Geomorphic setting	Dominant mangrove	Dominant saltmarsh	Feldspar horizons	SOM sample depth
Ukerebagh Island, Tweed River	Marine Sand delta, saline	*Rhizophora stylosa*, *Avicennia marina*	*Sporobolus virginicus*	Mangrove 9 Saltmarsh 9	0.2 m
Kooragang Island (Hunter River)	Fluvial silt delta, brackish to saline	*Avicennia marina*	*Sporobolus virginicus*	Mangrove 9 Saltmarsh 9	1.0 m
Berowra Creek, Hawkesbury River	Tributary fluvial deltaic silts, brackish	*Avicennia marina*	*Juncus kraussii*	Mangrove 9 Saltmarsh 9	1.0 m
MarraMarra Ck, Hawkesbury River	Tributary fluvial deltaic silts, brackish	*Avicennia marina*	*Juncus kraussii*	Mangrove 9 Saltmarsh 9	1.0 m
Big Bay, Hawkesbury River	Mud/silt basin, brackish	*Avicennia marina*	*Juncus kraussii*	Mangrove 9 Saltmarsh 9	0.2 m
Homebush Bay, Parramatta River	Restored Tributary delta, brackish/saline	*Avicennia marina*	*Sarcocornia quinqueflora*	Mangrove 9 Saltmarsh 9	0.2 m
Minnamurra estuary	Fluvial silt delta, brackish to saline	*Avicennia marina*	*Sarcocornia quinqueflora*	Mangrove 9 Saltmarsh 9	0.2 m
Currambene Creek, Jervis Bay	Marine sand delta, saline	*Avicennia marina*	*Sarcocornia quinqueflora* *Juncus kraussii*	Mangrove 9 Saltmarsh 9	1.0 m
Cararma Inlet, Jervis Bay	Marine sand delta, saline	*Avicennia marina*	*Sarcocornia quinqueflora*	Mangrove 9 Saltmarsh 9	1.0 m
Westernport Bay (4 locations)	Muddy estuarine embayment, saline	*Avicennia marina*	*Tecticornia* spp.	Mangrove 36 Saltmarsh 36	1.0 m[a]

[a] Values derived from Livesley and Andrusiak (2012).

To support interpretation of carbon isotope signatures, it was necessary to survey potential carbon sources. There are several published values of autotrophic carbon signatures for wetlands of the region (Saintilan et al., 2007; Saintilan and Mazumder, 2010), however, these did not include mangrove and saltmarsh root material, or provide an indication of variation in shoot and root $\delta^{13}C$ along salinity gradients and across geomorphic settings. The Hawkesbury estuary was used to survey variation in plant $\delta^{13}C$ because of the wide array of geomorphic settings of contrasting phyisco-chemical properties (Saintilan, 1997), ranging from muddy brackish riverine environments, to saline marine sand flats. Mangrove shoot and root material was sampled across this gradient at five sites, (Fig. 2), and *Juncus kraussii* where this occurred at one site. Saltmarsh plant shoot material was also sampled at the estuary mouth, including the C_4 grass *Sporobolus virginicus*, the C_3 rush *J. kraussii*, and the C_3 succulent *Sarcocornia quinqueflora.* Several studies have indicated an enrichment in $\delta^{13}C$ with decomposition, though evidence is equivocal (Garten et al., 2007). At Allens Creek we measured carbon isotopic composition of fresh and decomposing mangrove leaf, and fresh and ancient (1900 BP) mangrove root material (Fig. 2).

2.3. Laboratory techniques: bulk density, percent carbon and delta C

Plant samples collected for isotopic fingerprinting of potential source materials were thoroughly rinsed with Milli-Q water prior

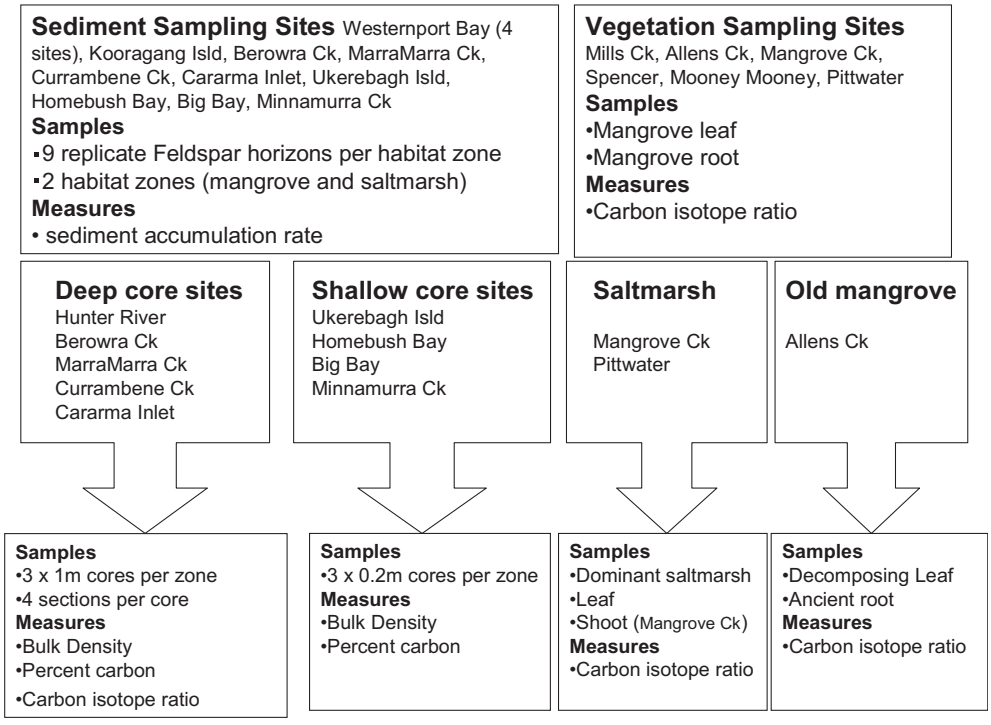


Fig. 2. Schematic of vegetation, sediment and core sampling strategy.

to processing. Leaves were cut from the plant and placed into labelled petri dishes ready for drying. Only leaf matter from each plant was used in each replica. Plant materials were oven dried at 60 °C for 72 h then ground to a fine powder with a Retsch three-dimensional Vibrator Mill (Type-MM-2:Haan, Germany) for stable isotope analysis. To determine soil bulk density, samples were oven dried to constant weight at 60 °C. Dry sample weight was determined and dry soil bulk density was estimated as the ratio between the dry sample weight (g) and the wet sample volume (cm^3).

Dried sediment samples were acidified by adding 0.1 N hydrochloric acid for an hour and then gently rinsed with Milli-Q water to remove acid remaining in sediments, dried to constant weight at 60 °C and ground to a fine powder with mortar and pestle for isotopic analysis (Mazumder et al., 2010). Isotopic analysis was done at the Australian Nuclear Science and Technology Organisation (ANSTO) in Sydney, Australia. Powdered and homogenised sediment and dried plant samples were loaded into tin capsules and analysed with a continuous flow isotope ratio mass spectrometer (CF-IRMS), model Delta V Plus (Thermo Scientific Corporation, USA) interfaced with an elemental analyser (Thermo Fisher Flash 2000 HT EA, Thermo Electron Corporation, USA). The data are reported relative to IAEA secondary standards that have been certified relative to VPDB for carbon. A two point calibration is employed to normalise the data, utilising standards that bracket the samples being analysed. Two quality control references were also included in each run. Results are accurate to 1% for C % and ±0.3 per mill for $\delta^{13}C$. Isotopic ratios for carbon, reported as $\delta^{13}C$, were calculated as:

$$\delta^{13}C = \delta R_{\mathrm{P/reference}} = \frac{R_p - R_{\mathrm{reference}}}{R_{\mathrm{reference}}}$$

where $R = {}^{\circ}/_{\circ}$

2.4. Statistical methods

Generalised linear models provide an integrated approach to statistical analysis for data sets that may not meet the assumptions required for classical linear models, such as normal distribution (Lindsey, 1997). The technique developed by Nelder and Wedderburn (1972), enables analysis of data from a range of distributions (normal, binomial, Poisson and gamma) that are transformed to linear distribution by a link function.

Preliminary analyses were employed to identify appropriate model distributions and link functions (Table 2). Generalised linear models were employed to establish relationships between:

1. rates of vertical accretion measured derived from feldspar marker horizons, vegetation type (mangrove and saltmarsh) and tidal range at study sites
2. carbon store, vegetation community types (mangrove, *Sporobolus/Sarcocornia* saltmarsh, and *Juncus* saltmarsh), and geomorphic settings (fluvial or marine) at study sites
3. shoot and root $\delta^{13}C$ at the five Hawkesbury sites
4. soil carbon concentration, carbon bulk density and $\delta^{13}C$, soil depth and vegetation type (mangrove and saltmarsh) at study sites

3. Results

3.1. Sediment accumulation

The major driver of accretion was found to be vegetation type ($p < 0.0001$), tidal range and the position of the flat in the tidal range ($p = 0.0005$), though there was a significant interaction effect between tide influences and vegetation ($p = 0.0499$, Table 2: Model a). Sedimentation rate was higher for mangrove than saltmarsh corresponding to their differing positions in the tidal range. The rate of surface sediment accumulation was higher in *Juncus* (1.76 (±1.0) mm y^{-1}) than in the *Sarcocornia/Sporobolus* association (1.11 (±0.08) mm y^{-1}). No latitudinal trends were apparent in carbon density for either mangrove or saltmarsh, although the estimates for the southernmost site, Westernport Bay, were the lowest recorded in both communities.

3.2. Variation in carbon and delta carbon within and between cores

The amount of carbon stored within soils (Mg ha^{-1}) varied across three vegetation categories (mangrove > *Juncus* saltmarsh > *Sarcocornia/Sporobolus* saltmarsh; $p < 0.0001$) and geomorphic setting (fluvial > marine) though the relationship was weak ($p = 0.0699$, Table 2: Model b). There was no carbon store interaction effect between vegetation communities and geomorphology ($p = 0.8186$, Table 2: Model b). Post hoc analyses indicated significant differences between *Sarcocornia/Sporobolus* saltmarsh carbon store and mangrove carbon store ($p = 0.0027$), and *Juncus* saltmarsh carbon store ($p = 0.0060$).

Table 2
Results from generalised linear model analyses.

Model	Variables			GLM model			Significance		
	Dependent variable	Effect variable 1	Effect variable 2	Distribution	Link function	Whole model	Effect 1	Effect 2	Interaction
a	Vertical accretion	Vegetation (mangrove, saltmarsh)	Tidal range	Normal	Identity	**$p < 0.0001$**	**$p < 0.0001$**	**$p = 0.0005$**	**$p = 0.0499$**
b	Carbon store	Vegetation (mangrove, saltmarsh, rushes)	Geomorphic setting (fluvial, marine)	Normal	Identity	**$p = 0.0002$**	**$p < 0.0001$**	$p = 0.0699$	$p = 0.8186$
c	$\delta^{13}C$	Soil depth (0–10 cm, 20–30 cm, 50–60 cm, 80–90 cm)	Vegetation type (mangrove, saltmarsh)	Normal	Identity	$p = 0.1379$	**$p = 0.0197$**	$p = 0.7594$	$p = 0.9587$
d	$\delta^{13}C$	Soil depth (0–10 cm, 20–30 cm, 50–60 cm, 80–90 cm)	Geomorphic setting (fluvial, marine)	Normal	Identity	**$p < 0.0001$**	**$p = 0.0014$**	**$p < 0.0001$**	**$p = 0.0733$**
e	% Carbon	Soil depth (0–10 cm, 20–30 cm, 50–60 cm, 80–90 cm)	Vegetation type (mangrove, saltmarsh)	Exponential	Reciprocal	**$p = 0.0066$**	**$p = 0.0005$**	$p = 0.9960$	$p = 0.8716$
f	Carbon bulk density	Soil depth (0–10 cm, 20–30 cm, 50–60 cm, 80–90 cm)	Vegetation type (mangrove, saltmarsh)	Normal	Identity	$p = 0.0625$	**$p = 0.0121$**	$p = 0.7852$	$p = 0.2973$
g	$\delta^{13}C$	Source of carbon (Avicennia root, leaf)	Study site (Allens Creek, Monemone, Pittwater, Spencer)	Normal	Identity	**$p < 0.0001$**	**$p < 0.0001$**	$p = 0.1518$	**$p = 0.0002$**

Bold values are statistically significant at $p = 0.05$.

Soil $\delta^{13}C$ becomes progressively enriched with depth ($p = 0.0197$, Table 2: Model c). The extent of enrichment appears to interact with sites ($p = 0.0002$, Table 2: Model d), being highest in sandy marine settings (Fig. 3). $\delta^{13}C$ is inversely correlated with percent carbon at all sites, with the exception of the Berowra Creek saltmarsh. Both percent carbon ($p = 0.0005$, Table 2: Model e) and carbon bulk density ($p = 0.0121$, Table 2: Model f) decreased with depth and vegetation type had little effect on this relationship. Analyses indicated that consistent down-core enrichment in $\delta^{13}C$ (mean $1.6 \pm 1.6‰$) corresponds to a loss of carbon (Table 3).

3.3. Carbon isotope ratios of source materials

Carbon isotope signatures divided autotrophs into two groups; relatively depleted woody plants and relatively enriched grasses. Emergent C_3 woody plants occupying the mangrove and saltmarsh $\delta^{13}C$ were depleted: *Sacrocornia quinqueflora* ($-26.25 \pm 0.6‰$); *Juncus kraussii* (shoot: $-27.03 \pm 1.8‰$), *Aegiceras corniculatum* ($-26.74 \pm 1.7‰$) and *Avicennia marina* ($-27.63 \pm 0.7‰$). The C_4 grass *Sporobolus virginicus* was relatively enriched ($-15.36 \pm 1.4‰$), as was the seagrass *Zostera capricorni* ($-12.54 \pm 0.4‰$), which, though C_3, derived its carbon from the water column.

The grey mangrove *Avicennia marina* is the dominant plant in the region by above-ground biomass, and average leaf longevity is little more than a year (Duke, 1990). Litter fall from *A. marina* therefore represents an important potential carbon source. No difference was found in carbon isotopic composition between fresh ($\delta^{13}C$: $-27.63 \pm 0.7‰$) and decomposing leaves ($\delta^{13}C$: $-26.21 \pm 1.8‰$).

A significant difference was found in $\delta^{13}C$ between *Avicennia marina* root and shoot samples across five sites of contrasting physico-chemical characteristics on the Hawkesbury River ($p < 0.0001$ Table 2: Model g). $\delta^{13}C$ in *A. marina* root and shoot samples did not vary between the five study sites ($p = 0.1518$), but there was a significant interaction found in $\delta^{13}C$ in *A. marina* root or shoot samples and study sites ($p = 0.0002$); this was caused by the greater difference between root and shoot $\delta^{13}C$ in the downstream Pittwater site (Table 2: Model g). No difference was found in carbon isotopic composition between fresh roots ($\delta^{13}C$: $-24.4 \pm 0.157‰$) and roots dating to 1700 BP ($\delta^{13}C$: $-24.6‰$) at the Allens Creek site. No difference was detected between shoot and root $\delta^{13}C$ for *Juncus kraussii*, the only saltmarsh species in the region forming extensive root systems (shoot $\delta^{13}C$: $-27.03 \pm 1.8‰$; root $-26.05 \pm 0.4‰$: Table 4).

4. Discussion

4.1. Variation in surface carbon accumulation rates between settings

Surface carbon accumulation rate is a function of sedimentation rate and the density of carbon within the sediment. Mangrove and *Juncus* saltmarsh showed a similar rate of carbon accumulation above feldspar horizons over a 10-year period and rates comparable to estimates globally (Table 5). Rates of carbon accumulation within the *Sporobolus/Sarcocornia* saltmarsh association were lower than the other communities sampled, and in some cases appreciably lower. This may be associated with two factors. First, the position of the saltmarsh in the upper intertidal zone receives a lower frequency, depth and duration of inundation than the lower intertidal zone occupied by mangrove. This limits the vertical accretion rate, in common with observations elsewhere (Alongi, 2009; Krauss et al., 2010; Sanders et al., 2010) and for this reason the results should not be extrapolated to sites where saltmarsh grows lower in the intertidal range. The position of saltmarsh in the tidal range explains the differences between these estimates and estimates from northern hemisphere studies cited in Chmura et al. (2003). Secondly, the productivity and biomass of the vegetation is

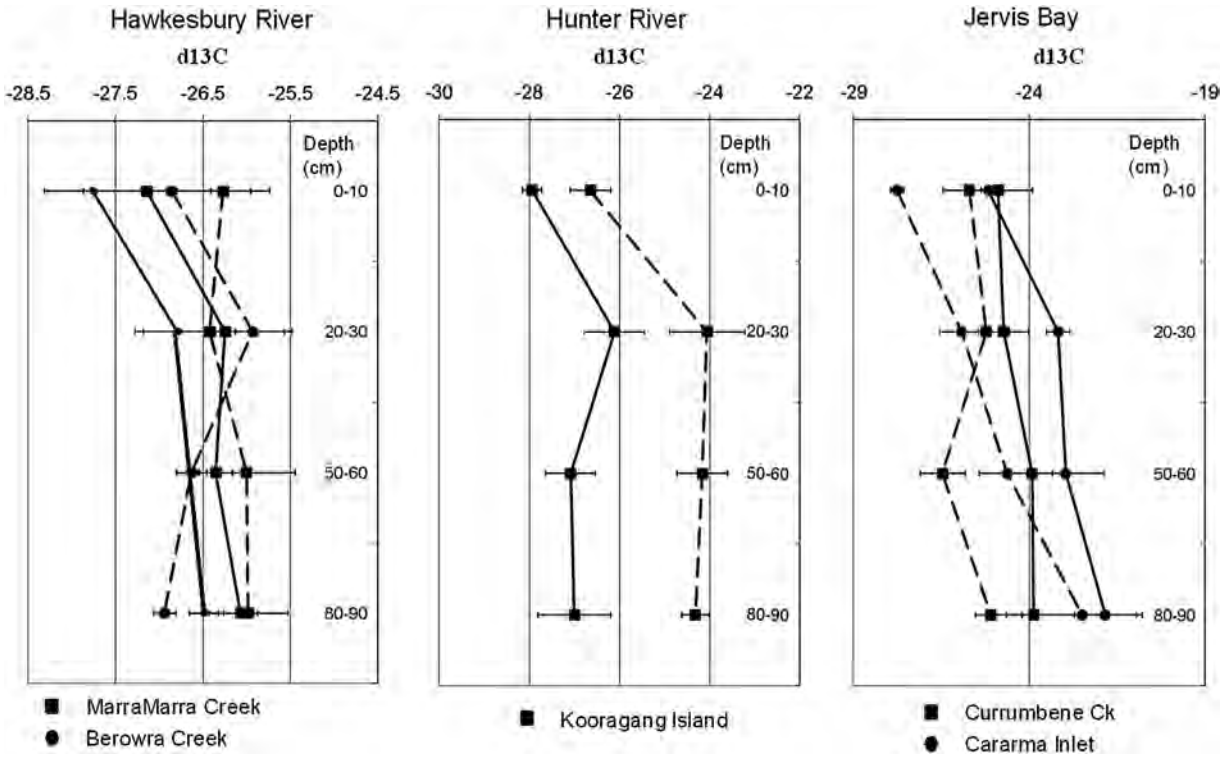


Fig. 3. Changes in $\delta^{13}C$ with depth in sediment cores extracted from mangrove (solid line) and saltmarsh (dashed line).

Table 3
Soil percentage carbon, carbon density and carbon store. Mean and standard deviation (SD).

Location	Saltmarsh						Mangrove					
Variable	Content		C Density		$\delta^{13}C$		Content		C Density		$\delta^{13}C$	
Depth	%C	SD	g cm^{-3}	SD	‰	SD	%C	SD	g cm^{-3}	SD	‰	SD
MarraMarra												
0–10 cm	12.7	3.1	0.03	0.02	−26.3	0.5	10.0	2.0	0.031	0.002	−27.1	0.7
20–30 cm	11.3	2.5	0.032	0.004	−26.4	0.9	8.1	0.8	0.037	0.007	−26.2	0.1
50–60 cm	9.0	3.7	0.035	0.004	−26.0	0.6	6.4	3.4	0.042	0.015	−26.4	0.2
80–90 cm	8.6	2.5	0.035	0.007	−26.0	0.5	4.3	3.9	0.026	0.017	−26.1	0.2
0–100 cm	Carbon store (Mg ha^{-1}) 343 ± 44						Carbon store (Mg ha^{-1}) 343 ± 110					
Berowra Creek												
0–10 cm	13.9	3.8	0.026	0.004	−26.9	0.9	13.7	5.4	0.027	0.006	−27.7	0.6
20–30 cm	10.3	2.2	0.030	0.008	−25.9	0.5	10.1	1.1	0.030	0.004	−26.8	0.4
50–60 cm	12.0	1.0	0.036	0.005	−26.6	0.2	n.d.		n.d.		n.d.	
80–90 cm	8.1	0.7	0.029	0.001	−26.9	0.1	3.3	1.2	0.028	0.015	−26.5	0.2
0–100 cm	Carbon store (Mg ha^{-1}) 311 ± 31						Carbon store (Mg ha^{-1}) 285 ± 74					
Kooragang Island												
0–10 cm	23.5	5.4	0.031	0.001	−26.6	0.5	21.7	0.1	0.034	0.006	−27.9	0.2
20–30 cm	4.4	1.4	0.034	0.006	−24.1	0.8	6.3	2.1	0.029	0.005	−26.1	0.7
50–60 cm	0.7	0.1	0.007	0.024	−24.2	0.6	5.8	1.0	0.024	0.008	−27.1	0.6
80–90 cm	0.3	0.1	0.003	0.001	−24.3	0.3	5.1	0.9	0.024	0.001	−27.0	0.8
0–100 cm	Carbon store (Mg ha^{-1}) 130 ± 27						Carbon store (Mg ha^{-1}) 261 ± 35					
Cararma Inlet												
0–10 cm	24.3	5.7	0.037	0.005	−27.7	0.2	22.3	6.6	0.036	0.015	−25.2	0.2
20–30 cm	0.5	0.2	0.006	0.002	−25.9	0.6	17.6	7.2	0.040	0.016	−23.2	0.3
50–60 cm	0.8	0.6	0.010	0.007	−24.6	0.8	7.5	10.5	0.018	0.012	−23.0	1.1
80–90 cm	0.6	0.2	0.008	0.001	−22.5	1.7	1.9	2.1	0.018	0.018	−21.8	0.8
0–100 cm	Carbon store (Mg ha^{-1}) 110 ± 26						Carbon store (Mg ha^{-1}) 241 ± 143					
Currambene Creek												
0–10 cm	13.4	7.0	0.042	0.010	−25.7	0.8	1.4	0.3	0.011	0.003	−24.9	1.0
20–30 cm	11.9	7.0	0.049	0.014	−25.2	0.7	1.9	0.6	0.013	0.003	−24.7	0.7
50–60 cm	1.8	0.6	0.013	0.002	−26.5	0.6	2.7	0.01	0.018	0.003	−23.9	0.6
80–90 cm	1.7	0.4	0.013	0.002	−25.1	0.5	2.0	0.2	0.015	0.002	−23.8	1.3
0–100 cm	Carbon store (Mg ha^{-1}) 61.2 ± 51						Carbon store (Mg ha^{-1}) 25.2 ± 20					

reportedly lower for saltmarsh than mangrove in southeastern Australia (Clarke and Jacoby, 1994), although the rate of sediment delivery may be a more important driver of sediment and carbon accumulation than *in-situ* production. The association demonstrated between tidal range and surface accumulation rate suggests most of the carbon accumulating above the feldspar horizon is allocthonous.

Our results indicate that rates of accretion are therefore dependent on both vegetation community, and the elevation of the community within the tidal range. Accretion therefore declines under stable sea-level conditions, as the elevation of the marsh increases and inundation and vegetation characteristics change (Morris et al., 2002). However, low to moderate rates of sea-level rise provide an opportunity for sustained accretion and sequestration over periods of time meaningful for REDD + valuation. Palaeostratigraphic work by Hashimoto et al. (2006) on the Richmond River, NSW, demonstrated that mangroves were able to maintain a rate of vertical accumulation of 5 mm y^{-1} over 900 years during the latter phases of the post-glacial marine transgression. Soil organic matter in these cores was consistently between 18 and 20%, equating to a rate of carbon sequestration of 2.75 Mg C ha^{-1} y^{-1}, a figure very close to the average rate estimated using contemporary data for the region (2.50 Mg C ha^{-1} y^{-1}). This rate of carbon sequestration is therefore sustainable over higher rates of sea-level rise than that so far encountered in southeast Australia during the historic period, though the peats were dominated by Rhizophoraceae rather than *Avicennia marina*, the dominant temperate mangrove.

Table 4
Macrophyte leaf and root $\delta^{13}C$ at 5 sites on the Hawkesbury river.

Site:	Distance from entrance (km)	Site conditions (Saintilan, 1997)	Species sampled ($n = 5$ unless specified)	Leaf $\delta^{13}C$ ‰ (SD)	Whole root $\delta^{13}C$ ‰ (SD)
Mills Creek	54.5	Fluvial muds and silts, brackish	*A. marina* *Ae. corniculatum*	−27.9 (1.23) −30.3.(0.063)	−24.7 (0.165)
Allens Creek	34	Fluvial muds and silts, brackish	*A. marina* *Ae. corniculatum*	−27.7 (0.48) Decomposing −26.21 (1.8) −28.9 (0.496)	−24.4 (0.157) Ancient −24.6
Mangrove Creek	33	Estuarine silts, brackish	*Juncus kraussii* ($n = 2$)	−27.03 (1.8)	−26.05 (0.4)
Spencer	29.5	Estuarine silts, brackish to hypersaline-upper intertidal	*A. marina* *Ae. corniculatum*	−27.3 (0.066) −28.6 (0.16)	−24.7 (0.19)
Mooney Mooney	16.5	Estuarine silts, Saline to brackish	*A. marina*	−28.3 (0.13)	−24.3 (0.07)
Pittwater	4	Marine sand delta, sea-water salinity	*A. marina* *S. virginicus* *S. quinqueflora*	−28.3 (1.13) −15.36 (1.4) −26.25 (0.6)	−23.3 (0.34)

Table 5
Global estimates of carbon accumulation in mangrove and saltmarsh from this study[1], Fujimoto 2004[2], Chmura et al. 2003[3]. Australian saltmarsh includes *Juncus acutus* (j) and the *Sporobolus/Sarcocornia* association (s).

Saltmarsh		Mangrove	
Region	Mg C ha^{-1} y^{-1} (s.d.)	Region	Mg C ha^{-1} y^{-1} (s.d.)
SE Aust (j)[1]	2.07 (1.32)	SE Aust[1]	2.56 (2.24)
SE Aust (s)[1]	0.46 (0.37)	NE Aust[3]	1.48 (1.18)
NE Atlantic[3]	2.49 (2.02)	W Pacific[3]	5.4 (2.22)
Gulf of Mexico[3]	2.96 (3.53)	Gulf of Mexico[3]	2.14 (1.53)
Mediterranean[3]	1.61 ($n = 1$)	Vietnam[3]	5.24 (4.09)
NE Pacific[3]	2.06 (1.83)		
NW Atlantic[3]	1.74 (1.54)		

We did not measure gaseous flux in this study, however, previous studies in mangrove and saltmarsh wetlands have shown that carbon accumulation can be offset by methane emissions (Sotomayor et al., 1994; Allen et al., 2007). The only published values for southeast Australian are from Westernport Bay (Livesley and Andrusiak, 2012), where emissions from mangrove were low (between 9.7 and 405.8 μg C m^{-2} h^{-1}), and for saltmarsh negligible (1.8–4.2 μg C m^{-2} h^{-1}). Nitrous oxide emissions from both vegetation types were also low.

4.2. Variation in sediment organic matter

In some circumstances, an enrichment in $\delta^{13}C$ with depth in a coastal wetland soil profile can indicate a change in community composition from C_3 to C_4 dominated plants. Choi et al. (2001) suggested that a shift from −23‰ to −17‰ at depth was the result of contributions changing from *Juncus roemerianus* (C_3) to C_4 plants at depth. The common C_4 saltmarsh plant on the east Australian coast *Sporobolus virginicus*, could be responsible for enrichment in cores, and this is a likely explanation of the relative enrichment of the Kooragang saltmarsh core compared to the adjacent mangrove (Fig. 3). The common seagrass plant *Zostera* is also enriched ($\delta^{13}C \sim -12‰$), deriving carbon from the water column rather than atmospheric CO_2. This may explain the enrichment at depth of the Currambene Creek cores, which adjoin and may have encroached seagrass beds.

However, in most cases soil carbon is too depleted in $\delta^{13}C$ for *Sporobolus virginicus* or seagrass to be making an important contribution. While soil carbon is enriched in comparison to mangrove and C_3 saltmarsh shoot material, we have demonstrated that mangrove roots are significantly enriched compared to mangrove leaves, and the profiles generally fit between the mangrove leaf and mangrove root signatures. Other studies have shown a higher rate of decomposition in leaf litter 0.28–1.53% day^{-1} (Middleton and McKee, 2001; Poret et al., 2007) than mangrove roots (0.10–0.28% day^{-1} (Middleton and McKee, 2001)). Down-core enrichment may be explained by the incremental loss of the relatively depleted leaf material, and the increasing contribution of recalcitrant root carbon. The difference between leaf and root $\delta^{13}C$ is greatest in sandy marine deltaic sites, based on the Pittwater samples, where a 5‰ root enrichment was observed. This may be sufficient to explain the greater down-core enrichment of sandy marine sites at Currambene Creek and Cararma Inlet though, as indicated above, seagrass carbon may also be making a contribution.

Geomorphic setting likely exerts an influence over carbon store. Brackish fluvial environments dominated by silts and muds exhibited a greater retention of carbon down-core, especially in the two Hawkesbury River sites, and relatively high carbon density continuing to 1.0 m depth. This is likely to be a function of variation in plant biomass between settings, and the preservation potential of the soil medium, being lower in more aerated sandy substrates. These sites maintain carbon stores of 250–350 Mg ha^{-1}, with no difference between sites dominated by mangrove or the dominant saltmarsh in these locations, *Juncus kraussii*. Saintilan (1997) estimated *Avicennia marina* living root biomass as approximately 110 Mg C ha^{-1} at Big Bay, Hawkesbury River, indicating a significant contribution of living material to carbon store in the upper metre. Sites situated on sandy marine deltas supported significantly lower carbon stores (25–250 Mg ha^{-1}) regardless of vegetation type. These lower values are primarily due to the sharp loss of carbon with depth, though this does not necessarily mean carbon is lost rapidly. Carbon retrieved at 0.7 m from the Cararma Inlet site dated to 1920 ± 90 BP (Saintilan and Wilton, 2001).

The results support studies applying biomarkers in affirming the importance of autocthonous carbon in saline marshes. Tanner et al. (2010) used compound-specific isotope analyses to show that saltmarsh plants dominated the carbon isotope signal of sediment organic matter in a Maine saltmarsh for more than three millenia. Our results indicate that mangrove root material possibly dominates soil organic carbon in all settings, with the exception of *Juncus* saltmarsh in brackish environments in which the relatively depleted *Juncus* roots dominate soil organic carbon.

The *Sporobolus virginicus/Sarcocornia quinqueflora* association is the most widespread saltmarsh vegetation community on the Australian east coast (Adam et al., 1988), and contributes carbon to estuarine foodwebs across the region (Guest and Connolly, 2004; Mazumder et al., 2011). The standing biomass of this community is relatively low compared to *Juncus kraussii* (Congdon and McComb, 1980; Clarke and Jacoby, 1994), and roots are shallow. Notwithstanding, the density of soil carbon within this community, though lower than the other vegetation types measured in this study, and the *Sclerostegia* saltmarsh measured by Livesley and Andrusiak (2012), is within the range of averages for saltmarshes in the northern hemisphere. Tidally-borne carbon may contribute significantly to soil organic matter in this community.

5. Conclusions

Our results indicate that variation in carbon store and accumulation rate on coastal wetland settings of southeastern Australia is driven primarily by hydro-geomorphic setting rather than vegetation type per se, notwithstanding the dominant contribution of in-situ vegetation to recalcitrant carbon. No difference in rate of accumulation or carbon store was observed between sites dominated by the saltmarsh *Juncus kraussii* and the mangrove *Avicennia marina*, with both communities showing strong differences between fluvial deltaic and marine deltaic settings, with the latter being appreciably lower. Accumulation rate above feldspar horizons was a function of tidal range and position in the tidal prism.

Carbon density decreased down-core, though more rapidly in sandy marine settings than fluvial mud/silt environments. The decrease in carbon was reflected in an enrichment in $\delta^{13}C$. Neither mangrove leaf or root material showed appreciable enrichment with decomposition. We therefore interpret down-core enrichment as an increase in the relative contribution of mangrove root material to soil carbon, given the consistent enrichment observed in mangrove root compared to mangrove leaves from the same trees across a range of settings. The result suggests an important contribution of in-situ plant material to carbon store, while surface carbon accumulation appears dominated by allocthonous sources.

Given the consistent accretion of these environments over hundreds of years (Saintilan and Hashimoto, 1999) the dominance of root carbon in soil carbon at depth suggests a relatively low residence time for allochthonous, tidally-borne carbon (including

leaf litter) in these systems. Studies of accretion using feldspar horizons should therefore be used cautiously in assessing contributions from this source to "permanent" carbon of the type required under REDD + frameworks. Several recent studies have demonstrated the potential of organic markers in clarifying sources of carbon in coastal sedimentary environments (Tanner et al., 2010; Wang et al., 2011), and the potential of compound-specific isotope analysis has not yet been fully realised in distinguishing between possible carbon sources in these settings.

Acknowledgements

Accretion measures were funded by the Australian Commonwealth Government through the Coast and Clean Seas Initiative and the NSW Environmental Trust. Don Cahoon is thanked for providing guidance in the establishment of the measurement network. Suzanne Hollins (ANSTO) supported SI sample analysis and Barbara Neklapilova (ANSTO) and Scott Allchin (ANSTO) assisted with sample preparation and analysis.

References

Adam, P., Wilson, N.C., Huntley, B., 1988. The phytosociology of coastal saltmarsh vegetation in New South Wales. Wetlands (Australia) 7, 35–57.
Allen, D.E., Dalal, R.C., Rennenberg, H., Meyer, R.L., Reeves, S., Schmidt, S., 2007. Spatial and temporal variation of nitrous oxide and methane flux between subtropical mangrove sediments and the atmosphere. Soil Biology and Biochemistry 39, 622–631.
Alongi, D.M., 2009. The Energetics of Mangrove Forests. Springer, Dordrecht.
Alongi, D.M., 2011. Carbon payments for mangrove conservation: ecosystem constraints and uncertainties of sequestration potential. Environmental Science and Policy 14, 462–470.
Anglesen, A., 2009. Realising REDD+: National Strategy and Policy Options. Center for International Forestry Research, Bogor.
Bouillon, S., Borges, A.V., Castañeda-Moya, E., Diele, K., Dittmar, T., Duke, N.C., Kristensen, E., Lee, S.Y., Marchand, C., Middelburg, J.J., Rivera-Monroy, V.H., Smith, T.J., Twilley, R.R., 2008. Mangrove production and carbon sinks: a revision of global budget estimates. Global Biogeochemical Cycles 22.
Cahoon, D.R., Lynch, J.C., Hensel, P., Boumans, R., Perez, B.C., Segura, B., Day Jr., J.W., 2002. High-precision measurements of wetland sediment elevation: I. Recent improvements to the Sedimentation-Erosion Table. Journal of Sedimentary Research 72, 730–733.
Chmura, G.L., Anisfeld, S.C., Cahoon, D.R., Lynch, J.C., 2003. Global carbon sequestration in tidal, saline wetland soils. Global Biogeochemical Cycles 17, 1111.
Choi, Y., Wang, Y., 2004. Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. Global Biogeochemical Cycles 18, GB4016.
Choi, Y., Wang, Y., Hsieh, Y.-P., Robinson, L., 2001. Vegetation succession and carbon sequestration in a coastal wetland in northwest Florida: evidence from carbon isotopes. Global Biogeochemical Cycles 15, 311–319.
Clarke, P.J., Jacoby, C.A., 1994. Biomass and above-ground productivity of salt-marsh plants in South-eastern Australia. Australian Journal of Marine and Freshwater Research 45, 1521–1528.
Congdon, R.A., McComb, A.J., 1980. Productivity and nutrient content of Juncus kraussii in an estuarine marsh in south-western Australia. Australian Journal of Ecology 5, 221–234.
Dalrymple, R.W., Zaitlin, B.A., Boyd, R., 1992. Estuarine facies models; conceptual basis and stratigraphic implications. Journal of Sedimentary Research 62, 1130–1146.
DeLaune, R.D., Patrick, W.D., Lindau, C.W., Smith, C.J., 1990. Nitrous oxide and method emission from Gulf Coast wetlands. In: Bouwman, A.F. (Ed.), Soils and the Greenhouse Effect. John Wiley, New York, pp. 497–502.
Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nature Geoscience 4, 293–297.
Duarte, C.M., Middelburg, J., Caraco, N., 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2, 1–8.
Duke, N.C., 1990. Phenological trends with latitude in the mangrove tree Avicennia marina. The Journal of Ecology 78, 113–133.
Ehleringer, J.R., Buchmann, N., Flanagan, L.B., 2000. Carbon isotope ratios in belowground carbon cycle processes. Ecological Applications 10, 412–422.
Fujimoto, K., 2004. Below-ground carbon sequestration of mangrove forests in the Asia-Pacific region. In: Vannucci, M. (Ed.), Mangrove Management and Conservation: Present and Future. United Nations University Press, Tokyo.
Garten, C.T., 2006. Relationships among forest soil C isotopic composition, partitioning, and turnover times. Canadian Journal of Forest Research 36, 2157–2167.
Garten, J.C., Hanson, P., Todd, J.D., Lu, B., Brice, D., 2007. Natural 15N and 13C abundance as indicators of forest N status and soil C dynamics. In: Lajtha, R.M.a.K. (Ed.), Stable Isotopes in Ecology and Environmental Science, second ed. Blackwell Science, Oxford.
Grace, J., Lloyd, J., MacIntyre, J., Miranda, A.C., Meir, P., Miranda, H.S., Mobre, C., Moncrieff, J., Massheder, J., Malhi, Y., Wright, I., Gash, J., 1993. Carbon dioxide uptake by undisturbed tropical rain forest in southwest Amazonia, 1993 to 1992. Science 270, 778–780.
Guest, M.A., Connolly, R.M., 2004. Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. Aquatic Ecology 38, 599–609.
Hashimoto, T.R., Saintilan, N., Haberle, S.G., 2006. Mid-holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond river estuary, New South Wales, Australia. Geographical Research 44, 63–76.
Heap, A.D., Bryce, S., Ryan, D.A., 2004. Facies evolution of Holocene estuaries and deltas: a large-sample statistical study from Australia. Sedimentary Geology 168, 1–17.
Howe, A.J., Rodríguez, J.F., Saco, P.M., 2009. Surface evolution and carbon sequestration in disturbed and undisturbed wetland soils of the Hunter estuary, southeast Australia. Estuarine, Coastal and Shelf Science 84, 75–83.
Krauss, K., Cahoon, D., Allen, J., Ewel, K., Lynch, J., Cormier, N., 2010. Surface elevation change and susceptibility of different Mangrove zones to sea-level rise on Pacific high Islands of Micronesia. Ecosystems 13, 129–143.
Lindsey, J.K., 1997. Applying Generalized Linear Models. Springer, New York.
Livesley, S.J., Andrusiak, S.M., 2012. Temperate mangrove and salt marsh sediments are a small methane and nitrous oxide source but important carbon store. Estuarine, Coastal and Shelf Science 97, 19–27.
Mazumder, D., Iles, J., Kelleway, J., Kobayashi, T., Knowles, L., Saintilan, N., Hollins, S., 2010. Effect of acidification on elemental and isotopic compositions of sediment organic matter and macro-invertebrate muscle tissues in food web research. Rapid Communications in Mass Spectrometry 24, 2938–2942.
Mazumder, D., Saintilan, N., Williams, J.R., Szymczak, R., 2011. Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. Marine and Freshwater Research 62, 11–19.
Middleton, B.A., McKee, K.L., 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. Journal of Ecology 89, 818–828.
Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea-levels. Ecology 83, 2869–2877.
Nelder, J.A., Wedderburn, R.W.M., 1972. Generalized linear models. Journal of the Royal Statistical Society 135, 370–384.
Nellemann, C., Corcoran, E., Duarte, C.M., Valdés, L., DeYoung, C., Fonseca, L., Grimsditch, G.E., 2009. Blue Carbon. A Rapid Response Assessment. United Nations Environment Programme, GRID-Arendal, Norway.
Pidgeon, E., 2009. Carbon sequestration by coastal marine habitats: important missing sinks. In: Laffoley, D., Grimsditch, G. (Eds.), The Management of National Coastal Carbon Sinks. IUCN, Gland, Switzerland.
Poffenbarger, H., Needelman, B., Megonigal, J., 2011. Salinity influence on methane emissions from tidal marshes. Wetlands 31, 831–842.
Poret, N., Twilley, R.R., Rivera-Monroy, V.H., Coronado-Molina, C., 2007. Belowground decomposition of mangrove roots in Florida coastal Everglades. Estuaries and Coasts 30, 491–496.
Roy, P.S., 1984. New south Wales estuaries: their origin and evolution. In: Thom, B.G. (Ed.), Coastal Geomorphology in Australia. Academic Press, Sydney, Australia, pp. 99–121.
Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of South-east Australian estuaries. Estuarine, Coastal and Shelf Science 53, 351–384.
Saenger, P., Snedaker, S.C., 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. Oecologia 96, 293–299.
Saintilan, N., 1997. Mangroves as successional stages on the Hawkesbury Rivers. Wetlands(Australia) 16, 99–107.
Saintilan, N., 1998. Photogrammetric survey of the Tweed River wetlands. Wetlands (Australia) 17, 74–82.
Saintilan, N., Hashimoto, R., 1999. Mangrove-saltmarsh dynamics on a prograding bayhead delta in the Hawkesbury River estuary, New South Wales, Australia. Hydrobiologia 413, 95–102.
Saintilan, N., Hossain, K., Mazumder, D., 2007. Linkages between adjacent seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. Wetlands Ecology and Management 15, 277–286.
Saintilan, N., Mazumder, D., 2010. Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. Marine and Freshwater Research 61, 615–620.
Saintilan, N., Wilton, K., 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetlands Ecology and Management 9, 409–420.
Sanders, C.J., Smoak, J.M., Naidu, A.S., Sanders, L.M., Patchineelam, S.R., 2010. Organic carbon burial in a mangrove forest, margin and intertidal mud flat. Estuarine. Coastal and Shelf Science 90, 168–172.
Sotomayor, D., Corredor, J., Morell, J., 1994. Methane flux from mangrove sediments along the Southwestern coast of Puerto Rico. Estuaries 17, 140–147.
Tanner, B.R., Uhle, M.E., Mora, C.I., Kelley, J.T., Schuneman, P.J., Lane, C.S., Allen, E.S., 2010. Comparison of bulk and compound-specific $\delta^{13}C$ analyses and determination of carbon sources to salt marsh sediments using n-alkane distributions (Maine, USA). Estuarine, Coastal and Shelf Science 86, 283–291.
Wang, J., Dodla, S., DeLaune, R., Hudnall, W., Cook, R., 2011. Soil carbon characteristics in two Mississippi river deltaic Marshland profiles. Wetlands 31, 157–166.

AGU PUBLICATIONS

JGR

Journal of Geophysical Research: Biogeosciences

RESEARCH ARTICLE
10.1002/2017JG003775

Key Points:
- Multiple ecosystem shifts were observed within the surface 1 m of blue carbon sediments
- Preservation of inputs from prior ecosystem formation can make large contributions to contemporary carbon stocks
- Heterogeneity of historical influence needs to be accounted for in regional assessments of carbon storage

Supporting Information:
- Supporting Information S1

Correspondence to:
J. J. Kelleway,
jeffrey.kelleway@mq.edu.au

Citation:
Kelleway, J. J., N. Saintilan, P. I. Macreadie, J. A. Baldock, H. Heijnis, A. Zawadzki, P. Gadd, G. Jacobsen, and P. J. Ralph (2017), Geochemical analyses reveal the importance of environmental history for blue carbon sequestration, *J. Geophys. Res. Biogeosci.*, *122*, 1789–1805, doi:10.1002/2017JG003775.

Received 18 JAN 2017
Accepted 23 JUN 2017
Accepted article online 30 JUN 2017
Published online 21 JUL 2017

©2017. American Geophysical Union. All Rights Reserved.

Geochemical analyses reveal the importance of environmental history for blue carbon sequestration

J. J. Kelleway[1,2,3], N. Saintilan[2], P. I. Macreadie[4], J. A. Baldock[5], H. Heijnis[6], A. Zawadzki[6], P. Gadd[6], G. Jacobsen[6], and P. J. Ralph[1]

[1]Climate Change Cluster, University of Technology Sydney, Ultimo, New South Wales, Australia, [2]Department of Environmental Sciences, Macquarie University, Sydney, New South Wales, Australia, [3]Now at Department of Environmental Sciences, Macquarie University, Sydney, New South Wales, Australia, [4]School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Burwood, Victoria, Australia, [5]CSIRO Agriculture and Food, Glen Osmond, South Australia, Australia, [6]Australian Nuclear Science and Technology Organisation, Lucas Heights, New South Wales, Australia

Abstract Coastal habitats including saltmarshes and mangrove forests can accumulate and store significant blue carbon stocks, which may persist for millennia. Despite this implied stability, the distribution and structure of intertidal-supratidal wetlands are known to respond to changes imposed by geomorphic evolution, climatic, sea level, and anthropogenic influences. In this study, we reconstruct environmental histories and biogeochemical conditions in four wetlands of similar contemporary vegetation in SE Australia. The objective is to assess the importance of historic factors to contemporary organic carbon (C) stocks and accumulation rates. Results from the four cores—two collected from marine-influenced saltmarshes (Wapengo marine site (WAP-M) and Port Stephens marine site (POR-M)) and two from fluvial influenced saltmarshes (Wapengo fluvial site (WAP-F) and Port Stephens fluvial site (POR-F))—highlight different environmental histories and preservation conditions. High C stocks are associated with the presence of a mangrove phase below the contemporary saltmarsh sediments in the POR-M and POR-F cores. ^{13}C nuclear magnetic resonance analyses show this historic mangrove root C to be remarkably stable in its molecular composition despite its age, consistent with its position in deep sediments. WAP-M and WAP-F cores did not contain mangrove root C; however, significant preservation of char C (up to 46% of C in some depths) in WAP-F reveals the importance of historic catchment processes to this site. Together, these results highlight the importance of integrating historic ecosystem and catchment factors into attempts to upscale C accounting to broader spatial scales.

1. Introduction

1.1. Organic Carbon in Coastal Ecosystems

Coastal vegetated habitats (saltmarshes, mangrove forests, and seagrass beds) provide an important ecosystem service through the capture and long-term storage of organic carbon (C). This capacity to sequester "blue carbon" is dependent upon three broad ecosystem factors: (1) high productivity in converting CO_2 into plant biomass C [*Alongi*, 2002; *Nixon*, 1980], (2) effective trapping of particulate organic C originating from within the ecosystem (autochthonous C) and/or from external sources (allochthonous C) [*Kennedy et al.*, 2010], and (3) biogeochemical conditions within sediments which slow the decay of organic material [*Fourqurean et al.*, 2012; *Kristensen et al.*, 2008; *McLeod et al.*, 2011]. In concert, these factors may allow C-rich sediments and biomass to continue to accrete over centuries and millennia [*Lo Iacono et al.*, 2008; *McKee et al.*, 2007]. Consequently, coastal vegetated habitats generally contain higher belowground stocks of C over a given depth and accumulate C in surface sediments faster than most terrestrial habitats [*Fourqurean et al.*, 2012; *McLeod et al.*, 2011].

Much of the blue carbon accumulated over time is produced belowground by roots and rhizomes [*Pendleton et al.*, 2012], though contributions from other sources may be significant. A global assessment of seagrass C isotope values ($\delta^{13}C$), for example, revealed that on average ~50% of all C in surface seagrass sediments derives from nonseagrass sources [*Kennedy et al.*, 2010]. Contributions of autochthonous versus allochthonous inputs may vary substantially, however, among the different depositional settings in which blue carbon ecosystems are found [*Kelleway et al.*, 2016a; *Zhou et al.*, 2006]. Such variability may have implications for long-term C storage because the molecular composition (i.e., recalcitrance) of C inputs is

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

considered a key driver of decay rates [*Enríquez et al.*, 1993], including in blue carbon ecosystems [*Kristensen*, 1994]. For example, it was recently demonstrated that organic matter stability decreases among marine macrophytes in the order mangrove > saltmarsh plants > seagrass > macroalgae, consistent with variations in molecular composition among taxa [*Trevathan-Tackett et al.*, 2015]. Terrestrial inputs to marine sediments, including lignin-rich plant materials and char transported after catchment fires, have also been shown to have high resistance to decomposition [*Burdige*, 2007, and references therein; *Derenne and Largeau*, 2001].

Whatever the C source, the capacity of coastal wetlands to store carbon over the long-term is dependent upon the balance between inputs and their decay rate [*Kirwan et al.*, 2013]. Due to low oxygen diffusion in water-saturated sediments, microbial decomposition of C in blue carbon sediments occurs mainly through anaerobic metabolic pathways [*Howes et al.*, 1984; *King*, 1983; *Lord and Church*, 1983]. The decomposition of organic matter also increases the diversity of biomolecules in soils and sediments as microbes transform source materials, synthesize additional biochemicals for their own growth, and excrete products of metabolic activity [*Baldock et al.*, 2013; *Grandy and Neff*, 2008].

1.2. Understanding Blue Carbon Variability

Considerable research effort over the past decade has greatly improved blue carbon sequestration estimates over local, regional, and global scales. Spatial variability of C stocks and C accumulation rates has been assessed in terms of contemporary expressions of vegetation composition and structure [*Chen et al.*, 2015; *Kelleway et al.*, 2016b; *Ricart et al.*, 2015] as well as geomorphic and sedimentary properties [e.g., *Adame et al.*, 2010; *Donato et al.*, 2011; *Macreadie et al.*, 2017; *Serrano et al.*, 2016b]. Such studies based on contemporary ecosystem character improve our understanding of C stocks and surface processes and have applicability in upscaling estimates to broader spatial scales [e.g., *Duarte et al.*, 2013; *Pendleton et al.*, 2012]. They often fail, however, to capture the variability driven by subsurface processes such as deep root growth [*Lovelock et al.*, 2013] and the preservation (or decay) of deep organic matter which may have accumulated hundreds or thousands of years earlier [*Lo Iacono et al.*, 2008; *McKee et al.*, 2007]. Improved knowledge of surface and subsurface blue carbon processes will become increasingly important as coastal wetlands respond to changes imposed by geomorphic, climatic, sea level, and anthropogenic influences [*Kirwan and Megonigal*, 2013; *Swales et al.*, 2015; *Woodroffe et al.*, 1985].

In southeastern (SE) Australia, the dynamic nature of blue carbon ecosystems has been revealed through analyses of sediment cores collected throughout the region. Mangrove roots have been found preserved beneath contemporary saltmarsh surface in multiple locations [*Saintilan and Hashimoto*, 1999; *Saintilan and Wilton*, 2001]; however, this phenomenon is not universal [*Kelleway et al.*, 2016a; *Mitchell and Adam*, 1989]. It is possible that site-specific differences in the input and preservation of roots explain some of the of spatial variability in subsurface C density of saltmarsh sediments that is not readily explained by contemporary (surface) vegetation structure or sedimentary properties [*Kelleway et al.*, 2016a].

The current study aims to reconstruct environmental histories and biogeochemical conditions in four wetlands of similar contemporary vegetation in SE Australia. It will do this by combining high-resolution chemical profiles with discrete sampling of parameters informative of the wetland's developmental stage, organic matter stocks and sources, and preservation or processing of C. The objective is to assess the importance of historic C input and preservation to contemporary blue carbon stocks and C accumulation rates.

2. Materials and Methods

2.1. Study Setting

In SE Australia, saltmarsh and mangrove ecosystems are restricted to estuaries and marine embayments where hydrodynamic energy is sufficiently reduced to allow colonization and survival of plants [*West et al.*, 1985]. Within these estuaries and embayments the most recent phase of estuarine sedimentation was initiated about 7000–8000 years ago [*Roy*, 1984; *Roy and Thom*, 1981] though rates of infilling of individual valleys have varied spatially since then [*Roy et al.*, 2001]. The four sedimentary environments in SE Australian estuaries (marine tidal delta, central mud basin, fluvial delta, and riverine channel) have characteristic water quality and nutrient cycling/primary productivity signatures [*Roy et al.*, 2001]. Of these, the marine

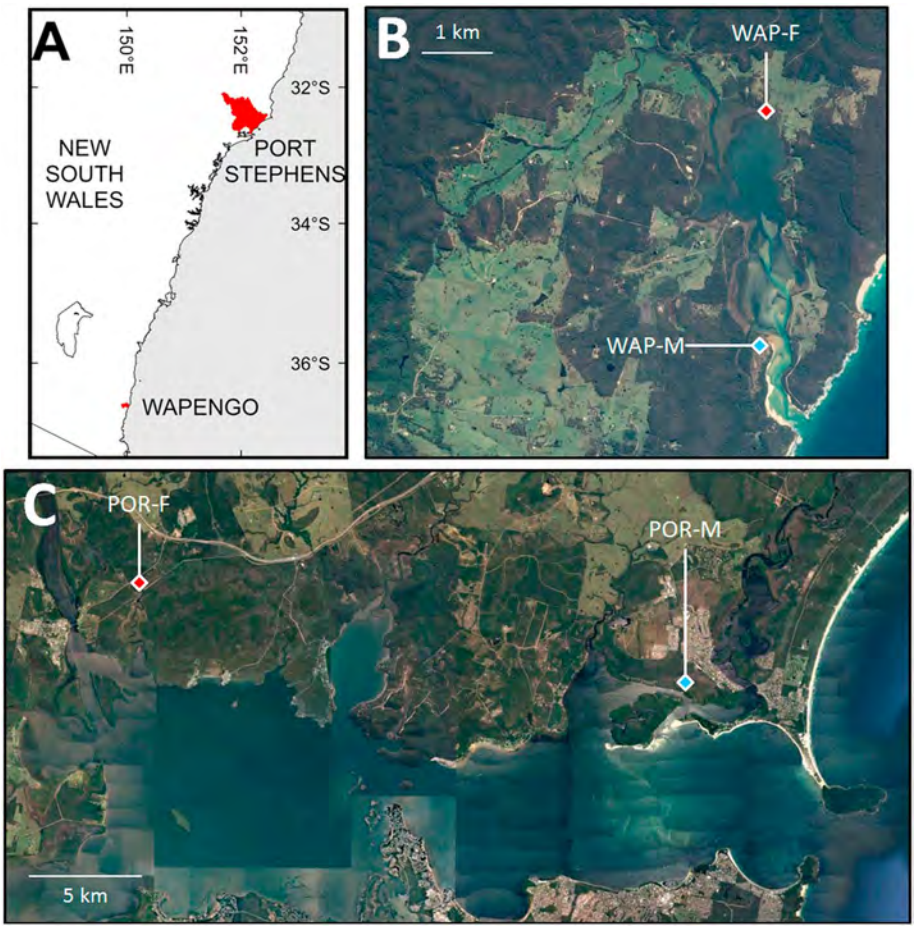


Figure 1. (a) Location of study estuaries along the New South Wales coast of SE Australia, (b) location of WAP-M and WAP-F in Wapengo Lagoon, and (c) location of POR-M and POR-F in the Port Stephens estuary.

tidal delta and fluvial delta represent depositional environments with distinctly different sedimentary sources, and as such these two zones will be a focus of this study.

SE Australian saltmarsh communities generally have low floral species richness, often being dominated by just one or two species [*Adam et al.*, 1988]. There are broad zonation patterns coinciding with surface elevation, whereby the majority of lower to midelevation saltmarsh is considered a single association dominated by the chenopod *Sarcocornia quinqueflora* and grass *Sporobolus virginicus* [*Zedler et al.*, 1995]. Data previously collected within the study region show that aboveground biomass of this association is low (*S. quinqueflora* mean = 320 g m^{-2}; *S. virginicus* mean = 350 g m^{-2}) relative to other saltmarsh types [*Clarke and Jacoby*, 1994]. Throughout mainland Australia, saltmarshes are generally bordered downslope by mangroves (the species *Avicennia marina* is dominant throughout the region) and supratidal forest or shrub communities to the higher, landward side.

The estuaries of Wapengo Lagoon and Port Stephens (Figure 1) were chosen for this study based on their dissimilarity in geomorphic type and stage of infilling. Within each estuary a saltmarsh near the estuary mouth was chosen as a "marine" influenced site, while a saltmarsh further up the estuary was chosen as a "fluvial" influenced site. For each site, a single sediment core was selected randomly from among five replicate cores from the midmarsh (i.e., the *Sarcocornia-Sporobolus* association) collected as part of a previous study [*Kelleway et al.*, 2016a].

2.2. Wapengo Lagoon

Wapengo Lagoon is a small, semimature barrier estuary (water area = 3.2 km^2; catchment area = 73 km^2) with an estimated tidal range of 0.45 m and average estuary depth of just 1.29 m below mean high tide [*Roy et al.*,

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2001; *Roper et al.*, 2011]. The contemporary extent of saltmarsh, mangrove forest, and seagrass beds in Wapengo Lagoon is 0.51, 0.56, and 0.42 km^2, respectively [*Creese et al.*, 2009]. While the upper Wapengo catchment is vegetated by native forests, much of the lower catchment has been cleared. Clearing likely occurred from the 1840s onward, when grazing and then timber milling operations expanded through the region [*NSW National Parks and Wildlife Service*, 2011]. In total, approximately 16% of the catchment has now been cleared [*Roper et al.*, 2011].

The Wapengo marine site (referred to hereafter as WAP-M) is located in the lower estuary, within Mimosa Rocks National Park. The succulent species *S. quinqueflora* (C3 photosynthetic pathway) is the dominant saltmarsh plant. The mangrove *Avicennia marina* (C3) occupies large areas of the site, but its distribution is scattered and restricted to dwarf shrubs within the vicinity of the coring location (~15 m away).

The Wapengo fluvial site (WAP-F) is located on a fluvial delta formed by the confluence of the main river into the estuary and an unnamed creek with a smaller subcatchment. The lower parts of this subcatchment, including the areas immediately upslope of WAP-F, have been extensively cleared for agriculture with small farm dams installed across drainage lines, sometime after the 1840s. The core was collected approximately 25 m from the small creek within a band of saltmarsh dominated by *S. quinqueflora*. Dwarf shrubs of *A. marina* are distributed across the fluvial delta, mostly in combination with the succulent saltmarsh shrub *Tecticornia arbuscular*, but neither occurred within 10 m of the coring location.

2.3. Port Stephens

Port Stephens is a tide-dominated, drowned valley estuary in the "youthful" stage of its geomorphic evolution [*Roy et al.*, 2001]. The main estuary has an area of 126 km^2 and catchment area of 4950 km^2 [*Roy et al.*, 2001]. In addition, two smaller estuaries—the Karuah River (3.9 km^2) and Myall River (7.5 km^2)—also feed into Port Stephens. Tidal range within the estuary mouth has been estimated as 1.01 m [*Roper et al.*, 2011] but is amplified up the estuary toward the Karuah River [*Roy and Boyd*, 1996]. The contemporary extent of saltmarsh, mangrove forest, and seagrass beds in Port Stephens is 10.63, 19.04, and 14.39 km^2, respectively [*Creese et al.*, 2009].

Port Stephens has a large flood-tide delta comprising shallow sand banks intersected by active tidal channels. The Port Stephens marine site (POR-M) is located in the intertidal-supratidal zone adjacent to this delta and comprises Pleistocene barrier sands overlaid by Holocene tidal delta sands [*Roy and Boyd*, 1996]. The sediment core was collected >100 m from the nearest open water in a meadow dominated by the C4 grass *S. virginicus*, but containing occasional *A. marina* mangrove trees in low-lying depressions. The nearest mangrove was situated approximately 25 m from the core.

A fluvial site (POR-F) was chosen within Yalimbah Creek, a tide-dominated creek which drains into the northwestern corner of Port Stephens. Yalimbah Creek consists of a small tidal (mostly unvegetated) channel bordered by muddy, vegetated intertidal, and supratidal flats, and meandering through a narrow valley incised in Permo-Carboniferous bedrock [*Roy and Matthei*, 1996]. Yalimbah Creek has a small catchment of approximately 14.5 km^2 (of which ~2.2 km^2 is intertidal), while the spring tidal range has been measured at 1.4 m [*Davies*, 2011]. This small catchment remains largely forested, though a small quarry at the top of the catchment commenced operation in 2000. The POR-F sediment core was collected with an area of *S. virginicus* saltmarsh located approximately 10 m from the edge of the main channel of Yalimbah Creek (i.e., a section of creek without mangrove frontage) and 10 m from the nearest mangrove (*A. marina*).

2.4. Field Collection and Measurement

At each site, a single sediment core of 50 mm diameter and approximately 1 m depth was randomly chosen from among five extracted from the *Sarcocornia-Sporobolus* midmarsh association for a previous study. Details of coring methods and data from the other four cores collected at each site are reported in *Kelleway et al.* [2016a]. Mean carbon stocks inclusive of all five *Sarcocornia-Sporobolus* cores, plus four cores collected from upper marsh rush communities, are reported in Table 1.

2.5. ITRAX

High-resolution logging of each core was undertaken using an ITRAX Core Scanner [*Croudace et al.*, 2006] to (1) inform the reconstruction of paleo-environments and determine provenance of sediments within each site and (2) identify distinct regions of interest (ROIs) within each core from which to subsample for

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1. Bulk Sediment and Carbon Accumulation Rates for Surface Sediments and C Store for Entire Core Profiles for Each of the Four Study Sites[a]

		Surface Accumulation Rates			C Store (0–100 cm)	
		Bulk Sediment		C	This Core	Site Mean[b]
Site	Depth Range (cm)	(mm yr^{-1})	(Mg ha^{-1} yr^{-1})	(Mg C ha^{-1} yr^{-1})	(Mg C ha^{-1})	(Mg C ha^{-1})
WAP-M	0–8	2	34.6 ± 1.6	0.8 ± 0.0	37.9	63.3 ± 12.9
	8–16	1	23.9 ± 2.2	0.1 ± 0.0		
WAP-F	0–11	1	5.8 ± 0.5	0.8 ± 0.1	176.0	193.1 ± 11.4
POR-M	0–6	1	7.0 ± 1.0	0.3 ± 0.0	156.0	164.0 ± 10.3
POR-F	0–16	2	18.7 ± 1.7	0.8 ± 0.1	204.5	166.2 ± 9.5

[a]Accumulation rates are based upon CIC (constant initial concentration) model of ^{210}Pb dating profiles, except WAP-M which is based upon a CRS model due to differing ^{210}Pb activities above and below 8 cm.
[b]Values derived by combining this core with replicate values reported in *Kelleway et al.* [2016a]. $N = 9$.

specific analyses (^{13}C nuclear magnetic resonance (NMR) and particle size analysis). Each core was scanned using a molybdenum tube set at 30 kV and 55 mA, with a dwell time of 10 s and step size of 1 mm. Six elemental ratios and related measures were selected for use as environmental proxies on the basis of their suitability in marine or estuarine sediments. In two of these ratios Ti was used as a divisor because of its stability and terrigenous provenance [*Rothwell and Croudace*, 2015].

The incoherent/coherent scattering ratio (inc/coh) was used as a qualitative indicator of organic matter content, with higher values of this ratio indicating increased organic content [*Burnett et al.*, 2011]. Ca/Ti was used to indicate Ca-rich marine sediment provenance (high Ca/Ti) or high terrigenous sediment delivery relative to Ca-rich marine sources (low Ca/Ti) [*Rothwell and Croudace*, 2015]. Si/Ti was used as a proxy for siliceous productivity, with biogenic Si derived from siliceous microfossils including diatoms [*Agnihotri et al.*, 2008]. In recent sediment samples, magnetic susceptibility (κ) is a measure of the amount of the mineral magnetite (or its oxidized derivative hematite) present by unit volume. Therefore, peaks in magnetic susceptibility may be an indicator of mineralogic inputs (mainly terrigenous soils); however, human-introduced magnetic materials and biogenic sources (including bacterially generated ferrimagnetic material) can also produce magnetic anomalies. Fe/κ is a sensitive proxy for magnetite diagenesis, with reductive diagenesis of Fe resulting in a significant magnetic susceptibility loss by the transformation of ferrimagnetic iron minerals to paramagnetic iron compounds (i.e., indicated by peaks in Fe/κ) [*Hofmann et al.*, 2005; *Rothwell and Croudace*, 2015; *van der Land et al.*, 2011]. Finally, Zr/Rb was used as a grain-size proxy as Zr resides mainly in coarser grains and Rb in clays [*Rothwell and Croudace*, 2015].

2.6. Radiometric Dating

Lead-210 (^{210}Pb) dating of surface sediments was undertaken to generate age profiles among surface sediments [*Appleby and Oldfield*, 1978] and to allow the calculation of both bulk sediment and C accumulation rates. For each core, six depth intervals (0–1, 2.5–3.5, 5–6, 7.5–8.5, 10–11, and 15–16 cm) were selected for preliminary analysis. Additional "fill-in" samples were analyzed as necessarily to improve the reliability of the age models. Samples were dried, measured for bulk density, and then processed to determine polonium-210 (^{210}Po) and radium-226 (^{226}Ra) activities by alpha spectrometry [*Atahan et al.*, 2015]. Unsupported ^{210}Pb activities were estimated as the difference between total ^{210}Pb activity (measured from ^{210}Po) and supported ^{210}Pb activity (measured from ^{226}Ra) [*Appleby and Oldfield*, 1978].

For three of the cores (WAP-F, POR-M, and POR-F) sediment chronology was determined using a constant initial concentration (CIC) model [*Appleby and Oldfield*, 1978]. For WAP-M, ^{210}Pb activities varied substantially between samples collected within the depth range of 0–8.5 cm (minimal decay in total ^{210}Pb and unsupported ^{210}Pb activity) and those collected from deeper intervals (significant decay). Consequently, we chose to use a constant rate of supply (CRS) model [*Appleby and Oldfield*, 1983] as we expect the mass accumulation rates to vary throughout this surface core chronology.

Eight samples (four plant root samples, two charcoal fragments, one bark fragment, and one shell fragment from the oyster *Saccostrea glomerata*) were selected from among the subsurface sediments of the cores for ^{14}C dating. The rationale for ^{14}C dating was primarily to determine the ages of preserved materials, rather

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

than to infer the ages of sedimentary strata. One root sample did not provide sufficient carbon to progress with the dating. Samples were pretreated to remove any external contaminants. The organic samples underwent acid-alkali-acid treatments to remove possible carbonate and humic acid contaminants, while the shell sample was cleaned by removing the surface with a dental drill, then washed in de-ionized water. Carbon from samples was converted to CO_2 using the sealed-tube method [*Hua et al.*, 2001] then converted to graphite by reduction using excess hydrogen in the presence of an iron catalyst at 600°C for 12 h. Once completed, the graphite and iron mixture was pressed into aluminum cathodes for ^{14}C measurement by accelerator mass spectrometry at Australian Nuclear Science and Technology Organisation (ANSTO) following methods outlined in *Fink et al.* [2004]. The results for the organic samples were calibrated against the SHCal13 calibration curve [*Hogg et al.*, 2013] using OxCal 4.2 [*Ramsey*, 2009]. A marine reservoir correction was applied to the marine shell sample, as C taken up from marine waters has an older apparent radiocarbon age associated with long C residence times in the deep ocean. This calibration was based upon the global marine calibration curve [*Reimer et al.*, 2013] but also takes into account a regional deviation (ΔR) of 3 ± 69 specific to southeast Australia [*Ulm*, 2006].

2.7. Elemental and Isotopic Analysis of C and N

In order to calculate and compare C accumulation and C stocks among the four cores, 15 specific depth intervals (10 × 5 cm depth intervals between 0 and 50 cm; 5 × 10 cm intervals between 50 and 100 cm) were analyzed for bulk density and %C. Stable isotope ($\delta^{13}C$) and elemental ratio (C:N) values were also calculated for these depth intervals to assist in identifying the provenance of organic matter. Dried sediment samples were homogenized and ground into a fine powder using a ball mill. The "Champagne test" [*Jaschinski et al.*, 2008] was used to determine if samples contained inorganic C. Only four samples (all from WAP-M core depths >60 cm) contained sufficient carbonate C to cause reaction with HCl. Subsequently, these samples were subject to acid washing with 1 M HCl and shaken for 24 h prior to centrifugation, rinsing with MilliQ water and redrying prior to analysis. Organic %C, %N, and $\delta^{13}C$ were measured for all samples using an isotope ratio mass spectrometry-elemental analyzer (Thermo DeltaV) at University of Hawaii (HILO). Organic C density (g C cm^{-3}) was determined by multiplying %C/100 by bulk density for each depth interval. Total C stock (Mg C ha^{-1}) was calculated by integrating the 15 depth interval measures over the 0–100 cm depth range.

2.8. ^{13}C NMR

Solid-state ^{13}C NMR (nuclear magnetic resonance) spectroscopy was used to characterize the molecular composition of organic C of all bulk (i.e., inclusive of roots, rhizomes, and sediments) ROI samples [*Baldock et al.*, 2004] and to determine the mechanisms by which organic carbon may have been preserved in marine environments [*Dickens et al.*, 2006]. Briefly, dried, homogenized, and ground sediment samples were treated with 2% hydrofluoric acid [*Skjemstad et al.*, 1994] to remove paramagnetic materials and concentrate C for ^{13}C NMR analyses. Cross-polarization ^{13}C NMR spectra were acquired using a 200 Avance spectrometer (Bruker Corporation, Billerica, MA, USA) following the instrument specifications, experimental procedures, and spectral processing outlined by *Baldock et al.* [2013].

^{13}C NMR spectra (Figure S1 in the supporting information) were used to determine the proportional allocation of C to each of eight spectral regions via integration of acquired signal intensity. The eight regions and the dominant form of carbon represented by each region were as follows: alkylC (0–45 ppm), *N*-alkyl/methoxyl (45–60 ppm), *O*-alkyl (60–95 ppm), Di-*O*-alkyl (95–110 ppm), aryl (110–145 ppm), *O*-aryl (145–165 ppm), amide/carboxyl (165–190 ppm), and ketone (190–215 ppm) [*Baldock and Smernik*, 2002]. A molecular mixing model described by *Nelson and Baldock* [2005] was then used to estimate the proportion of key biomolecule components (carbohydrate, protein, lignin, lipid, pure carbonyl, and char) contributing to total C within each ROI. Each of the spectral regions listed above were used as inputs to the molecular mixing model, with amide/carboxyl and ketone combined into a single value (165–215 ppm). The N:C ratio of each ROI was also used to constrain the mixing model [*Baldock et al.*, 2004].

2.9. Grain Size Analysis

Grain size distribution of sediment samples was measured using a laser diffraction particle size analyzer (LS 230; Beckman Coulter, Germany) with an analytical range of 0–2000 μm to estimate the relative energy level present in the environment under which the sediment was transported and deposited [*Bartholomä and*

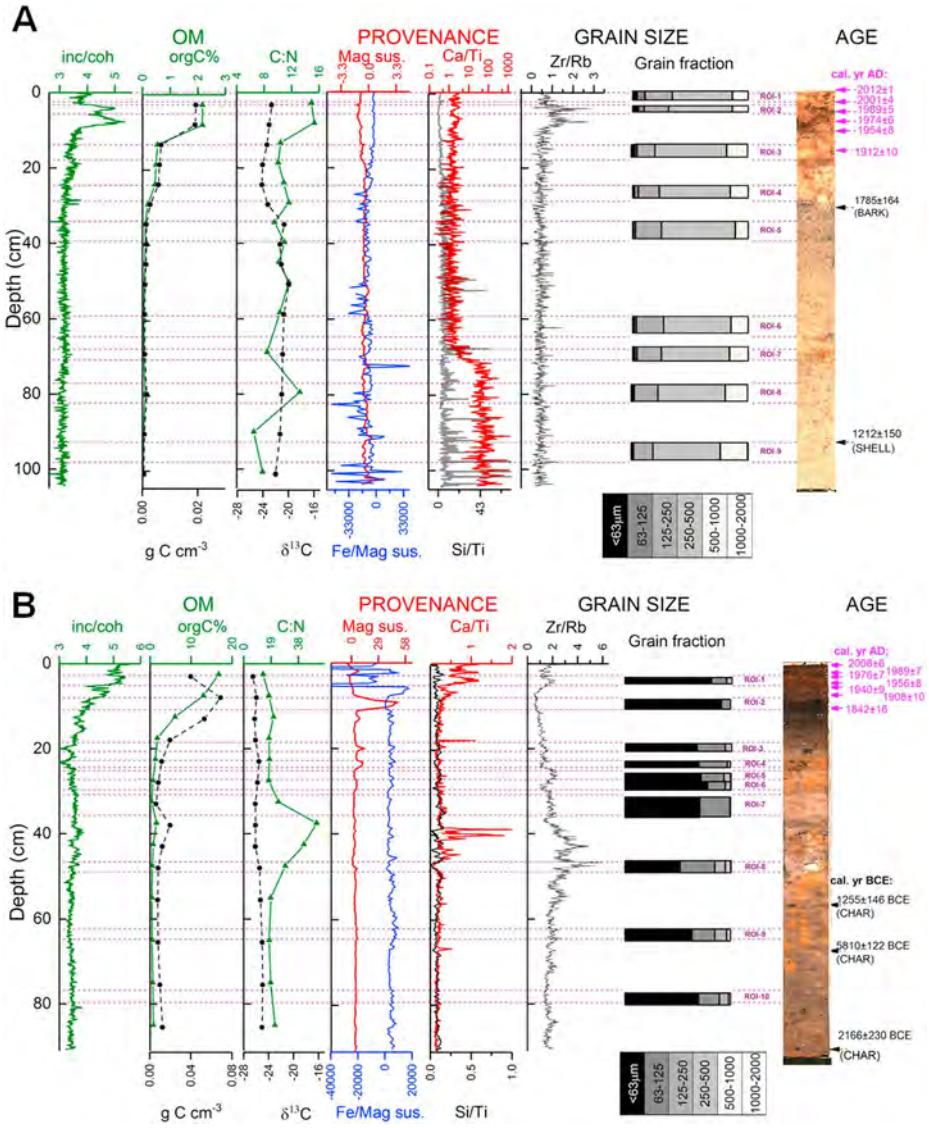


Figure 2. (a) WAP-M and (b) WAP-F core profiles derived from ITRAX core scanning, depth interval, and region of interest (ROI) sampling. Optical core image is presented on the right with ^{210}Pb derived ages presented for surface sediments (pink text) and calibrated ^{14}C ages of specific materials in deeper sections (black text). ROIs for discrete sampling of grain size analysis and molecular composition are labeled and marked by dashed lines.

Flemming, 2007]. Sediments were oxidized with H_2O_2 to remove organic matter and treated with HCl to remove carbonates prior to analysis.

3. Results

3.1. WAP-M

The Wapengo marine core (Figure 2a) displays surface horizons with moderate C densities associated with recent belowground biomass inputs, overlaying OC-poor marine sands, and shells which show little (~20–30 cm depth) to no (> 30 cm depth) visible record of plant tissue preservation. Radiocarbon dating of deposited materials—tree bark at 30 cm dated to 1785 ± 164 cal years AD and an oyster shell fragment at 91 cm dated to 1212 ± 150 cal years AD (Table 2)—suggests *maximum* long-term surface accretion rates of 1.8 ± 1.8 mm yr^{-1} and 1.2 ± 0.2 mm yr^{-1}, respectively. Recent accumulation rates measured by ^{210}Pb were rapid, relative to the other cores, but were also unique in showing a marked difference in surface accumulation rates in recent (0–8 cm) versus deeper (8–16 cm) sediments (Table 1 and Figure S2).

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 2. Details of Samples Subjected to Radiocarbon Dating

Site	Lab ID	Depth (cm)	Dated Material	Radiocarbon age ^{14}C year B.P.	1σ Error	Mean Calibrated Age cal year B.P. (±2σ)	Mean Calibrated Calendar Age cal year A.D./B.C.E. (±2σ)
WAP-M	OZT467	29.7–30.7	tree bark	190	30	165 ± 164	1785 ± 164 A.D.
	OZT468	90.1–91.2	oyster shell fragment (*Saccostrea glomerata*)	1180	35	738 ± 150[a]	1212 ± 150 A.D.[a]
WAP-F	OZT469	57.0–58.0	char fragment	3055	35	3205 ± 146	1255 ± 146 B.C.E.
	OZT471	58.0–69.0	char fragment	6965	50	7760 ± 122	5810 ± 122 B.C.E.
	OZT472	92.0–93.0	char fragment	3790	70	4116 ± 230	2166 ± 230 B.C.E.
POR-M	OZT535	54.8–55.9	plant root	1820	30	1688 ± 108	262 ± 108 A.D.
	OZT464	86.3–87.4	plant root	1475	35	1331 ± 52	619 ± 52 A.D.
POR-F	OZT465	65.3–66.5	plant root	755	40	648 ± 86	1302 ± 86 A.D.
	OZT466	108.0–109.2	plant root	Modern			

[a]Calibrated using ΔR = 3 ± 69 years [*Ulm*, 2006].

Overall, WAP-M had the lowest C stocks of the cores in the present study (Table 1). C density was high in the contemporary root zone (0–10 cm) where C was characterized by high proportions of carbohydrates and lignin (Figure 4). With depth, the proportion of carbohydrate C and carbonyl C declined, most substantially below the contemporary root zone (i.e., ROIs 4 and 5). These declines coincided with increases in the proportions of both proteinaceous and lipid C, while lignin C persisted downcore. Grain size distributions included a greater proportion of $<$250 μm sediments in contemporary strata (ROIs 1 and 2) but were more coarse and uniform from ROI-3 and below.

3.2. WAP-F

The Wapengo fluvial core (Figure 2b) is characterized by dense organic-rich materials within the surface horizon (0– ~15 cm) and multiple depositional facies downcore. Roots were encountered occasionally below the contemporary root zone to the base of the core, but became increasingly sparse with depth. These regions of sparse, fine roots were consistently depleted in δ^{13}C. A fragment of the volcanic rock pumice was found at 47 cm, while coarse charcoal fragments were present within depositional strata across the entire depth range of the core.

The highest C densities of any core (i.e., 0.04–0.07 g C cm^{-3}) were observed in the surface sediments of WAP-F. Here autochthonous plant contributions (roots, rhizomes, and detritus) were visibly dominant, though ^{13}C NMR analysis showed a substantial contribution (22%) of char in ROI-2. The peak in C density (0.07 g C cm^{-3}) also coincided with three indicators of catchment sedimentation: (1) a significant peak in magnetic susceptibility, (2) low Ca:Ti values, and 3) fine sediment delivery (96% $<$ 63 μm). Below the contemporary root/rhizome zone, C density maintained a baseline of ~0.01 g C cm^{-3} (25–90 cm) with a slight increase associated with a char-rich section between 35 and 40 cm. This baseline C density remained relatively constant despite the decline in the presence of plant roots and rhizomes. Carbohydrates and lignin exhibited substantial decline with depth and were replaced by char, lipids, and to a lesser extent protein and carbonyl C.

3.3. POR-M

The POR-M core shows broad similarity to WAP-M in that both display mineral profiles consistent with a vegetated wetland phase sitting above coarser sediments of apparent marine origin (Figure 3a). In the case of POR-M, however, the fining of sediments was more substantial and extended to a greater depth (~30 cm). Contemporary (up to ~100 year B.P.) bulk sediment and C accumulation rates were also much lower than in WAP-M (Table 1 and Figure S3). Despite this, C stocks over 1 meter of depth were more than four times higher in POR-M relative to WAP-M.

Decays in %C were mirrored by shifts in the character of C from carbohydrate-rich (ROI 1) to carbohydrate poor (ROI 4) strata and a depletion in δ^{13}C from −17.6‰ (ROI 1) to −25.5‰ (ROI 4). Below ~25 cm, C density increased to a peak 0.028 g C cm^{-3} and there was a concomitant increase in C:N relative to surface sediments. Visual inspection of the core readily identified partially decayed *Avicennia marina* mangrove roots increasing in density from ~25 cm and persisting to the bottom of the core. In contrast to the shift in C composition observed with depth in the surface sediments, C within the historic mangrove root zone (i.e., ROIs 6–11)

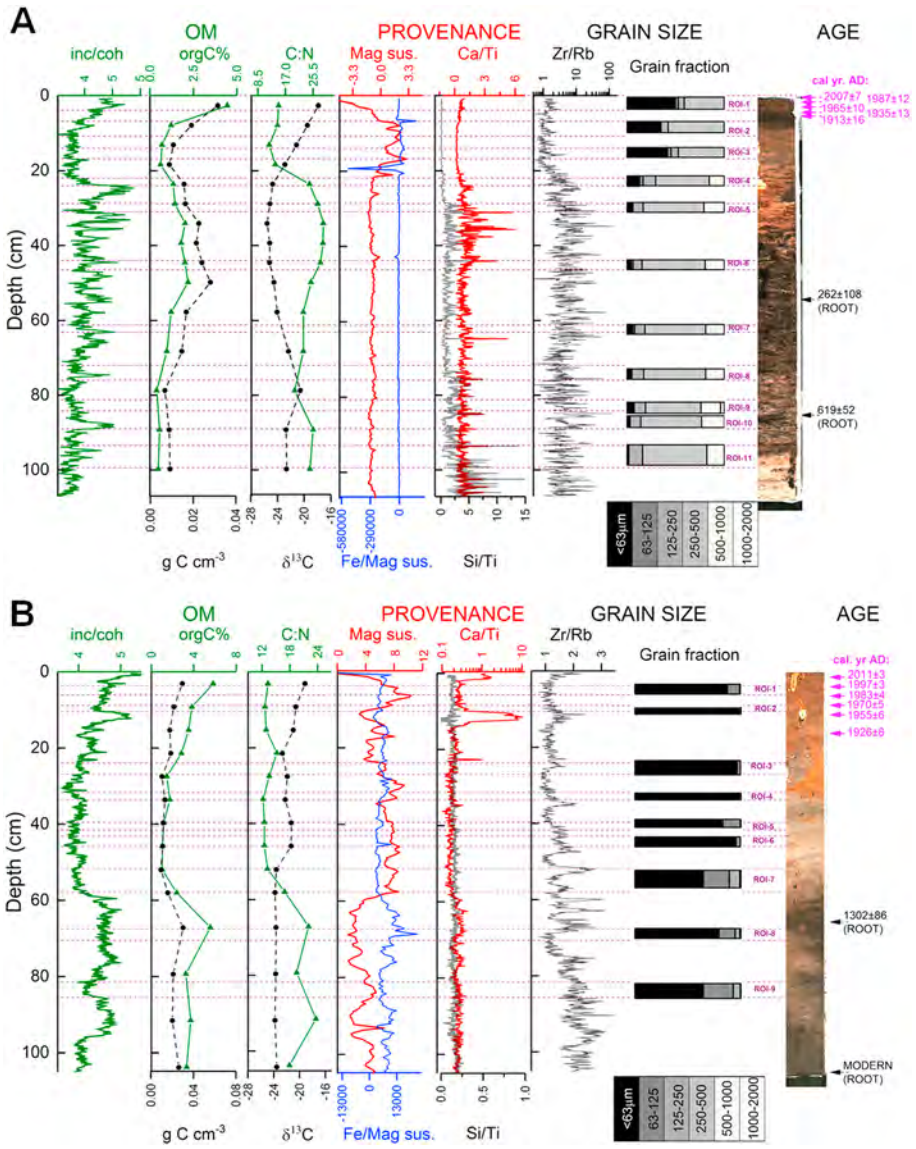


Figure 3. (a) POR-M and (b) POR-F core profiles derived from ITRAX core scanning, depth interval, and region of interest (ROI) sampling. Optical core image is presented on the right with ^{210}Pb derived ages presented for surface sediments (pink text) and calibrated ^{14}C ages of specific materials in deeper sections (black text). ROIs for discrete sampling of grain size analysis and molecular composition are labeled and marked by dashed lines.

appeared stable (Figure 4). That is, plant-derived functional groups dominated, though with the selective retention of lignin relative to carbohydrates. The mineral composition (elevated Ca/Ti and Si/Ti); low magnetic susceptibility and dominance of coarse grains (indicated by both elevated Zr/Rb and discrete measurements of grain size) indicate marine sedimentary inputs below ~30 cm.

3.4. POR-F

POR-F contained the highest C stocks over 100 cm of the four cores studied. Surface C accumulation rates were similar to WAP-F, with both higher than those of the marine cores (Table 1 and Figure S3). A large, contemporary mangrove pneumatophore and associated fine roots were observed in the surface sediments (see core image in Figure 3b), coinciding with peaks in inc/coh and %C. Bulk δ^{13}C values in the surface 50 cm sat between those of the more enriched roots of the C4 saltmarsh plant *S. virginicus* (−14.6 to −14.9‰) and the more depleted *A. marina* pneumatophore (−27.4 to −27.9‰) collected from the site, while C:N was mostly constant in the surface 50 cm.

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

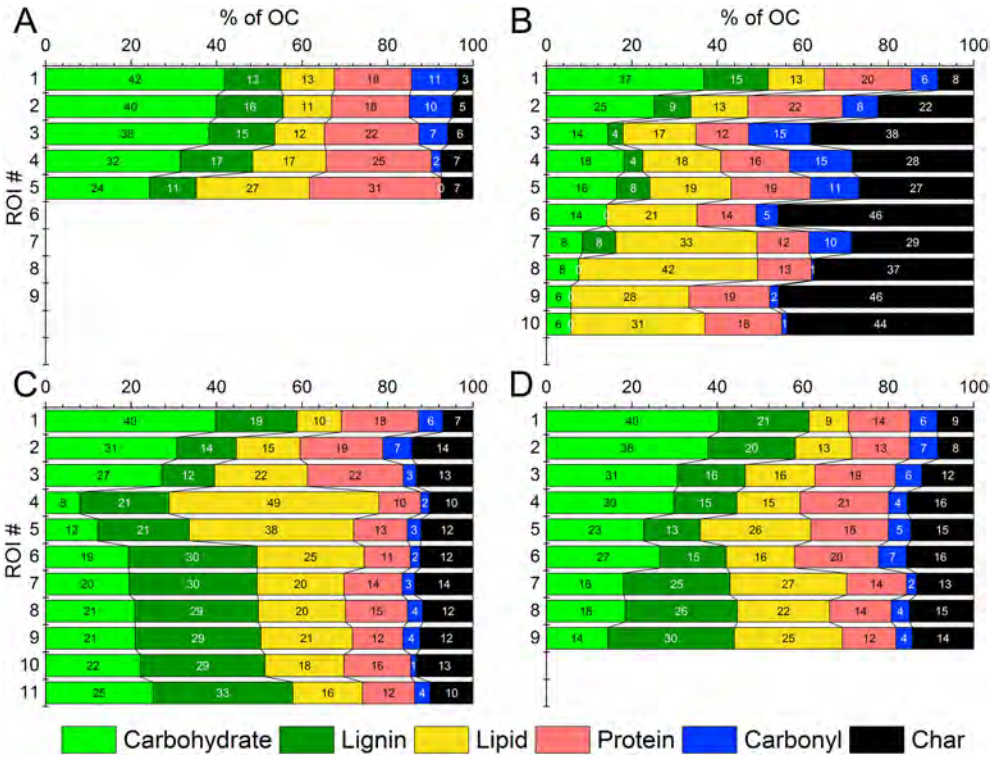


Figure 4. Proportional (%) contributions of six biomolecule groups to organic C in ROIs located throughout the depth range of the four study cores: (a) WAP-M, (b) WAP-F, (c) POR-M, and (d) POR-F. C density was insufficient to obtain reliable ^{13}C NMR spectra for WAP-M ROIs 6–9. For the location of each ROI in each core see corresponding plots in Figures 2 and 3.

Below ~50 cm, sedimentary properties underwent a marked shift, with a broadening of the grain size distribution. Visual inspection of this zone revealed an accumulation of partially decayed *A. marina* mangrove roots, like that seen in POR-M. Radiocarbon analyses of *A. marina* roots at 65 cm and 108 cm returned dates of 1302 ± 86 cal years AD and "modern" (i.e., at or after 1956/7), respectively (Table 2). Like in POR-M, the accumulation of mangrove roots was mirrored by increases in subsurface C:N (Figure 3). While the relative contribution of carbohydrates declined with depth in the POR-F core, there was a marked preservation of plant derived C—mostly lignin—below ROI 6. This decline in carbohydrate C was matched by a relative increase in the contribution of lipids.

4. Discussion

Our detailed analysis of saltmarsh cores revealed different environmental histories and C preservation conditions among the four study sites. Based on the data presented, we interpret the WAP-M core as shifting from a high energy, subtidal elevation (with shell hash at 70 cm and below) to mineral sediments dominated by coarse sands and later to the contemporary (last ~100 years), vegetated saltmarsh surface. The distribution of fine roots only and deposition of strandline materials—e.g., pumice [*Ward and Little*, 2000] and char—in WAP-F points to a predominantly vegetated, intertidal, to lower supratidal history with no evidence of mangrove or upland tree colonization. At POR-M, the substantial shift in grain size and shift toward terrigenous sediment provenance above ~30 cm is consistent with the capacity of mangrove pneumatophores to slow water movement, and trap fine sediments [*Furukawa and Wolanski*, 1996]. This sedimentary change, along with the downcore distribution of preserved plant roots, leads us to interpret a historic mangrove colonization (i.e., ~30 cm depth) of previously unvegetated (probably subtidal to lower intertidal) sediments. Although sampled within saltmarsh vegetation, the POR-F core is strongly influenced by both saltmarsh and mangrove belowground biomass, with the latter including both modern and preserved, historic inputs.

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

4.1. Implications for Blue Carbon Research

Among-site variability has important implications for attempts to characterize blue carbon based on contemporary environmental conditions. Our results suggest that contemporary vegetation structure is likely to be a poor predictor of both C stocks and C accumulation rates. That is, we found approximately threefold, fivefold, and sixfold differences in bulk accumulation, C stock, and C accumulation rates, respectively, among sites characterized by the same vegetation association [*Zedler et al.*, 1995]. For SE Australian saltmarshes this may not be particularly surprising, given that sedimentary factors (rather than vegetation factors) have been identified to be important in predicting saltmarsh C stocks [*Kelleway et al.*, 2016a; *Macreadie et al.*, 2017]. Surface expressions of sediment character and geomorphic setting, however, still fail to account for much of the variability observed in the present study. For example, there are stark differences among the two marine tidal delta cores—WAP-M exhibits faster surface C accumulation, but very low C store, while POR-M exhibits the opposite—slow surface C accumulation, but high C store (Table 1).

The two fluvial cores show some similarity to one another, including above average C stocks relative to regional estimates (regional mean = 164 Mg C ha^{-1}) [*Kelleway et al.*, 2016a] and C accumulation rates for *Sarcocornia-Sporobolus* association saltmarshes (0.46 Mg C ha^{-1} yr^{-1}) [*Saintilan et al.*, 2013]. These similarities occur despite substantial differences in bulk accumulation rates at the two sites (Table 1). That is, the POR-F surface is accumulating bulk materials which are lower in %C, but at a faster rate (2 mm yr^{-1}), which is consistent with accumulation dominated by mineral sediments. In contrast, the exceptionally slow surface accumulation rate and high %C in WAP-F suggest low mineral inputs relative to plant organic matter inputs. Finally, apart from WAP-M, there is also considerable deviation in C stocks from site mean values for each of the cores analyzed in this study (Table 1), despite the expectation of similar geomorphic influences at the within-site scale.

Together, these findings indicate that simple delineations of contemporary vegetation structure and geomorphic setting are not sufficient to explain the spatial variability in blue carbon stocks and accumulation processes. Instead, we need to consider the broader factors of ecosystem stability and environmental change, including historic differences in vegetation and geomorphic processes and the role of C preservation/degradation over time.

4.2. Ecosystem Stability and Environmental Change

Growing interest in blue carbon is based largely upon the potential of saltmarsh, mangrove, and seagrass ecosystems to store C over centennial and millennial time scales. Such a capacity implies an inherent stability within these ecosystems, which is somewhat incongruous with their location within some dynamic areas of estuaries and the coastal ocean [*Dalrymple et al.*, 1992; *Roy et al.*, 2001; *Woodroffe et al.*, 1985]. There are a small number of studies demonstrating exceptional ecosystem stability among seagrass and mangrove ecosystems that were integral to the development of the blue carbon concept. Among these was the discovery of Mediterranean seagrasses which have persisted for over ~5000 years, with continued ecosystem function in the form of C sequestration [*Lo Iacono et al.*, 2008]. That study pointed to stability in local (subtidal) environmental conditions as an important factor in the persistence of seagrass and associated C sequestration. Furthermore, the capacity of intertidal mangrove ecosystems to persist up to 7500 years in the Caribbean, while building belowground C stocks up to 10 m in depth over this time, demonstrates exceptional ecosystem resilience in the face of changing sea level [*McKee et al.*, 2007]. While there are likely to be other instances where either environmental stability or ecosystem resilience leads to ecosystem persistence (and consequently long-term blue carbon accumulation), the results of our study demonstrate that this in not always the case. In fact, our study shows that multiple distinct ecosystem shifts (e.g., unvegetated ➔ mangrove ➔ saltmarsh) may be represented throughout just the surface meter of some blue carbon habitats. This therefore raises important questions—what do ecosystem shifts mean for rates of blue carbon accumulation and storage and what are implications for upscaling blue carbon estimates to broader spatial scales?

4.2.1. Ecosystem Shifts Influence C

Our study shows that ecosystem transitions associated with the geomorphic evolution of estuarine sediments have important implications for C storage. This difference is most evident in the two marine cores where shifts from unvegetated sediments to saltmarsh sediments occurred at both sites. In WAP-M, C inputs appear to be restricted to saltmarsh vegetation which probably only within the past ~100 years. Consequently, this site contains the lowest C stocks (Table 1). Much higher C stocks at POR-M are due in

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

large part to the occurrence of an intermediate mangrove phase, which persisted for ~300 years or more (Table 2). The downcore expansion of mangrove roots at that time appears to have substantially increased belowground C stocks (Figure 3a). Similarly, the persistence of old and modern mangrove C inputs at POR-F are responsible for much of the overall C stock measured in that core (Figure 3b).

Our records of ecosystem shifts from unvegetated or mangrove-vegetated intertidal to lower supratidal vegetation (saltmarsh) are broadly consistent with the gradual infilling of estuaries proposed by geomorphic models of estuary evolution [*Roy*, 1984; *Roy et al.*, 2001], whereby fluvial deltas prograde seaward, and (depending on entrance conditions) marine deltas prograde landward. The prograding deltas thereby infill the former mangrove zones with sediments to an extent that their elevation rises in respect to the tidal frame where conditions favor saltmarsh vegetation. Based on evolutionary models, we expect that similar ecosystem shifts would be preserved in similar situations throughout the region.

In this study, mangrove roots were preserved within cores collected from Port Stephens—a drowned river valley in an intermediate evolutionary phase and a broad tidal range. In the nearby Hawkesbury River estuary (also a drowned river estuary in an intermediate state of infilling) *Saintilan and Hashimoto* [1999] found mangrove root systems dating from 500 to 1700 years B.P. preserved ~30 cm below the contemporary saltmarsh surface, highlighting a mangrove to saltmarsh transition associated with the development of the fluvial delta in this location. Similarly, preserved root material at similar depths (from 20 cm below the contemporary surface) also indicated the evolution of sediment surface (relative to local sea level) in the marine settings of Currumbene Creek and Cararma Inlet further south in NSW [*Saintilan and Wilton*, 2001]. At other saltmarsh sites, however, relics of the supratidal tree *Casuarina glauca* within the contemporary saltmarsh [e.g., *Kelleway et al.*, 2016a] indicate a drop in surface elevation relative to local sea level, highlighting the complexity of geomorphic change within estuaries in the same region. Further, while the spatial coverage of blue carbon research has grown throughout the region in recent years, the record of ecosystem shifts below contemporary surface sediments in the region still remains largely unexplored.

Importantly, the preservation of historic blue carbon stocks in settings which have since undergone ecosystem change is not limited to our study region of SE Australia. Across northern Australia, stratigraphic evidence of extensive mangrove root networks below contemporary sedgelands, grasslands, and unvegetated flats was used to demonstrate the occurrence of a "big mangrove swamp" phase in that region between 5500–7000 years B.P. [*Woodroffe et al.*, 1985]. Similarly, extensive coring of Mekong River delta sediments has revealed mangrove, saltmarsh, and tidal flat development below contemporary floodplain and anthropogenic sediments [*Hanebuth et al.*, 2012]. To date, the C storage associated with preserved blue carbon in such locations remains uncalculated, though it may be substantial given the sizes of the deltaic systems involved. Similarly, evidence of successional patterns in mangrove vegetation in locations as diverse as the Mekong delta [*Li et al.*, 2012] to Florida in the southeast USA [*Ball*, 1980] also remain unquantified in terms of their influence on blue carbon stocks.

4.2.2. Catchment History and Land Use

Environmental changes which do not involve a shift in ecosystem structure may also influence the quantity and quality of C which accumulates in coastal habitats. Recent studies in Australian seagrass beds, for example, have demonstrated shifts in the amount and source of C accumulating in seagrass sediments after post-European settlement modifications to local catchments [*Macreadie et al.*, 2012; *Serrano et al.*, 2016a]. In the present study, evidence of catchment disturbance is most obvious in the WAP-F core where a massive peak in magnetic susceptibility (an indicator of catchment erosion and subsequent deposition) in ROI-2 coincides with the timing of land-clearing for agricultural purposes in the region [*NSW National Parks and Wildlife Service*, 2011]. Such sedimentation events may play an important role in the preservation of C by shortening oxygen exposure times and creating a reducing environment below which C remineralization efficiency declines [*Kristensen*, 2000; *Kristensen et al.*, 2008]. More recently, the construction of small farm dams across drainage lines upslope of the saltmarsh has probably created effective sediment traps, starving the wetland of sediments and resulting in extremely slow contemporary surface accumulation relative to other fluvial sites in the region (Table 1) [*Rogers et al.*, 2006].

The role of catchment processes becomes even more distinct in the deeper, pre-European sediments of WAP-F. Here mixing model outputs show char C accounted for almost half of all C in some deep ROIs. The proportion increase in char C in deeper sediments (relative to modern surface sediments) partly reflects

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the selective preservation of recalcitrant char with time, highlighting the primary importance of C character to preservation in marine sediments [*Dickens et al.*, 2006]. Variations in char contribution to these deep sediments (shifting from 27% to 46% among adjacent ROIs), however, highlight the temporal variability of char accumulation. Episodic events, including the timing of fires, but also mobilization (e.g., flood) and subsequent deposition (flood and/or tidal deposition) events, dictate the movement of this terrestrial C to blue carbon habitats. It is difficult to determine whether climatic conditions (such as El Niño–Southern Oscillation intensification) or Aboriginal burning practices explain char distribution downcore [*Macreadie et al.*, 2015] though both may play a role. The disparate radiocarbon dates of char fragments in this core profile (Figure 2b and Table 2) suggest that much of this material may be old char which has been redistributed within the catchment. In any case, their ages of 3205 ± 146, 7760 ± 122, and 4116 ± 230 calibrated (cal) year B.P., respectively, highlight the long-term preservation potential of this form of C.

Black C typically contributes ~2–30% of the carbon stock of marine sediments [*Burdige*, 2007], incorporating both char and geological sources [*Dickens et al.*, 2004]. Our char values for many strata within the WAP-F core not only exceeded these marine values but are also high relative to estimates of black C in fire-prone Australian terrestrial soils [*Lehmann et al.*, 2008; *Baldock et al.*, 2013]. Visual inspection of WAP-F clearly showed that fire-derived char was largely responsible for the high C contents measured in that core. Overall, this contribution from char warrants broader research on the contribution of char C to blue carbon stocks, with our preliminary research suggesting that (1) char C contributions may be substantial, (2) is likely to be spatially variable with increased contribution in sites subject to fluvial influence, and (3) is likely to be temporally dependent on catchment processes.

4.3. Preservation of Blue C

In all four cores, declines in C density were matched by shifts in molecular composition in near-surface sediments (Figure 4). This indicates degradation of C that has accumulated during the contemporary saltmarsh phase and is most apparent in the young (~100 year old) saltmarsh at WAP-M. Here C density and C molecular composition display down-core profiles which are broadly consistent with patterns of C decomposition typically seen in terrestrial soils [e.g., *Melillo et al.*, 1989; *Rovira and Vallejo*, 2002]. Such patterns are contrasted sharply by the preservation of mangrove roots in the POR-M and (to a lesser extent) POR-F cores. The preservation of bulk mangrove roots for at least ~1800 years (POR-M) and ~800 years (POR-F), respectively, suggests a greater C preservation capacity of *A. marina* roots relative to the contemporary *Sarcocornia-Sporobolus* vegetation. This could be due in part to the refractory nature of mangrove roots [*Bianchi et al.*, 2013; *McKee et al.*, 2007; *Middleton and McKee*, 2001] as evidenced by the selective preservation of lignin C apparent in both cores. However, preservation of some more labile biomolecules (e.g., carbohydrate contents >20% in some deeper ROIs) suggests that other factors associated with deep C preservation may also be important. Principal among these are low microbial activity associated with anaerobic and/or low nutrient conditions [*Kristensen et al.*, 2008; *Schmidt et al.*, 2011].

The effective preservation of mangrove roots has broader implication for blue carbon storage, as mangroves are currently expanding their range globally into saltmarsh ecosystems [*Saintilan et al.*, 2014]. While a recent study has shown that mangrove root development into and above the historic saltmarsh sediment increases total C stocks over a period of 70 years [*Kelleway et al.*, 2016b], the implications for longer-term preservation remain unclear. The findings of enhanced preservation of mangrove root C relative to saltmarsh root and rhizome C in the present study suggest that mangrove encroachment may also lead to longer-term C storage. Clearly though, further research is required here, especially regarding the likely preservation of tissues from a broader range of saltmarsh and mangrove species associated with this global phenomenon of encroachment.

Finally, although appearing less stable than their underlying mangrove roots, the contemporary saltmarsh surface may be playing an important role in the preservation of deeper C stocks. Shallow rooted saltmarsh plants and sediment accumulation associated with the saltmarsh phase appear to effectively cap the belowground mangrove deposits. This is particularly important where the protrusion of pneumatophores and bioturbation by mangrove fauna may result in increased oxygen diffusion deep into the sediment profile and cause enhanced rates of C remineralization and translocation of CO_2 gas from deeper sediments [*Kristensen et al.*, 2008]. By covering such features, saltmarsh materials effectively remove the historic mangrove C stocks from the oxidizing zone of the surface sediments and confine them to deeper sediments

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

where microbial remineralization is less efficient. The capacity of saltmarsh vegetation to bind sediments under hydrological phenomena such as sea level rise or tidal forces [*Feagin et al.*, 2009] may also be an important factor in preventing future loss of deeper C stocks.

5. Conclusions

The dynamic nature of estuaries, and specifically their intertidal and lower supratidal zones, means that the environmental history of a site is likely to be a key determinant of current C stocks. Factors including the age of current vegetation communities, the character of preceding vegetation, and biogeochemical conditions may all influence the storage and preservation of organic matter throughout the 0–100 cm depth range (and probably deeper). Specifically, the regional heterogeneity of mangrove root accumulation under contemporary saltmarshes in SE Australia introduces a substantial source of variability when blue carbon stock estimates are upscaled to larger spatial scales based upon contemporary landscape features such as contemporary vegetation maps. In many instances the nature of historic conditions and ecosystem change is difficult to ascertain. Consequently, historical information is largely excluded from regional blue carbon models.

To incorporate the variability introduced by environmental history, researchers and managers will need to find (or generate) information sources which integrate current landscape features with measured or modeled information regarding the geomorphic and vegetation history of locations of interest. In some instances, stratigraphic reconstructions of estuarine or coastal evolution may reveal organic subhorizons indicative of alternate blue carbon habitats. Similarly, acid sulfate soil mapping and modeling [e.g., *Smith et al.*, 2003] may alert users to the distribution of organic-rich subsoils in coastal areas. In some cases, these areas may now support habitats where blue carbon vegetation has been succeeded (e.g., contemporary supratidal floodplains). Where adequate information is not available, targeted sampling and reconstruction of environmental histories may be necessary. Although historically such studies may have been arduous and prohibitively time-consuming, more recent technological advances (such as ITRAX and ^{13}C NMR instruments utilized in this study) may partly ease this cost. Information gained from such studies which reconstruct environmental conditions associated with evolution of blue carbon habitats over past and recent time periods will become increasingly important as coastal wetlands around the world become subject to further anthropogenic, climatic, and sea level-related changes.

Acknowledgments

We thank the many individuals who assisted with field collection, sample preparation, and laboratory analyses, including Frederic Cadera, Janine McGowan, Bruce Hawke, Jack Goralewski, and Fiona Bertuch. Field collections were undertaken in accordance with NSW Office of Environment and Heritage scientific license SL101217 and NSW Department of Primary Industries Scientific Permit P13/0058-1.0. We also thank NSW National Parks and Wildlife Service for supporting access to conservation reserves for fieldwork. This research was supported by the Plant Functional Biology and Climate Change Cluster, CSIRO Coastal Carbon Cluster, and an Australian Institute of Nuclear Science and Engineering AINSE grant (ALNGRA14004) and PGRA grant (ALNSTU11903). We acknowledge the financial support from the Australian Government for the Centre for Accelerator Science at ANSTO through the National Collaborative Research Infrastructure Strategy (NCRIS). P.M. was supported by an Australian Research Council DECRA Fellowship (DE130101084). Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.t6j7f.

References

Adam, P., N. Wilson, and B. Huntley (1988), The phytosociology of coastal saltmarsh vegetation in New South Wales, *Wetlands (Australia)*, *7*(2), 35–85.

Adame, M. F., D. Neil, S. F. Wright, and C. E. Lovelock (2010), Sedimentation within and among mangrove forests along a gradient of geomorphological settings, *Estuarine Coastal Shelf Sci.*, *86*(1), 21–30.

Agnihotri, R., M. A. Altabet, T. D. Herbert, and J. E. Tierney (2008), Subdecadally resolved paleoceanography of the Peru margin during the last two millennia, *Geochem. Geophys. Geosyst.*, *9*, Q05013, doi:10.1029/2007GC001744.

Alongi, D. M. (2002), Present state and future of the world's mangrove forests, *Environ. Conserv.*, *29*(3), 331–349.

Appleby, P., and F. Oldfield (1978), The calculation of lead-210 dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment, *Catena*, *5*(1), 1–8.

Appleby, P., and F. Oldfield (1983), The assessment of ^{210}Pb data from sites with varying sediment accumulation rates, *Hydrobiologia*, *103*, 29–35, doi:10.1007/BF00028424.

Atahan, P., H. Heijnis, J. Dodson, K. Grice, P. Le Métayer, K. Taffs, S. Hembrow, M. Woltering, and A. Zawadzki (2015), Pollen, biomarker and stable isotope evidence of late Quaternary environmental change at Lake McKenzie, southeast Queensland, *J. Paleolimnol.*, *53*(1), 139–156.

Baldock, J. A., and R. J. Smernik (2002), Chemical composition and bioavailability of thermally altered *Pinus resinosa* (red pine) wood, *Org. Geochem.*, *33*(9), 1093–1109, doi:10.1016/S0146-6380(02)00062-1.

Baldock, J. A., C. Masiello, Y. Gelinas, and J. Hedges (2004), Cycling and composition of organic matter in terrestrial and marine ecosystems, *Mar. Chem.*, *92*(1), 39–64.

Baldock, J. A., J. Sanderman, L. M. Macdonald, A. Puccini, B. Hawke, S. Szarvas, and J. McGowan (2013), Quantifying the allocation of soil organic carbon to biologically significant fractions, *Soil Res.*, *51*(8), 561, doi:10.1071/sr12374.

Ball, M. C. (1980), Patterns of secondary succession in a mangrove forest of southern Florida, *Oecologia*, *44*(2), 226–235.

Bartholomä, A., and B. W. Flemming (2007), Progressive grain-size sorting along an intertidal energy gradient, *Sediment. Geol.*, *202*(3), 464–472, doi:10.1016/j.sedgeo.2007.03.010.

Bianchi, T. S., M. A. Allison, J. Zhao, X. Li, R. S. Comeaux, R. A. Feagin, and R. W. Kulawardhana (2013), Historical reconstruction of mangrove expansion in the Gulf of Mexico: Linking climate change with carbon sequestration in coastal wetlands, *Estuarine Coastal Shelf Sci.*, *119*, 7–16.

Burdige, D. J. (2007), Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets?, *Chem. Rev.*, *107*(2), 467–485.

Burnett, A. P., M. J. Soreghan, C. A. Scholz, and E. T. Brown (2011), Tropical East African climate change and its relation to global climate: A record from Lake Tanganyika, tropical East Africa, over the past 90+ kyr, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *303*(1–4), 155–167, doi:10.1016/j.palaeo.2010.02.011.

Chen, Y., G. Chen, and Y. Ye (2015), Coastal vegetation invasion increases greenhouse gas emission from wetland soils but also increases soil carbon accumulation, *Sci. Total Environ.*, *526*, 19–28.

Clarke, P. J., and C. A. Jacoby (1994), Biomass and above-ground productivity of salt-marsh plants in south-eastern Australia, *Mar. Freshwater Res.*, *45*(8), 1521–1528.

Creese, R., T. Glasby, G. West, and C. Gallen (2009), Mapping the habitats of NSW estuaries, Rep., 95 pp., Industry & Investment NSW, Port Stephens, NSW, Australia.

Croudace, I. W., A. Rindby, and R. G. Rothwell (2006), ITRAX: Description and evaluation of a new multi-function X-ray core scanner, *Geol. Soc. London Spec. Publ.*, *267*, 51.

Dalrymple, R. W., B. A. Zaitlin, and R. Boyd (1992), Estuarine facies models: Conceptual basis and stratigraphic implications: Perspective, *J. Sediment. Res.*, *62*(6).

Davies, G. (2011), Downstream changes in the cross-sectional shape of tidal channels.

Derenne, S., and C. Largeau (2001), A review of some important families of refractory macromolecules: Composition, origin, and fate in soils and sediments, *Soil Sci.*, *166*(11), 833–847.

Dickens, A. F., J. A. Baldock, R. J. Smernik, S. G. Wakeham, T. S. Arnarson, Y. Gélinas, and J. I. Hedges (2006), Solid-state ^{13}C NMR analysis of size and density fractions of marine sediments: Insight into organic carbon sources and preservation mechanisms, *Geochim. Cosmochim. Acta*, *70*(3), 666–686, doi:10.1016/j.gca.2005.10.024.

Dickens, A. F., Y. Gelinas, C. A. Masiello, S. Wakeham, and J. I. Hedges (2004), Reburial of fossil organic carbon in marine sediments, *Nature*, *427*(6972), 336–339.

Donato, D. C., J. B. Kauffman, D. Murdiyarso, S. Kurnianto, M. Stidham, and M. Kanninen (2011), Mangroves among the most carbon-rich forests in the tropics, *Nat. Geosci.*, *4*(5), 293–297.

Duarte, C. M., I. J. Losada, I. E. Hendriks, I. Mazarrasa, and N. Marbà (2013), The role of coastal plant communities for climate change mitigation and adaptation, *Nat. Clim. Change*, *3*(11), 961–968.

Enríquez, S., C. M. Duarte, and K. Sand-Jensen (1993), Patterns in decomposition rates among photosynthetic organisms: The importance of detritus C:N:P content, *Oecologia*, *94*(4), 457–471.

Feagin, R., S. Lozada-Bernard, T. Ravens, I. Möller, K. Yeager, and A. Baird (2009), Does vegetation prevent wave erosion of salt marsh edges?, *Proc. Natl. Acad. Sci. U.S.A.*, *106*(25), 10,109–10,113.

Fink, D., M. Hotchkis, Q. Hua, G. Jacobsen, A. Smith, U. Zoppi, D. Child, C. Mifsud, H. van der Gaast, and A. Williams (2004), The Antares AMS facility at ANSTO, *Nucl. Instrum. Methods Phys. Res., Sect. B*, *223*, 109–115.

Fourqurean, J. W., C. M. Duarte, H. Kennedy, N. Marbà, M. Holmer, M. A. Mateo, E. T. Apostolaki, G. A. Kendrick, D. Krause-Jensen, and K. J. McGlathery (2012), Seagrass ecosystems as a globally significant carbon stock, *Nat. Geosci.*, *5*(7), 505–509.

Furukawa, K., and E. Wolanski (1996), Sedimentation in mangrove forests, *Mangrove Salt Marshes*, *1*(1), 3–10.

Grandy, A. S., and J. C. Neff (2008), Molecular C dynamics downstream: The biochemical decomposition sequence and its impact on soil organic matter structure and function, *Sci. Total Environ.*, *404*(2–3), 297–307, doi:10.1016/j.scitotenv.2007.11.013.

Hanebuth, T. J. J., U. Proske, Y. Saito, V. L. Nguyen, and T. K. O. Ta (2012), Early growth stage of a large delta—Transformation from estuarine-platform to deltaic-progradational conditions (the northeastern Mekong River Delta, Vietnam), *Sediment. Geol.*, *261–262*, 108–119, doi:10.1016/j.sedgeo.2012.03.014.

Hofmann, D. I., K. Fabian, F. Schmieder, B. Donner, and U. Bleil (2005), A stratigraphic network across the subtropical front in the central South Atlantic: Multi-parameter correlation of magnetic susceptibility, density, X-ray fluorescence and δ^{18}O records, *Earth Planet. Sci. Lett.*, *240*(3), 694–709.

Hogg, A., Q. Hua, P. Blackwell, M. Niu, C. Buck, T. Guilderson, T. Heaton, J. Palmer, P. Reimer, and R. Reimer (2013), SHCal13 southern hemisphere calibration, 0-50,000 cal yr BP, *Radiocarbon 55*, 1889–1903.

Howes, B. L., J. W. Dacey, and G. M. King (1984), Carbon flow through oxygen and sulfate reduction pathways in salt marsh sediments, *Limnol. Oceanogr.*, *29*, 1037–1051.

Hua, Q., G. Jacobsen, U. Zoppi, E. Lawson, A. Williams, A. Smith, and M. McGann (2001), Progress in radiocarbon target preparation at the ANTARES AMS Centre, *Radiocarbon*, *43*(2; PART A), 275–282.

Jaschinski, S., T. Hansen, and U. Sommer (2008), Effects of acidification in multiple stable isotope analyses, *Limnol. Oceanogr. Methods*, *6*(1), 12–15, doi:10.4319/lom.2008.6.12.

Kelleway, J. J., N. Saintilan, P. I. Macreadie, and P. J. Ralph (2016a), Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes, *Ecosystems*, doi:10.1007/s10021-016-9972-3.

Kelleway, J. J., N. Saintilan, P. I. Macreadie, C. G. Skilbeck, A. Zawadzki, and P. J. Ralph (2016b), Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes, *Global Change Biol.*, *22*, 1097–1109, doi:10.1111/gcb.13158.

Kennedy, H., J. Beggins, C. M. Duarte, J. W. Fourqurean, M. Holmer, N. Marbà, and J. J. Middelburg (2010), Seagrass sediments as a global carbon sink: Isotopic constraints, *Global Biogeochem. Cycles*, *24*, GB4026, doi:10.1029/2010GB003848.

King, G. M. (1983), Sulfate reduction in Georgia salt marsh soils: An evaluation of pyrite formation by use of ^{35}S and ^{55}Fe tracers, *Limnol. Oceanogr.*, *28*, 987–995.

Kirwan, M. L., J. A. Langley, G. R. Guntenspergen, and J. P. Megonigal (2013), The impact of sea-level rise on organic matter decay rates in Chesapeake Bay brackish tidal marshes, *Biogeosciences*, *10*(3), 1869–1876, doi:10.5194/bg-10-1869-2013.

Kirwan, M. L., and J. P. Megonigal (2013), Tidal wetland stability in the face of human impacts and sea-level rise, *Nature*, *504*(7478), 53–60, doi:10.1038/nature12856.

Kristensen, E. (1994), Decomposition of macroalgae, vascular plants and sediment detritus in seawater: Use of stepwise thermogravimetry, *Biogeochemistry*, *26*(1), 1.

Kristensen, E. (2000), Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals, *Hydrobiologia*, *426*(1), 1–24.

Kristensen, E., S. Bouillon, T. Dittmar, and C. Marchand (2008), Organic carbon dynamics in mangrove ecosystems: A review, *Aquat. Bot.*, *89*(2), 201–219.

Lehmann, J., J. Skjemstad, S. Sohi, J. Carter, M. Barson, P. Falloon, K. Coleman, P. Woodbury, and E. Krull (2008), Australian climate–carbon cycle feedback reduced by soil black carbon, *Nat. Geosci.*, *1*(12), 832–835, doi:10.1038/ngeo358.

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Li, Z., Y. Saito, L. Mao, T. Tamura, Z. Li, B. Song, Y. Zhang, A. Lu, S. Sieng, and J. Li (2012), Mid-Holocene mangrove succession and its response to sea-level change in the upper Mekong River delta, Cambodia, *Quat. Res.*, *78*(2), 386–399, doi:10.1016/j.yqres.2012.07.001.

Lo Iacono, C., M. A. Mateo, E. Gràcia, L. Guasch, R. Carbonell, L. Serrano, O. Serrano, and J. Dañobeitia (2008), Very high-resolution seismo-acoustic imaging of seagrass meadows (Mediterranean Sea): Implications for carbon sink estimates, *Geophys. Res. Lett.*, *35*, L18601, doi:10.1029/2008GL034773.

Lord III, C. J., and T. M. Church (1983), The geochemistry of salt marshes: Sedimentary ion diffusion, sulfate reduction, and pyritization, *Geochim. Cosmochim. Acta*, *47*(8), 1381–1391, doi:10.1016/0016-7037(83)90296-X.

Lovelock, C. E., M. F. Adame, V. Bennion, M. Hayes, J. O'Mara, R. Reef, and N. S. Santini (2013), Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of south East Queensland, Australia, *Estuaries Coasts*, *37*(3), 763–771, doi:10.1007/s12237-013-9702-4.

Macreadie, P. I., K. Allen, B. P. Kelaher, P. J. Ralph, and C. G. Skilbeck (2012), Paleoreconstruction of estuarine sediments reveal human-induced weakening of coastal carbon sinks, *Global Change Biol.*, *18*(3), 891–901, doi:10.1111/j.1365-2486.2011.02582.x.

Macreadie, P. I., T. C. Rolph, R. Boyd, C. J. Schroder-Adams, and C. G. Skilbeck (2015), Do ENSO and coastal development enhance coastal burial of terrestrial carbon?, *PLoS One*, *10*(12), e0145136, doi:10.1371/journal.pone.0145136.

Macreadie, P. I., et al. (2017), Carbon sequestration by Australian tidal marshes, *Sci. Rep.*, *7*, 44071, doi:10.1038/srep44071.

McKee, K. L., D. R. Cahoon, and I. C. Feller (2007), Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation, *Global Ecol. Biogeogr.*, *16*(5), 545–556.

McLeod, E., G. L. Chmura, S. Bouillon, R. Salm, M. Björk, C. M. Duarte, C. E. Lovelock, W. H. Schlesinger, and B. R. Silliman (2011), A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2, *Front. Ecol. Environ.*, *9*(10), 552–560, doi:10.1890/110004.

Melillo, J. M., J. D. Aber, A. E. Linkins, A. Ricca, B. Fry, and K. J. Nadelhoffer (1989), Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter, in *Ecology of Arable Land—Perspectives and Challenges*, pp. 53–62, Springer, Dordrecht, Holland.

Middleton, B. A., and K. L. McKee (2001), Degradation of mangrove tissues and implications for peat formation in Belizean island forests, *J. Ecol.*, *89*(5), 818–828, doi:10.1046/j.0022-0477.2001.00602.x.

Mitchell, M., and P. Adam (1989), The relationship between mangrove and saltmarsh communities in the Sydney region, *Wetlands (Australia)*, *8*(2), pp. 37–46.

Nelson, P. N., and J. A. Baldock (2005), Estimating the molecular composition of a diverse range of natural organic materials from solid-state ^{13}C NMR and elemental analyses, *Biogeochemistry*, *72*(1), 1–34, doi:10.1007/s10533-004-0076-3.

Nixon, S. W. (1980), Between coastal marshes and coastal waters: A review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry, URI, Marine Advisory Service, Publications Unit.

NSW National Parks and Wildlife Service (2011), Mimosa Rocks National Park Plan of Management, Rep. 978 1 74293 219 4, 86 pp., Dep. of Environ., Clim. Change and Water.

Pendleton, L., D. C. Donato, B. C. Murray, S. Crooks, W. A. Jenkins, S. Sifleet, C. Craft, J. W. Fourqurean, J. B. Kauffman, and N. Marbà (2012), Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems, *PLoS One*, *7*(9), e43542.

Ramsey, C. B. (2009), Bayesian analysis of radiocarbon dates, *Radiocarbon*, *51*(1), 337–360.

Reimer, P. J., E. Bard, A. Bayliss, J. W. Beck, P. G. Blackwell, C. B. Ramsey, C. E. Buck, H. Cheng, R. L. Edwards, and M. Friedrich (2013), IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP, *Radiocarbon*, *55*(4), 1869–1887.

Ricart, A. M., P. H. York, M. A. Rasheed, M. Pérez, J. Romero, C. V. Bryant, and P. I. Macreadie (2015), Variability of sedimentary organic carbon in patchy seagrass landscapes, *Mar. Pollut. Bull.*, *100*(1), 476–482.

Rogers, K., K. M. Wilton, and N. Saintilan (2006), Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia, *Estuarine Coastal Shelf Sci.*, *66*(3–4), 559–569, doi:10.1016/j.ecss.2005.11.004.

Roper, T., B. Creese, P. Scanes, K. Stephens, R. Williams, J. Dela-Cruz, G. Coade, B. Coates, and M. Fraser (2011), Assessing the condition of estuaries and coastal lake ecosystems in NSW, *NSW State Catchments 2010*, 239.

Rothwell, R. G., and I. W. Croudace (2015), Twenty years of XRF core scanning marine sediments: What do geochemical proxies tell us?, in *Micro-XRF Studies of Sediment Cores*, pp. 25–102, Springer, Dordrecht, Holland.

Rovira, P., and V. R. Vallejo (2002), Labile and recalcitrant pools of carbon and nitrogen in organic matter decomposing at different depths in soil: An acid hydrolysis approach, *Geoderma*, *107*(1–2), 109–141, doi:10.1016/S0016-7061(01)00143-4.

Roy, P. (1984), New South Wales Estuaries: Their Origin and Evolution, in *Coastal Geomorphology in Australia*, edited by B. G. Thom, pp., 99–121, Academic Press, Sydney.

Roy, P., and R. Boyd (1996), Quaternary geology of southeast Australia: A tectonically stable, wave-dominated, sediment deficient margin, Field Guide to the Central New South Wales Coast, IGCP Project# 367, paper presented at International Conference, Sydney.

Roy, P., and L. Matthei (1996), Late Cainozoic clay deposits in the Port Stephens area, New South Wales, *Aust. J. Earth Sci.*, *43*(4), 395–400.

Roy, P., R. Williams, A. Jones, I. Yassini, P. Gibbs, B. Coates, R. West, P. Scanes, J. Hudson, and S. Nichol (2001), Structure and function of south-east Australian estuaries, *Estuarine Coastal Shelf Sci.*, *53*(3), 351–384.

Roy, P. S., and B. G. Thom (1981), Late Quaternary marine deposition in New South Wales and southern Queensland—An evolutionary model, *J. Geol. Soc. Aust.*, *28*(3–4), 471–489, doi:10.1080/00167618108729182.

Saintilan, N., and T. Hashimoto (1999), Mangrove-saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia, *Hydrobiologia*, *413*, 95–102.

Saintilan, N., and K. Wilton (2001), Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia, *Wetl. Ecol. Manage*, *9*(5), 409–420.

Saintilan, N., K. Rogers, D. Mazumder, and C. Woodroffe (2013), Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands, *Estuarine Coastal Shelf Sci.*, *128*, 84–92.

Saintilan, N., N. C. Wilson, K. Rogers, A. Rajkaran, and K. W. Krauss (2014), Mangrove expansion and salt marsh decline at mangrove poleward limits, *Global Change Biol.*, *20*(1), 147–157, doi:10.1111/gcb.12341.

Schmidt, M. W., et al. (2011), Persistence of soil organic matter as an ecosystem property, *Nature*, *478*(7367), 49–56, doi:10.1038/nature10386.

Serrano, O., P. Lavery, P. Masque, K. Inostroza, J. Bongiovanni, and C. Duarte (2016a), Seagrass sediments reveal the long-term deterioration of an estuarine ecosystem, *Global Change Biol.*, doi:10.1111/gcb.13195.

Serrano, O., P. S. Lavery, C. M. Duarte, G. A. Kendrick, A. Calafat, P. York, A. Steven, and P. Macreadie (2016b), Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems?, *Biogeosci. Discuss.*, *2016*, 1–24, doi:10.5194/bg-2015-598.

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Skjemstad, J., P. Clarke, J. Taylor, J. Oades, and R. Newman (1994), The removal of magnetic materials from surface soils-a solid state ^{13}C CP/MAS NMR study, *Soil Res.*, *32*(6), 1215–1229.

Smith, J., P. van Oploo, H. Marston, M. D. Melville, and B. C. T. Macdonald (2003), Spatial distribution and management of total actual acidity in an acid sulfate soil environment, McLeods Creek, northeastern NSW, Australia, *Catena*, *51*(1), 61–79, doi:10.1016/S0341-8162(02)00069-3.

Swales, A., S. J. Bentley, and C. E. Lovelock (2015), Mangrove-forest evolution in a sediment-rich estuarine system: Opportunists or agents of geomorphic change?, *Earth Surf. Processes Landforms*, *40*(12), 1672–1687, doi:10.1002/esp.3759.

Trevathan-Tackett, S. M., J. J. Kelleway, P. I. Macreadie, J. Beardall, P. Ralph, and A. Bellgrove (2015), Comparison of marine macrophytes for their contributions to blue carbon sequestration, *Ecology*, *96*(11), 3043–3057.

Ulm, S. (2006), Australian marine reservoir effects: A guide to ΔR values, *Aust. Archaeol.*, *63*, 57–60.

van der Land, C., F. Mienis, H. de Haas, H. C. de Stigter, R. Swennen, J. J. G. Reijmer, and T. C. E. van Weering (2011), Paleo-redox fronts and their formation in carbonate mound sediments from the Rockall Trough, *Mar. Geol.*, *284*(1–4), 86–95, doi:10.1016/j.margeo.2011.03.010.

Ward, W., and I. Little (2000), Sea-rafted pumice on the Australian east coast: Numerical classification and stratigraphy, *Aust. J. Earth Sci.*, *47*(1), 95–109.

West, R. J., C. Thorogood, T. Walford, and R. Williams (1985), *An Estuarine Inventory for New South Wales, Australia*, pp. 1–140, Fisheries Bulletin, Department of Agriculture New South Wales, Sydney, Australia.

Woodroffe, C. D., B. G. Thom, and J. Chappell (1985), Development of widespread mangrove swamps in mid-Holocene times in northern Australia, *Nature*, *317*(6039), 711–713.

Zedler, J., P. Nelson, and P. Adam (1995), Plant community organization in New South Wales saltmarshes: Species mosaics and potential causes, *Wetlands (Australia)*, *14*(1), 1–18.

Zhou, J., Y. Wu, J. Zhang, Q. Kang, and Z. Liu (2006), Carbon and nitrogen composition and stable isotope as potential indicators of source and fate of organic matter in the salt marsh of the Changjiang estuary, China, *Chemosphere*, *65*(2), 310–317, doi:10.1016/j.chemosphere.2006.02.026.

21698961, 2017, 7, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1002/2017JG003775 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

Biogeosciences Discussions
Open Access
EGU

Sediment and carbon accumulation vary among vegetation assemblages in a coastal saltmarsh

Jeffrey J. Kelleway[1,2], Neil Saintilan[2], Peter I. Macreadie[1,3], Jeffrey A. Baldock[4], Peter J. Ralph[1]

[1]Plant Functional Biology and Climate Change Cluster, School of Life Sciences, University of Technology Sydney, Ultimo, NSW 2007, Australia
[2]Department of Environmental Sciences, Macquarie University, Sydney, NSW 2109, Australia
[3]School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Victoria 3216, Australia
[4]CSIRO Land and Water/Sustainable Agriculture Flagship, Glen Osmond, SA 5064, Australia

Correspondence to: J. J. Kelleway (jeffrey.kelleway@mq.edu.au)

Abstract. Coastal saltmarshes are dynamic, intertidal ecosystems which are increasingly being recognised for their contributions to ecosystem services, including carbon (C) accumulation and storage. The survival of saltmarshes and their capacity to store C under rising sea levels, however, is partially reliant upon surface sedimentation rates and influenced by a combination of physical and biological factors. In this study, we use several complementary methods to assess short-term (days) deposition and medium-term (months) accretion dynamics within three saltmarsh vegetation types common throughout southeast (SE) Australia.

We found that surface accretion varies among vegetation assemblages, with medium-term (19 month) bulk accretion rates in the upper marsh rush (*Juncus*) assemblage (1.74 ± 0.13 mm y^{-1}) consistently in excess of estimated local sea level rise (1.15 mm y^{-1}). Accretion was lower and less consistent in both the succulent (*Sarcocornia*) (0.78 ± 0.18 mm y^{-1}) and grass (*Sporobolus*) (0.88 ± 0.22 mm y^{-1}) assemblages located lower in the tidal frame. Short-term (6 d) experiments showed deposition within *Juncus* plots to be dominated by autochthonous organic inputs with C deposition rates ranging from 0.41 ± 0.15 g C cm^{-2} y^{-1} (neap tidal period) to 0.87 ± 0.16 g C cm^{-2} y^{-1} (spring tidal period), while minerogenic inputs and lower C deposition dominated *Sarcocornia* (0.03 ± 0.01 to 0.23 ± 0.03 g C cm^{-2} y^{-1}) and *Sporobolus* (0.06 ± 0.01 to 0.15 ± 0.03 g C cm^{-2} y^{-1}) assemblages.

Elemental (C:N), isotopic ($\delta^{13}C$), mid infrared (MIR) and ^{13}C NMR analyses revealed little difference in either the source or character of materials being deposited among neap versus spring tidal periods. Instead, these analyses point to substantial redistribution of materials within the *Sarcocornia* and *Sporobolus* assemblages, compared to high retention and preservation of organic inputs in the *Juncus* assemblage. By combining medium-term accretion quantification with short-term deposition measurements and chemical analyses we have gained novel insights into biophysical processes responsible for regional differences in surface dynamics among key saltmarsh vegetation assemblages. Our results suggest that unless belowground processes (e.g. root production) make substantial contributions to surface elevation gain, then *Sarcocornia* and *Sporobolus* assemblages may be particularly susceptible to changes in sea level, with implications for the future structure and function of these saltmarsh areas.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

1 Introduction

1.1 Coastal wetlands

Coastal saltmarshes are dynamic ecosystems, vegetated by herbs, grasses and rushes that are found in a range of sedimentary settings along low-energy coastlines. Globally, vegetation type and floristic assemblage have been used to classify broad types of saltmarsh (Adam, 1990; Adam, 2002). At the local scale, vegetation zonation is one of the most striking ecological features of many saltmarshes, reflecting the elevation requirements of a small number of dominant species, although mosaics of species within a zone are also common (Adam, 2002; Hickey and Bruce, 2010). Whilst the biodiversity values and exceptional productivity of coastal wetlands have been long recognised, increasing attention is now being focused upon ecosystem services such as carbon (C) accumulation and storage (Chmura et al., 2003; Duarte et al., 2013), and the response of these coastal ecosystems to changes in climate (Kirwan and Mudd, 2012) and sea level (Rogers et al., 2013).

Surface elevation and sedimentation dynamics are central to both coastal wetland survival under rising sea level (Baustian et al., 2012; Kirwan and Megonigal, 2013; Kirwin et al., 2016) and to the delivery and storage of organic matter (OM) (Duarte et al., 2013; Lovelock et al., 2013). Saltmarsh sediments may be minerogenic (dominated by mineral inputs) or organogenic (dominated by biomass and litter production and/or allochthonous OM inputs), although most sediments comprise both mineral and organic fractions (Adam, 2002; Baustian et al., 2012). Consequently, sediment properties and surface dynamics may be influenced by both physicochemical and biological factors. Physical drivers of accretion (the vertical accumulation of sediment) in intertidal wetlands include the suspended sediment supply of inundating waters (Zhou et al., 2007); as well as the tidal range of a site and position within the tidal range (Ouyang and Lee, 2014; Saintilan et al., 2013; van Proosdij et al., 2006). High tides may play an important role in importing sediment into saltmarshes (Rosencranz et al., 2015), while low-tide rainfall may act to redistribute or export materials, including particulate organic carbon (Chen et al., 2015).

Numerous studies have investigated the interactions between vegetation and marsh surface dynamics, although the majority of these studies have focussed on the genus *Spartina* (e.g. Baustian et al., 2012; Mudd et al., 2010; Mudd et al., 2009; Nyman et al., 2006). Broadly, these studies have shown that the presence of vegetation may have a significant positive influence on surface accretion through: 1) accumulating organic matter; and 2) helping to trap mineral sediments (Morris et al., 2002; Mudd et al., 2010; Nyman et al., 2006). Comparative studies of the effect of vegetation composition in the intertidal zone, however, vary from no difference in accretion among different vegetation species in the wetland (e.g. Culberson et al., 2004) to sizeable differences among mangroves and different saltmarsh species (e.g. Saintilan et al., 2013).

1.2 C storage

Globally, the rate of sediment carbon accumulation is extremely high in saltmarshes, relative to terrestrial and most coastal ecosystems, with a mean ± SE accumulation rate of 0.024 ± 0.003 g C cm^{-2} y^{-1} (Ouyang and Lee, 2014). While much of this C is produced belowground by roots and rhizomes, contributions from aboveground sources may be significant (Boschker et al., 1999; Zhou et al., 2006). Sources of aboveground C may include both autochthonous (produced within the community) and allochthonous (deposited from outside the community) OM, although their relative contributions may vary within and among saltmarsh settings (Kelleway et al., 2016a).

Regardless of OM source, the capacity of coastal wetlands to store carbon in the long-term remains dependent upon the balance between OM inputs and their decay (Kirwan et al., 2013). While there is considerable debate as

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

to which factors most influence the long-term retention of C in soil pools, litter quality has long been identified as a key driver of decay rates (Cleveland et al., 2014; Enríquez et al., 1993; Josselyn and Mathieson, 1980; Kristensen, 1994) and is of particular relevance to C stock accumulation on the sediment surface.

1.3 Measuring surface deposition and accretion

A variety of methods have been developed for measuring and monitoring surface dynamics in tidal wetlands (for reviews see Nolte et al., 2013; Thomas and Ridd, 2004). These include techniques relevant to short-term *deposition* events (of sediments and plant litter) through to medium- and long-term measures of *accretion* or *accumulation* (the net effect of multiple deposition and removal events) as well as *surface-elevation change*. Methods also vary in their effectiveness of trapping and retaining different materials, meaning a combination of techniques may be required to identify the different physical and biotic influences on deposition and accretion (Nolte et al., 2013). In this study, we use several methods to assess short-term (days) deposition and medium-term (months) accretion dynamics within three saltmarsh vegetation assemblages common throughout southeast (SE) Australia. We hypothesise that: 1) deposition and accretion will vary among assemblages, in accordance with differences in vegetation structure and location within the saltmarsh; and 2) the source and character of material deposited will vary temporally according to tidal inundation patterns. This study also presented an opportunity to compare wetland sedimentation methods. Together, we expect this information will improve our understanding of how materials (including C) accumulate in coastal wetlands and how these ecosystems might respond under rising sea level.

2 Methods

2.1 Study setting

Towra Point Nature Reserve is located within the oceanic embayment Botany Bay, approximately 16 km south of central Sydney, Australia's largest city. The intertidal estuarine wetland complex at this site is the largest remaining within the Sydney region and is listed as a Ramsar Wetland of International Importance. Within the site, a large saltmarsh area adjacent to Weeney Bay was chosen as a study site (Fig. 1) as this area exhibits vegetation zonation typical of SE Australian saltmarshes. The lower saltmarsh is bordered by the mangrove *Avicennia marina*, beyond which seagrass meadows (including *Posidonia australis*) occur within the subtidal zone. In some areas the upslope limit of saltmarsh extends into small patches of the supratidal trees *Casuarina glauca* and *Melaleuca ericifolia*, but for the most part is bordered by a levee which was constructed between 1947 and 1951. Previous investigation has revealed vegetation zonation across the site coinciding with elevation measurements and tidal extent modelling (Hickey and Bruce, 2010).

Saltmarsh within this site comprises two broad vegetation communities – an association of the perennial succulent *Sarcocornia quinqueflora* (C3 photosynthetic pathway) and the perennial grass *Sporobolus virginicus* (C4 photosynthetic pathway), mostly intermixed across the lower and middle marsh. The upper marsh assemblage is dominated by the rush *Juncus kraussii* (C3), with *S. virginicus* (C4) ubiquitous as a sub-dominant lower stratum across this assemblage.

Fifteen plots were selected for study on the basis of saltmarsh vegetation zonation – five plots randomly chosen within the *Juncus*-dominated assemblage, and 10 plots strategically selected within the *Sarcocornia-Sporobolus*

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

association (five plots vegetated exclusively by *Sarcocornia,* and five vegetated exclusively by *Sporobolus*). Hereafter, these three assemblages are referred to by genus (*Sarcocornia; Sporobolus; Juncus*), while reference to the plant species themselves involves the species name (*S. quinqueflora; S. virginicus; J. kraussii*).

Data previously collected within the study region showed a substantial difference in aboveground biomass of the rush assemblage (Juncus mean = 1116 g m^{-2}), compared to that of the non-rush assemblages (*Sarcocornia* mean = 320 g m^{-2}; *Sporobolus* mean = 350 g m^{-2}) - importantly, there do not appear to be distinct seasonal patterns of biomass stock for any of these species (Clarke and Jacoby, 1994). Both *Sarcocornia* and *Sporobolus* are perennial species, while *J. kraussii* culms undergo initiation and senescence throughout the year, but with peak culm initiation before and after summer flowering and fruiting (Clarke and Jacoby, 1994). Belowground biomass data are rare, though on the basis of data presented by Clarke and Jacoby (1994) we have calculated a mean aboveground : belowground biomass ratio of 1.5 for *Juncus*. No belowground data have been reported for either *Sarcocornia* and *Sporobolus*. More broadly, the saltmarshes of southeast (SE) Australia have been classified within the temperate group of saltmarshes which also includes those of Europe, the Pacific coast of North America, Japan and South Africa (Adam, 1990). These are distinct from the well-studied *Spartina*-dominated marshes of North America's Atlantic coast.

Tides along the New South Wales coast are semidiurnal (two flood and two ebb periods each lunar day) with a maximum spring tidal range of 2.0 m (Roy et al., 2001). Astronomical (i.e. predicted) maxima occur during the new moon in summer and during the full moon in winter (spring tides). Tidal inundation to and recession from the study area occurs via Weeney Bay, with the causeway acting as a barrier to surface water exchange with the western section of the Nature Reserve and Woolooware Bay. The linear rate of sea level rise in Botany Bay since local records commenced in 1981 is 1.15 mm y^{-1} (Kelleway et al., 2016b).

2.2 Elevation measurement

Within each plot, elevation was measured using a modified version of the tidal inundation method described by English et al. (1994), whereby three vertical rods marked with water-soluble dye were inserted into the ground immediately prior to a summer spring tide (23/01/2015; measured tidal height of 1.897 m above lowest astronomical tide (LAT) datum at nearest tidal gauge). Depth of inundation above the saltmarsh surface was measured immediately after the tide receded and subtracted from the predicted tide height to obtain an estimate of surface elevation. Care was taken during the measurement procedure and in the selection of a calm day (to minimise wind and waves effects) to minimise discrepancies between measurements at different plots. Comparison of three replicate rods revealed a standard error of the mean < 1.3 cm for each plot.

2.3 Feldspar marker horizons

The feldspar marker horizon (MH) technique (Cahoon and Turner, 1989) has been proposed as a suitable method to investigate the effects of aboveground vegetation structure on the accretion (vertical accumulation) of material on the marsh surface over the medium-term (Nolte et al., 2013). A total of 45 feldspar MHs were installed across the study site on 23 January 2014, comprising three replicates in each of the 15 study plots. Accretion was determined at later dates as the height difference between the marsh surface and the feldspar (i.e., the material accumulated above the MH), and was recorded as the mean of three replicate measurements from within the marker horizon at each sampling event. Measurements were taken 11, 13, 15, 17 and 19 months after installation.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

During the later sampling events many MHs in *Sarcocornia* and *Sporobolus* plots became increasingly difficult to discern within the sediment, probably due to bioturbation and mixing of sediments (Cahoon and Turner, 1989; Krauss et al., 2003). Consequently, monitoring of all plots was terminated after 19 months.

2.4 Sedimentation traps

Two complementary types of sedimentation trap were installed concurrently for the purpose of quantifying short-term deposition of materials among the three vegetation assemblages. First, pre-weighed, 50 mL centrifuge vials (30 mm mouth diameter; 115 mm depth) were placed into the ground, so that the 'lip' of each tube was 10 mm above the ground surface. This vial method has a bias towards the collection of non-buoyant materials washing over the mouth of the tube (i.e. mineral matter) and a bias against collection of coarse and/or buoyant materials, including large fragments of plant litter. Second, a modified version of the filter paper method described by Reed (1989) and Adame et al. (2010) was used to quantify 'passive' sedimentation and litter accretion on the saltmarsh surface. Pre-weighed 90 mm hydrophilic nylon filters (pore size 0.45µm) were placed over 90 mm upturned plastic Petri dishes, and attached to the sediment by two small staples, so that the nylon filter lay level with the sediment surface. The resolution of this method, using a 90 mm filter has been calculated as 0.0015 mg cm^{-2} (Thomas and Ridd, 2004).

Three replicates of each short-term trap were installed at the centre of each of the study areas described above during the summer of 2014/15. Traps were deployed for 6 d (12 high tides) periods on four instances, on the basis of tide chart predictions. Two neap ('December neap' and 'January neap') periods were selected to reflect periods when high tides were at their lowest. While these neap periods were intended to measure periods without any inundation, higher than predicted tides occurred in both neap periods. Although unconfirmed, inundation of some plots within lower elevation zones of the study area were expected to have occurred at least once during the December neap (up to 80% of *Sarcocornia* plots and 100% of *Sporobolus* plots) and/or the January neap (up to 60% of *Sarcocornia* plots only) (Table S1). Two other periods ('December spring' and 'January spring') were selected as maximum saltmarsh inundation events with between five and ten high tides inundating each plot in each period (Table S1). Although unintended, the fact that a small number of inundations were likely captured during neap tides more accurately reflects the differences in tidal behaviour that naturally occurs among the three vegetation assemblages (i.e. lower elevation assemblages are subject to a greater number of high tides throughout the year than higher elevation assemblages). Consequently, all results from short-term measures were considered in the context of these varied inundation patterns.

Great care was taken not to disturb sediments or litter collected on, or surrounding the removable traps during their installation and collection. Filters with visible crab-excavated sediment (n = 23/180) or physically upturned during inundation (n = 3 January spring inundation only) were excluded from analysis, although all plant (autochthonous and allochthonous) materials were retained for analysis as we considered these to be largely unaffected by crab excavation.

In the laboratory, vials were centrifuged, the supernatant decanted and vial placed in an oven for drying. All samples and vessels (filters and centrifuge vials) were dried at 60°C until constant weight was achieved (≤ 72 h) and subtracted from initial vessel mass to obtain the dry weight of material collected. In addition, all identifiable litter was removed from each filter, identified to the species level and weighed. Litter samples of the main saltmarsh species encountered (*S. quinqueflora, S. virginicus* and *J. kraussii*), wrack of the seagrass *Posidonia*

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

australis and macroalga *Hormosira banksii*, fresh leaves of the mangrove *Avicennia marina,* as well as composite samples of all residual sediment (mineral component and unidentified organic matter; referred hereafter as 'residue') from filters were also prepared for chemical analyses.

2.5 Elemental and isotopic analysis

Dried aboveground plant biomass, litter and residues were homogenised and ground into a fine powder using a ball mill. The 'Champagne test' (Jaschinski et al., 2008) was used to determine that no residue samples contained inorganic C. Consequently, acidification of samples was deemed unnecessary. Organic %C, %N, and $\delta^{13}C$ were measured for all samples using an Isotope Ratio Mass Spectrometry – Elemental Analyzer (Thermo DeltaV) at University of Hawaii (HILO).

2.6 MIR

Diffuse reflectance mid-infrared (MIR) spectroscopy was used to assess the composition of biomass, litter and residue samples. MIR spectroscopy characterises the bulk composition and is therefore inclusive of both mineral and organic components. Spectra were acquired using a Nicolet 6700 FTIR spectrometer (Thermo Fisher Scientific Inc., Waltham, MA, USA) following the specifications and procedures outlined by Baldock et al. (2013a). Spectra were acquired over 8000–400 cm^{-1} with a resolution of 8 cm^{-1}, but were truncated to 6000–600 cm^{-1}. Spectra were baseline-corrected using a baseline-offset transformation and then mean-centred using the Unscrambler 10.2 software (CAMO Software AS, Oslo, Norway) before conducting principal component analysis (PCA).

2.7 ^{13}C NMR

Solid-state ^{13}C nuclear magnetic resonance (NMR) spectroscopy was used to quantify the contribution of C functional groups to live plant biomass, litter and residue samples. Residue samples were treated with 2% hydrofluoric acid (HF) according to the method of Skjemstad et al. (1994) to remove paramagnetic materials and concentrate organic C for ^{13}C NMR analyses. Cross-polarization ^{13}C NMR spectra were acquired using a 200 MHz Avance spectrometer (Bruker Corporation, Billerica, MA, USA) following the instrument specifications, experimental procedures and spectral processing outlined by Baldock et al. (2013b). ^{13}C NMR data are presented as the proportion of integral area under each of eight chemical shift regions corresponding to main types of organic functional groupings found in natural organic materials: Alkyl C (0-45 ppm), *N*-Alkyl/Methoxyl (45-60 ppm), *O*-Alkyl (60-95 ppm), Di-*O*-Alkyl (95-110 ppm), Aryl (110-145 ppm), *O*-Aryl (145-165 ppm), Amide/Carboxyl (165-190 ppm) and Ketone (190-215 ppm) (Baldock and Smernik, 2002).

2.8 Statistical analyses

Separate simple linear regression analyses were conducted using all feldspar MH measurements for each of the three vegetation assemblages for the purpose of obtaining accumulation rates over 19 months and to assess the strength of linear fits for these data. Bulk short-term deposition variables (bulk material collected in vials; bulk material collected on filters) were log-transformed to achieve normality and analysed with separate linear mixed models, to test main and interactive effects of vegetation assemblage (*Sarcocornia*, *Sporobolus*, *Juncus*) and tidal event (repeated measures: December neap, December spring, January neap, January spring). Elevation was

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

included as a covariate for each of these analyses. Covariance structure was selected for each model through comparison of Akaike's Information Criterion (AIC) of four covariance structures (unstructured, compound symmetry, diagonal, scaled identity). Where main effects presented significance differences ($P < 0.05$), post hoc tests (with conservative Bonferroni adjustment) were used to determine difference among levels of vegetation and tidal event factors. Statistical analyses were performed using SPSS v19 (IBM, USA), Origin Pro 2015 (OriginLab, USA) and PRIMER v6 (PRIMER-E, UK).

2.8.1 Isotope mixing model

A two-source, single isotope mixing model (Phillips, 2012) was used to estimate the proportion of C3 (f_1 in equation (1)) and C4 (f_2 in equation (2)) plants to the unidentified organic residue:

$$f_1 = \frac{\delta^{13}C_{residue} - \delta^{13}C_{C4}}{\delta^{13}C_{C3} - \delta^{13}C_{C4}} \quad (1)$$

$$f_2 = 1 - f_1 \quad (2)$$

where $C_{residue}$ denotes the residue organic C, C_{C3} denotes the $\delta^{13}C$ of the relevant C3 plants (*S. quinqueflora* litter for *Sarcocornia-Sporobolus* association residues or *J. kraussii* litter for *Juncus* assemblage residues) and C_{C4} denotes $\delta^{13}C$ of litter of the C4 species (*S. virginicus*).

2.8.2 MIR analysis

Principal components analysis (PCA) was performed using the transformed MIR spectra to: 1) identify differences in composition among samples due to sample type and vegetation assemblage; and 2) define the MIR spectral components most important to differentiating the samples. Loadings were plotted for the first two principal components to assist in the latter and to guide interpretation of differences in composition among samples.

3 Results

3.1 Feldspar MHs

Positive and consistent accretion was measured among *Juncus* plots throughout the entire 19 months, reflected in the moderate-strong linear fit ($R^2 = 0.68$; $P < 0.001$) and a mean accumulation rate with relatively low variance (1.74 ± 0.13 mm y^{-1}). In contrast, accumulation above the feldspar MHs was more varied and slower overall in the *Sarcocornia* ($R^2 = 0.16$; $P < 0.001$; 0.76 ± 0.18 mm y^{-1}) and *Sporobolus* plots ($R^2 = 0.14$; $P < 0.001$; 0.88 ± 0.22 mm y^{-1}) (Figure 2). Accretion varied both spatially and temporally within the *Sarcocornia* and *Sporobolus* assemblages. Across *Sporobolus* plots, there was relatively high accretion recorded at the 11-month interval, followed by multiple peaks and troughs in the amount of height of material measured above MHs, with some similarity among replicate plots in the timing of these (Fig 2b). After modest gains at the 11-month interval, *Sarcocornia* accretion diverged among plots with two plots (*Sarcocornia* 2 and 5) experiencing continued accretion, whilst *Sarcocornia* 3 and 4 appeared to lose surface material through the remainder of the study. The

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

pattern of accumulation and loss observed between 13-19 months at *Sarcocornia* 1 was mirrored in the nearby *Sporobolus* 1 plot.

3.2 Short-term deposition

3.2.1 Vials

Mean bulk material deposition rates as determined by vials were higher than filter bulk deposition rates across all sampling events and vegetation assemblages (Table 1). Observations of materials retained within vials suggested a dominance of mineral matter and unidentified detritus, except in *Juncus* plots where *Juncus kraussii* fragments were the dominant material.

Deposition varied significantly among tidal events ($F_{6, 42} = 10.01$; $P < 0.001$), with post-hoc tests revealing each event as significantly different to the others. Despite large differences in mean deposition among the three vegetation assemblages during December spring, January neap and January spring events (Table 1), vegetation assemblage was not a significant factor when elevation was included as a covariate ($F_{2, 45.8} = 1.06$; $P = 0.36$). There was, however, a significant event × assemblage interaction ($F_{6, 42} = 10.01$; $P < 0.001$), with deposition in *Sarcocornia* vials higher during January neap relative to December spring for *Sarcocornia* plots, but not so for *Sporobolus* and *Juncus* vials (Table 1). Deposition into vials was lowest for all three assemblages during December neap (Table 1) and was highest overall in *Sarcocornia* vials during January spring (100.78 ± 32.73).

Regression of the log (mass of material retained within vials) versus plot surface elevation revealed no clear relationship between the two variables during the December neap period (Fig. S1a), but significant negative relationships ($P<0.001$, $R^2>0.35$) existed for all other time periods (Fig. S1b-d). That is, there were broad trends of higher sedimentation at lower elevation plots than higher elevation plots during these periods.

3.2.2 Filters

Retention of bulk materials on filters also varied among all four tidal periods ($F_{3, 109.3} = 48.82$; $P < 0.001$), with overall deposition highest in January spring, followed by December spring (Table 1, Fig. 3). Bulk deposition on filters varied among vegetation assemblages ($F_{2, 30.85} = 48.82$; $P = 0.004$), with lower deposition in *Sporobolus* plots relative to both *Sarcocornia* and *Juncus* plots across all tidal events (Fig. 3; Table 1). In contrast to the vials, there was no clear relationship between bulk material retained on filter papers and plot surface elevation during either of the neap or spring tidal events (Fig. S2).

Although the mass of bulk material retained on filters was similar across *Sarcocornia* and *Juncus* plots, Fig. 3 demonstrates that different materials were contributing to surface accumulation among the two vegetation assemblages. In *Juncus* plots, autochthonous plant litter (that is, from the dominant species *Juncus* kraussii and the sub-dominant species *Sporobolus* virginicus) contributed between 66% (December neap) and 78% (both December spring and January neap) of all deposited material. In contrast, litter contributions were low (≤ 12% of all deposited material) in both *Sarcocornia* and *Sporobolus* assemblages, regardless of tidal period. Contributions from identifiable allochthonous materials were low in all cases, with negligible quantities of *Posidonia australis* litter (recorded in five out of all 60 *Sporobolus* filters) and a single large piece of *Hormosira banksii* deposited on a *Sporobolus* filter during December spring – the latter was considered an outlier and was therefore excluded from Fig 3.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

Chemical analysis of the unidentified portion of material deposited on filters also highlights differences between the vegetation assemblages. The organic content (%C, %N) of unidentified material pooled across *Juncus* plots was much higher than for the other assemblages (Table S2), with this difference also apparent in the disparity between C accumulation rates in *Juncus* versus *Sarcocornia* and *Sporobolus* assemblages (Table 1).

3.3 Elemental and isotopic ratios

Elemental C:N ratios and $\delta^{13}C$ values of plant biomass, litter and unidentified residues are presented in Table 2. The biomass and litter samples of the C4 grass *Sporobolus* were more enriched in ^{13}C relative to those of the C3 species *Sarcocornia* and *Juncus* (Table 2). This distinction, however, was not as great for the unidentified residue samples, with $\delta^{13}C$ values from all assemblages sitting between the $\delta^{13}C$ values of the C3 and C4 saltmarsh plants. Outputs from the isotope mixing model (Table 1) highlighted differences in source contribution among the vegetation assemblages. *Sarcocornia* residues showed a higher contribution of C3 plant material during spring tides relative to the neap tides. Further, similar contribution from the host plant (i.e. C3 in *Sarcocornia* and C4 in *Sporobolus*) to residues was apparent for all tidal periods except January neap, when the C4 contribution to *Sporobolus* residue was higher. Overall, contributions of the host plant ranged from 59.6 – 77.5 % in *Sarcocornia* plots and 61.7 - 80.1% in *Sporobolus* plots.

Source contributions across the four tidal periods were most consistent in the *Juncus* assemblage, where estimates ranged between 78.8% and 84.6% for C3 plant material and 15.4 - 21.2% for C4 plant material. These contributions aligned well with visual observations of plant cover across plots (where the C3 plant *J. kraussii* is dominant over the C4 plant *S. virginicus* in approximately an 80:20% biomass mix). Quantification of litter fall onto filters, however, highlighted a skew towards *J. kraussii* litter (85.9 – 97.0%) over *S. virginicus* litter (3.0 – 14.1%) across the *Juncus* assemblage. Residue C:N ratios were also highest for *Juncus*, followed by *Sporobolus* then *Sarcocornia*. While *Juncus* litter samples had a higher C:N, relative to all other *Juncus* biomass (Table 2), this difference was not noted for *Sarcocornia* nor *Sporobolus*.

3.4 MIR and ^{13}C NMR

Together, the first two principal components explained 96.4% of the variation in MIR spectra of all samples assessed. A clear separation of residue samples from litter and biomass is apparent along PC1 (Fig 4A) with inspection of the loadings plot (Fig 4B) highlighting variation in the range 600-2000 cm^{-1} (quartz), and distinct troughs at 3400 cm^{-1} (water) and 2900 cm^{-1} (OM-alkyl). Residue samples are separated along PC2, with differentiation among vegetation assemblages, regardless of tidal event. The loadings plot for PC2 (Fig 4C) also exhibits variation in the range 600-2000 cm^{-1} (quartz), a peak at 2900 cm^{-1} (OM-alkyl) and also 3600-3700 cm^{-1} (kaolinite).

The proportions of C within each of eight organic functional groupings for each sample analysed with ^{13}C NMR are presented in Table 2. For all samples O-Alkyl C was the most abundant. O-Alkyl C content was higher in live plant biomass than litter for both *Sarcocornia*, but less so for *Sporobolus* and essentially unchanged for *Juncus*. Generally, residues were higher in Alkyl C, and Amide/Carboxyl C, and lower in O-Alkyl, Di-O-Alkyl and aromatics relative to litter and biomass samples. There were differences in residue C composition according to which vegetation assemblage they were collected from –aromatics (higher in *Juncus* and *Sporobolus*), Alkyl C

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

and Amide/Carboxyl (higher in *Sarcocornia*). There was high similarity between residues collected under the two different tides, however, for both the *Sarcocornia* and *Sporobolus* assemblages. These similarities among tides are mirrored in the similarity of the residue C:N values. There was insufficient residue material available for analysis from *Juncus* neap tide, even though samples were pooled across a large number of filters, further highlighting the small contribution of unidentifiable sedimentary components within this assemblage.

4 Discussion

In this study we have compared sediment and C accretion dynamics among three vegetation assemblages within an intertidal wetland complex. Our findings, across a range of methods, showed that there were substantial differences among assemblages in: 1) the types of materials deposited on the marsh surface; and 2) the quantities of material accumulated over 19 months. Here, we first consider the accumulation differences among assemblages over the medium-term, and then discuss the interactions among vegetation, physical and degradation processes which are likely driving these differences. We conclude with an assessment of the implications for C accumulation and storage, and response to relative sea level rise (RSLR).

4.1 Accretion varies among vegetation assemblages

Surface accretion above feldspar MHs over a period of 19 months and deposition within short-term sedimentation traps provide evidence of the multiple ways in which accretion dynamics differ between saltmarsh vegetation assemblages. First, feldspar MHs highlight a record of continued and consistent accretion across the upper marsh *Juncus* assemblage, amounting to a reliable ($R^2 = 0.68$) accretion rate of 1.74 ± 0.13 mm y^{-1} (Fig. 2). This value is remarkably similar to the mean accretion rate measured over 10 years above feldspar MHs of 1.76 mm y^{-1} by Saintilan et al. (2013) for *Juncus* saltmarshes across a range of sites in SE Australia. In contrast, accretion above MHs in *Sarcocornia* and *Sporobolus* assemblages varied substantially– both spatially and temporally – in our study (Fig. 2), possibly due in part to the influence of bioturbation and sediment mixing above MHs (Cahoon and Turner, 1989; Krauss et al., 2003). While our mean accretion estimates for both *Sarcocornia* and *Sporobolus* are lower than the regional estimate for *Sarcocornia*/*Sporobolus* associations (1.11 ± 0.08 mm y^{-1}) (Saintilan et al., 2013), this regional mean is within the 95% confidence interval for both species at Towra Point (Table 1). Critically, accretion rates in the *Juncus* assemblage consistently exceed contemporary rates of sea level rise within Botany Bay (1.15 mm y^{-1}), while mean accretion rates for both *Sarcocornia* and *Sporobolus* (and even the upper 95% confidence interval of *Sarcocornia)* are below the contemporary rate of sea level rise.

4.2 Processes driving spatial variability in deposition and accretion

One of the key strengths of using short-term accumulation methods is the ability to identify and quantify the composition of inputs which may be contributing to differences observed over the medium-term. In this study, a distinction was observed between the organogenic deposition which dominated the *Juncus* assemblage (where medium-term accretion rates were consistently high) and the minerogenic deposition of the *Sarcocornia* and *Sporobolus* assemblages (where medium-term accretion rates were lower and more varied). This distinction was best exemplified by the results of the filter method (Fig 3.), where differences in the contributions of autochthonous litter and the residual sediment (comprising mineral and organic residue components) were stark.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

There was further evidence of this in the vial results, where mineral-biased deposition was high in the lower elevation, non-rush assemblages, and low in the higher elevation *Juncus* assemblage during multiple experimental periods (Table 1; Fig. S1). Although higher than predicted tides likely influenced some short-term traps during neap experimental periods (Table S1), the fact that deposition into vials was lower during December neap (when up to 80% of *Sarcocornia* plots and 100% of *Sporobolus* plots would have been subjected to at least one tidal inundation) relative to January neap (up to 60% of *Sarcocornia* plots; no inundation of *Sporobolus* plots), suggests that this had a small impact relative to other influences.

Together, the vegetation assemblage scale differences in short-term deposition and longer-term accumulation patterns observed in this study suggest further consideration of the biological, physical and interactive processes which are most responsible for the dynamics of saltmarsh surface materials is warranted.

4.2.1 The role of vegetation

There are fundamental differences in vegetation structure and function which can at least partly account for the variations in the quantity and type of materials being retained in rush (*Juncus*) versus non-rush (*Sarcocornia* and *Sporobolus*) assemblages. First, *Juncus* assemblages have massive potential for direct organic sedimentation through the annual replacement of their significant aboveground biomass (1116 g m^{-2}) (Clarke and Jacoby, 1994). No clear patterns of annual turnover have been observed in *Sarcocornia* and *Sporobolus* assemblages, where standing biomass is only about one-third that of the *Juncus* assemblage (Clarke and Jacoby, 1994).

There may also be indirect vegetation effects on the deposition and accumulation of surface materials. For instance, the tall (~1 m), dense structure of the *Juncus* assemblage is likely to enhance: 1) the retention of autochthonous litter which may have otherwise been exported during tidal recession, and 2) the capture of mineral particles on plant stems (Morris et al., 2002; Mudd et al., 2004). Dense saltmarsh vegetation also has the capacity to enhance sedimentation by reducing the turbulent energy of inundating waters, with Mudd et al. (2010) demonstrating that this phenomenon was responsible for virtually all of the sedimentation increase observed when standing plant biomass of *Spartina alterniflora* was artificially increased. The high litter deposition rates we observed during neap tides (Fig. 3a,c) and the increased contribution of both mineral and litter components during spring tides (Fig 3b,d) suggested that each of these direct and indirect plant-mechanisms may be operating and contributing to the relatively high medium-term accretion rates within *Juncus* assemblages. This supported the first element of our first hypothesis - that assemblage differences can be (at least partly) explained by differences in vegetation structure.

4.2.2 The role of physical factors

Differences in suspended sediment supply and tidal flooding characteristics (tidal range, position within the tidal prism) have been identified as key physical drivers of saltmarsh accretion (Chmura and Hung, 2004; Rogers et al., 2014). Generally, lower elevation within the tidal frame and closer proximity to the source of tidal inundation result in higher sedimentation rates. This is because: (1) greater flooding depth allows for greater sediment volume and higher sedimentation, and (2) the increase in flooding duration increases the time for sediment deposition to occur (Baustian et al., 2012; Harter and Mitsch, 2003; Morris, 2007; Oenema and DeLaune, 1988). If these processes were operating in our site, we would have expected to observe higher sedimentation rates in the *Sarcocornia* and *Sporobolus* assemblages, which were generally both lower in the tidal frame (Table S1) and

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

nearer to tidal sources (Fig. 1). Indeed, when measurements relevant to the mineral component were considered, our results appeared to be consistent with this. First, overall mineral retention on filters (Fig. 3) was highest in the *Sarcocornia* and *Sporobolus* assemblages. Second, mineral-biased deposition into vials was shown to have a significant log-linear relationship with elevation during the periods of greatest tidal inundation (December spring, January spring), and during January neap when significant rainfall (Fig. S3) as well as some inundation of low elevation sites likely occurred (Table S2). These mineral deposition results were therefore supportive of the role of physical position within the saltmarsh towards differences among assemblages (i.e. part two of our first hypothesis).

Importantly, however, the deposition-elevation relationship expressed by the mineral component, did not apply when bulk results of the passive filter method were considered. With the mineral bias effectively removed, no clear relationship between elevation and bulk deposition was observed across any of the tidal periods (see Fig. S2). Instead, total deposition was similar between the minerogenic, lower elevation *Sarcocornia/Sporobolus* plots, and the organogenic, higher elevation *Juncus* plots.

The lack of an elevation relationship in terms of bulk material deposition is somewhat contrary to spatial patterns expected on the basis of physical sedimentary processes in the tidal zone. This disparity extended to medium-term accretion results, where lower marsh (*Sarcocornia* and *Sporobolus*) assemblages accrete at a slower rate than upper marsh (*Juncus*), both in our study, and regionally (Saintilan et al., 2013). This relationship doesn't necessarily downplay the importance of tidal influence on surface dynamics in SE Australian saltmarshes. An alternative explanation is that these physical processes, in interaction with biological factors, are instead remobilising and redistributing materials across the lower marsh assemblages, rather than depositing significant amounts of 'new' allochthonous material.

4.2.3 Redistribution of surface materials

The second hypothesis of our study was that the source and character of materials deposited would vary temporally with tidal inundation patterns. For the most part, however, this was not observed, with high degrees of within-assemblage similarity for neap and spring tide samples across the various analyses undertaken (Table 2; Fig. 4). Instead, our results provide multiple lines of evidence that point to the redistribution of surface materials across the saltmarsh, mediated by a range of biological, physical and interactive processes.

The first indication of redistribution of surface materials was the mismatch between rates of short-term bulk deposition and patterns of medium-term accretion among vegetation assemblages. This was best exhibited in the *Sarcocornia* plots, where short-term measures showed deposition to be as high or higher in *Sarcocornia* plots relative to the other assemblages (Table 1; Fig. 3), while medium-term accretion was actually lowest here (Fig. 2). This suggests that short-term measures in this assemblage were capturing materials which were being moved or redistributed across the saltmarsh, but not necessarily retained in a given location over longer time periods (i.e. months). While the short- versus medium-term discrepancy was not as large for the *Sporobolus* assemblage, the temporal variability in feldspar MH measurements (i.e. multiple peaks and troughs across the 19 month period for most plots) also suggested significant redistribution of materials over time in this assemblage. Such movement of materials within the *Sarcocornia* and *Sporobolus* assemblages also fits with the expectation that hydrodynamic energy, and therefore potential for sediment redistribution, would be highest in the saltmarsh zones lower in the tidal frame and located closer to tidal sources (Fig. 1, Table S1). We also attribute the fading of feldspar horizons

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

in many *Sarcocornia* and *Sporobolus* plots over time to mixing of sediments (Cahoon and Turner, 1989) in this active zone, with assistance from bioturbation (Cahoon and Turner, 1989; Krauss et al., 2003). In contrast, these temporal discrepancies and variations (including fading of MHs) were not observed in the *Juncus* assemblage, where hydrodynamic energy is expected to be greatly reduced as a result of both its position within the marsh and the influences of plant biomass (see discussion above).

Next, it was not expected that tidal inundation would substantially increase saltmarsh plant litter production. We therefore interpret the increased concentration of autochthonous litter in *Juncus* plots during spring tides relative to neap tides (Fig. 3) as evidence of the redistribution and trapping of autochthonous material within this assemblage. That is, the 'extra' spring tide litter was material that had been remobilised by inundating water and redistributed within the same community, resulting in a larger amount of material being caught on the *Juncus* filters. The fact that no identifiable *Juncus* litter was collected on any of the *Sporobolus* filters, despite their position being within the expected path of receding tides (Fig. 1), further highlights the retaining capacity within the *Juncus* assemblage. While it is not known over what scale the litter redistribution is occurring in the *Juncus* assemblage, we expect it to be highly localised, given the dense structure of standing vegetation here and its capacity to impede movement of coarse litter particles.

Finally, by placing our *Sarcocornia* and *Sporobolus* plots within small patches vegetated exclusively by either the C3 species (*S. quinqueflora*) or the C4 species (*S. virginicus*), we are able to estimate the contribution of each resident plant to the residue collected from within its assemblage. While the dominance of resident plant signatures suggested a strong autochthonous contribution in all instances (see mixing model results in Table 1), residue signatures across all tidal periods reveal a mixture of sources both present (i.e. the resident plant) or neighbouring (i.e. the other co-dominant plant in the association) to the plots. The fact that contributions of sources other than the resident plant were in the order of 20 – 40% (Table 1) during the neap tides suggest significant mixing across scales greater than the monospecific patches (i.e. several metres or more). While some of this movement of materials may have been due to the creep of the highest neap period tides into the lower elevation plots (though this appears small - see section 4.2), non-tidal agents such as redistribution by rainfall (Chen et al., 2015) and faunal activity (Guest et al., 2004) may have also contributed.

A two source (C3 plant v C4 plant) mixing model probably presents an overly simplified estimate of source matter contributions. This is because it does not account for other potential sources which have $\delta^{13}C$ values within or near the range of saltmarsh plant sources prescribed in the mixing model. These include mangroves (-28.7 ± 0.3 ‰), seagrass (-12.3 ‰), macroalgae (-17.7 ‰) and benthic algae (-15.0 ± 0.4 ‰). Of these, benthic algae would have the greatest potential to contribute to *Sarcocornia* residue, as vegetation is sparsest here (and therefore light penetration to benthos the greatest), while the MIR PC plot (Fig. 4) also points to a similarity in chemical composition between the two. However, the fact that *Sporobolus* residues are consistently depleted in ^{13}C, relative to both the resident plant (*S. virginicus*) and benthic algae, show that our interpretation of mixing between both C3 and C4 sources is warranted at least in that assemblage. In contrast, the constancy of isotope signatures and their overall similarity with the mix of C3- and C4-derived biomass in the *Juncus* plots provide further evidence of the autochthonous nature and trapping capacity of this assemblage.

Together, these findings allow several conclusions to be made about redistribution of surface materials. First, short-term deposition measures may capture a significant proportion of within-marsh redistribution and therefore may not necessarily equate with longer term accretion. Second, the capacity of vegetation to retain autochthonous

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

sedimentation appears to vary substantially among species assemblages. Third, redistribution is likely to be greatest in more exposed, lower-biomass assemblages. These findings also highlight the importance of considering redistributed materials in quantifications of wetland surface dynamics, and likely shortcomings for studies which attempt to assess surface dynamics using only short-term methods.

4.3 Implications for wetland function

Understanding the biological and physical feedbacks which affect surface dynamics is critical to the survival of intertidal wetlands and their associated ecosystem services, under changing environmental conditions (Kirwan and Megonigal, 2013). To this end, the data collected as part of this study reveal patterns of how C sequestration capacity, organic matter decomposition and vulnerability to sea level rise vary among saltmarsh assemblages.

4.3.1 C deposition and sequestration rates

The distinction between organogenic and minerogenic assemblages, and their respective locations within the tidal frame, has important implications for surface C sequestration rates. Here we estimate mean C deposition rates ranging from 0.03 to 0.23 g C cm^{-2} y^{-1} across the four tidal periods for the minerogenic *Sarcocornia* and *Sporobolus* assemblages and 0.41 to 0.87 g C cm^{-2} y^{-1} for the organogenic *Juncus* assemblage (Table 1). It should be noted that such short-term C deposition rates inclusive of plant litter will likely represent a massive overestimation of C that is retained and sequestered over longer timescales, due to diagenesis of deposited OM (Duarte and Cebrian, 1996), and the potential for materials to be redistributed or even exported by tidal and non-tidal processes (see section 4.2.3). Therefore, these deposition rates are not directly comparable to C accumulation rates determined by medium-term (e.g. feldspar MH) or longer term (e.g. radiometric dating) techniques. Notwithstanding this, the magnitude of the differences we report among assemblages above fit broadly with differences in regional estimates of C accumulation over the medium-term (10 y MH experiments) which have been estimated as 4.5 times higher in *Juncus* relative to *Sarcocornia-Sporobolus* saltmarsh (Saintilan et al., 2013). Similarly, our results are also in agreement with findings further north in Moreton Bay, where Lovelock et al. (2013) reported much higher C sequestration rates on oligotrophic sand island marshes dominated by *J. kraussii*, than *S. quinqueflora* dominated marshes on the western side of that bay.

4.3.2 Decomposition of organic matter varies among assemblages

We have assessed the chemistry of aboveground biomass, litter and unidentified residues through elemental (C:N) and spectrometric (MIR, ^{13}C NMR) methods. Together, these analyses have revealed insights into the fate of aboveground organic matter and the likelihood of their contribution to longer-term sedimentary carbon stocks. Most importantly, our results highlight among assemblage differences in the transformation of OM along the biomass-litter-sediment decay continuum.

Shifts in the bulk composition of materials was best seen in the principal components plots of MIR spectra, where biomass, litter and sediment residue samples varied across PC1 (Fig. 4a). Broadly, the separation of residues from litter and biomass was primarily due to the addition of mineral components in the residues, however, there was also evidence of a shift in alkyl OM. Specifically, the presence of a single peak at ~2900 cm^{-1} in the loadings plot (Fig. 4b) was indicative of a declining cellulose content across PC1, that is, in the general order live biomass – litter – residue. Importantly, cellulose also appears to be a factor in the separation of residues from the three

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

different saltmarsh assemblages along PC2 (Fig. 4c), suggesting higher content in the two *Juncus* samples, followed by *Sporobolus* and then *Sarcocornia* samples. This finding was confirmed by ^{13}C NMR data, which showed greater proportions of plant compounds (carbohydrates more broadly, as well as lignin) were retained within the *Juncus* litter and residue relative to the other species (Table 2). In contrast, the higher proportions of alkyl–C and amide/carboxyl–C within *Sarcocornia* and *Sporobolus* residues were indicative of higher protein and lipid contents, consistent with bacterial biomass and marine algae signatures (Dickens et al., 2006). However, they may also be partly explained by the selective retention of resistant plant waxes, such as suberin and cutan.

There are multiple mechanisms which may explain the greater retention of plant-derived C along the biomass-litter-residue pathway for *Juncus*, relative to the other assemblages. The simplest explanation is that a high turnover of *Juncus* biomass (and its exclusion of other sources through shading and/or structural impedance) ensures ample supply of plant-derived C to the benthos. Our data, however, reveal an important biomass-to-litter transformation in *Juncus* that was not observed in either the *Sarcocornia* or *Sporobolus* assemblage. That is, the C:N of *Juncus* litter increased substantially relative to live biomass. Such an increase is commonly observed in terrestrial (McGroddy et al., 2004) and marine (Stapel and Hemminga, 1997) plants and may be explained by the selective resorption of nutrients (but not carbon) by the plant prior to, or during, senescence (McGroddy et al., 2004; Stapel and Hemminga, 1997). Such a mechanism was supported by the constancy of molecular C composition between *Juncus* biomass and litter (Table 2). The selective resorption of N by a plant has important implications for the fate and processing of the resulting litter and residue, as tissue C:N is considered a primary determinant on saltmarsh organic matter decomposition (Minden and Kleyer, 2015). By retaining nutrients within the living tissues, the plant effectively decreases the lability of resulting litter and residual sediments and makes them less attractive to the microbial decomposer community (Reddy and DeLaune, 2008). This will have the effect of lowering OM remineralisation rates in *Juncus* relative to other assemblages, a result which also coincides with the bacterial biomass increases suggested for *Sarcocornia* and *Sporobolus*, but not apparent within the more recalcitrant *Juncus* residues (Table 2). Finally, there may also be an element of physical protection, with the closed structure of the *Juncus* assemblage potentially offering increased protection against decomposition with lower, more stable temperatures expected at ground level, relative to the more exposed *Sarcocornia* and *Sporobolus* assemblages.

Together, these data from SE Australia contribute to a broader pattern of plant assemblage differences in saltmarsh surface dynamics and C sequestration potential (Minden and Kleyer, 2015; Saintilan et al., 2013; Wang et al., 2003). They also highlight the likely processes behind the high capacity of *Juncus* saltmarshes to accumulate significant C stocks globally (0.034 g C cm^{-2} y^{-1}), relative to most other saltmarsh genera (mean C accumulation rate = 0.024 g C cm^{-2} y^{-1}) (Ouyang and Lee, 2013).

4.3.3 Vulnerability to sea level rise

There is growing evidence of the capacity of coastal wetlands to maintain surface elevation with relative sea level rise (RSLR), in certain situations, by increasing surface elevation through belowground production, enhanced trapping of sediments, or a combination of the two (Baustian et al., 2012; Kelleway et al., 2016b; McKee et al., 2007). Where wetland assemblages are unable to maintain a suitable elevation relative to inundating water levels then vegetation shifts may occur, including the loss of marsh vegetation (Day Jr et al., 1999; Day Jr et al., 2011; Rogers et al., 2006). While wetland surface elevation is a function of multiple factors, including belowground

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

production and decomposition, groundwater dynamics and sedimentary and regional subsidence (Cahoon et al., 1999; Rogers and Saintilan, 2008), the retention of aboveground inputs play a critical role in wetland survival under changing hydrological conditions (Day et al., 2011).

With this in mind, our medium-term accretion data suggest that *Sporobolus* and *Sarcocornia* assemblages may be particularly vulnerable to current RSLR, with mean surface accretion rates either lower (*Sarcocornia* = 0.92 mm y^{-1}) or only marginally higher (*Sporobolus* = 1.30 mm y^{-1}) than contemporary rates of local sea level rise within Botany Bay (1.15 mm y^{-1}). In fact, there is already evidence of this across much of the Towra Point Nature Reserve, as well as elsewhere in the region, where upslope encroachment of mangrove shrubs into *Sarcocornia-Sporobolus* association is occurring (Kelleway et al., 2016b). In contrast, vegetation change (either in the form of mangrove encroachment or dieback) has not been widely reported for *Juncus* assemblages across SE Australia over recent decades, suggesting relative stability during a time of changing sea levels. While belowground biomass production likely plays a role, average *Juncus* surface accretion rates (1.70 mm y^{-1} in this study; 1.76 mm y^{-1} regionally) in excess of local RSLR suggest a potential role of aboveground inputs towards maintaining surface elevation. Dependence upon organogenic inputs for accretion, however, also means the response of *Juncus* assemblages to RSLR may vary with shifts in productivity or decomposition dynamics (e.g. changes in climate and/or nutrient status). Under present conditions, at least, our analyses have shown these organic inputs to be relatively resistant to early decomposition. In all, our findings are also supportive of recent research which suggests organic sediment accretion may be of critical importance in marsh survival under RSLR, particularly in areas most removed from inorganic sediment delivery (D'Alpaos and Marani, 2015). Whether belowground organic matter production makes substantial contributions to Australian saltmarsh surface elevation dynamics and vulnerability to sea level rise remains unknown, and represent an important area for further research. Better understanding of the temporal dynamics of organic and mineral contributions to elevation maintenance is also required, including in relation to expected non-linear increases in sea level.

By combining medium-term accretion quantification with short-term deposition measurements and chemical analyses we have gained insights into the various processes behind observed differences in accretion among saltmarsh vegetation assemblages. While our study highlights assemblage scale differences in potential response to RSLR, it represents only a small part of the information needed to accurately predict the future of SE Australian saltmarsh assemblages. Further measures of short-term deposition and medium-term accretion across a broader range of geographical settings, longer-term studies of soil elevation change among assemblages and modelling of vegetation response thresholds are all required.

Acknowledgements

Charlie Hinchcliffe, Mikael Kim, Sarah Meoli and Frederic Cadera assisted with field measurements. Janine McGowan and Bruce Hawke assisted with sample preparation and spectroscopic methods. Field collections were undertaken in accordance with NSW Office of Environment and Heritage scientific licence SL101217 and NSW Department of Primary Industries Scientific Permit P13/0058-1.0. We also thank NSW National Parks and Wildlife Service for supporting access to Towra Point Nature Reserve. This research was supported by the CSIRO Coastal Carbon Cluster. PM was supported by an Australian Research Council DECRA Fellowship (DE130101084). Data from this research will be made public as part of the CSIRO Coastal Carbon Cluster.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

REFERENCES

Adam, P. (Ed.): Saltmarsh Ecology, Cambridge University Press, Cambridge, UK., 1990.
Adam, P.: Saltmarshes in a time of change, Environmental conservation, 29, 39-61, 2002.
Adame, M. F., Neil, D., Wright, S. F., and Lovelock, C. E.: Sedimentation within and among mangrove forests along a gradient of geomorphological settings, Estuarine, Coastal and Shelf Science, 86, 21-30, 2010.
Baldock, J. A., Hawke, B., Sanderman, J., and Macdonald, L. M.: Predicting contents of carbon and its component fractions in Australian soils from diffuse reflectance mid-infrared spectra, Soil Research, 51, 577, 2013a.
Baldock, J. A., Sanderman, J., Macdonald, L. M., Puccini, A., Hawke, B., Szarvas, S., and McGowan, J.: Quantifying the allocation of soil organic carbon to biologically significant fractions, Soil Research, 51, 561-576, 2013b.
Baldock, J. A. and Smernik, R. J.: Chemical composition and bioavailability of thermally altered *Pinus resinosa* (Red pine) wood, Organic Geochemistry, 33, 1093-1109, 2002.
Baustian, J. J., Mendelssohn, I. A., and Hester, M. W.: Vegetation's importance in regulating surface elevation in a coastal salt marsh facing elevated rates of sea level rise, Global Change Biology, 18, 3377-3382, 2012.
Boschker, H., De Brouwer, J., and Cappenberg, T.: The contribution of macrophyte-derived organic matter to microbial biomass in salt-marsh sediments: Stable carbon isotope analysis of microbial biomarkers, Limnology and Oceanography, 44, 309-319, 1999.
Cahoon, D. and Turner, R. E.: Accretion and canal impacts in a rapidly subsiding wetland II. Feldspar marker horizon technique, Estuaries, 12, 260-268, 1989.
Cahoon, D. R., Day Jr, J. W., and Reed, D. J.: The influence of surface and shallow subsurface soil processes on wetland elevation: A synthesis, Current Topics In Wetland Biogeochemistry, 3, 72-88, 1999.
Chen, S., Torres, R., and Goñi, M. A.: Intertidal zone particulate organic carbon redistribution by low-tide rainfall, Limnology and Oceanography, doi: 10.1002/lno.10077, 2015. n/a-n/a, 2015.
Chmura, G. L., Anisfeld, S. C., Cahoon, D. R., and Lynch, J. C.: Global carbon sequestration in tidal, saline wetland soils, Global Biogeochemical Cycles, 17, 22:21-22:12, 2003.
Chmura, G. L. and Hung, G. A.: Controls on salt marsh accretion: A test in salt marshes of Eastern Canada, Estuaries, 27, 70-81, 2004.
Clarke, P. J. and Jacoby, C. A.: Biomass and above-ground productivity of salt-marsh plants in south-eastern Australia, Marine and Freshwater Research, 45, 1521-1528, 1994.
Cleveland, C. C., Reed, S. C., Keller, A. B., Nemergut, D. R., O'Neill, S. P., Ostertag, R., and Vitousek, P. M.: Litter quality versus soil microbial community controls over decomposition: a quantitative analysis, Oecologia, 174, 283-294, 2014.
Culberson, S. D., Foin, T. C., and Collins, J. N.: The role of sedimentation in estuarine marsh development within the San Francisco Estuary, California, USA, Journal of Coastal Research, 2004. 970-979, 2004.
D'Alpaos, A. and Marani, M.: Reading the signatures of biologic–geomorphic feedbacks in salt-marsh landscapes, Advances in Water Resources, doi: http://dx.doi.org/10.1016/j.advwatres.2015.09.004, 2015. 2015.
Day Jr, J., Rybczyk, J., Scarton, F., Rismondo, A., Are, D., and Cecconi, G.: Soil accretionary dynamics, sea-level rise and the survival of wetlands in Venice Lagoon: a field and modelling approach, Estuarine, Coastal and Shelf Science, 49, 607-628, 1999.
Day, Jr, J., Kemp, G. P., Reed, D. J., Cahoon, D. R., Boumans, R. M., Suhayda, J. M., and Gambrell, R.: Vegetation death and rapid loss of surface elevation in two contrasting Mississippi delta salt marshes: The role of sedimentation, autocompaction and sea-level rise, Ecological Engineering, 37, 229-240, 2011.
Dickens, A. F., Baldock, J. A., Smernik, R. J., Wakeham, S. G., Arnarson, T. S., Gélinas, Y., and Hedges, J. I.: Solid-state 13C NMR analysis of size and density fractions of marine sediments: Insight into

© Author(s) 2017. CC-BY 3.0 License.

organic carbon sources and preservation mechanisms, Geochimica et Cosmochimica Acta, 70, 666-686, 2006.
Duarte, C. M. and Cebrian, J.: The fate of marine autotrophic production, Limnology and Oceanography, 41, 1758-1766, 1996.
Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., and Marbà, N.: The role of coastal plant communities for climate change mitigation and adaptation, Nature Climate Change, 3, 961-968, 2013.
English, S. S., Wilkinson, C. C., and Baker, V. V.: Survey manual for tropical marine resources, Australian Institute of Marine Science (AIMS), 1994.
Enríquez, S., Duarte, C. M., and Sand-Jensen, K.: Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content, Oecologia, 94, 457-471, 1993.
Guest, M. A., Connolly, R. M., and Loneragan, N. R.: Carbon movement and assimilation by invertebrates in estuarine habitats at a scale of metres, Marine Ecology Progress Series, 278, 27-34, 2004.
Harter, S. K. and Mitsch, W. J.: Patterns of short-term sedimentation in a freshwater created marsh, Journal of Environmental Quality, 32, 325-334, 2003.
Hickey, D. and Bruce, E.: Examining Tidal Inundation and Salt Marsh Vegetation Distribution Patterns using Spatial Analysis (Botany Bay, Australia), Journal of Coastal Research, doi: 10.2112/08-1089.1, 2010. 94-102, 2010.
Josselyn, M. N. and Mathieson, A. C.: Seasonal influx and decomposition of autochthonous macrophyte litter in a north temperature estuary, Hydrobiologia, 71, 197-207, 1980.
Kelleway, J. J., Saintilan, N., Macreadie, P. I., and Ralph, P. J.: Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes, Ecosystems, doi: 10.1007/s10021-016-9972-3, 2016a. 2016a.
Kelleway, J. J., Saintilan, N., Macreadie, P. I., Skilbeck, C. G., Zawadzki, A., and Ralph, P. J.: Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes, Global Change Biology, 22, 1097-1109, 2016b.
Kirwan, M. L., Langley, J. A., Guntenspergen, G. R., and Megonigal, J. P.: The impact of sea-level rise on organic matter decay rates in Chesapeake Bay brackish tidal marshes, Biogeosciences, 10, 1869-1876, 2013.
Kirwan, M. L. and Megonigal, J. P.: Tidal wetland stability in the face of human impacts and sea-level rise, Nature, 504, 53-60, 2013.
Kirwan, M. L. and Mudd, S. M.: Response of salt-marsh carbon accumulation to climate change, Nature, 489, 550-553, 2012.
Kirwan, M. L., Temmerman, S., Skeehan, E. E., Guntenspergen, G. R., and Fagherazzi, S.: Overestimation of marsh vulnerability to sea level rise, Nature Climate Change, 6, 253-260, 2016.
Krauss, K. W., Allen, J. A., and Cahoon, D. R.: Differential rates of vertical accretion and elevation change among aerial root types in Micronesian mangrove forests, Estuarine, Coastal and Shelf Science, 56, 251-259, 2003.
Kristensen, E.: Decomposition of macroalgae, vascular plants and sediment detritus in seawater - use of stepwise thermogravimetry, Biogeochemistry, 26, 1-24, 1994.
Lovelock, C. E., Adame, M. F., Bennion, V., Hayes, M., O'Mara, J., Reef, R., and Santini, N. S.: Contemporary Rates of Carbon Sequestration Through Vertical Accretion of Sediments in Mangrove Forests and Saltmarshes of South East Queensland, Australia, Estuaries and Coasts, 37, 763-771, 2013.
McGroddy, M. E., Daufresne, T., and Hedin, L. O.: Scaling of C: N: P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios, Ecology, 85, 2390-2401, 2004.
McKee, K. L., Cahoon, D. R., and Feller, I. C.: Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation, Global Ecology and Biogeography, 16, 545-556, 2007.
Minden, V. and Kleyer, M.: Ecosystem multifunctionality of coastal marshes is determined by key plant traits, Journal of Vegetation Science, 2015. 2015.

© Author(s) 2017. CC-BY 3.0 License.

Morris, J. T.: Ecological engineering in intertidial saltmarshes, Hydrobiologia, 577, 161-168, 2007.
Morris, J. T., Sundareshwar, P., Nietch, C. T., Kjerfve, B., and Cahoon, D.: Responses of coastal wetlands to rising sea level, Ecology, 83, 2869-2877, 2002.
Mudd, S. M., D'Alpaos, A., and Morris, J. T.: How does vegetation affect sedimentation on tidal marshes? Investigating particle capture and hydrodynamic controls on biologically mediated sedimentation, Journal of Geophysical Research: Earth Surface (2003–2012), 115, 2010.
Mudd, S. M., Fagherazzi, S., Morris, J. T., and Furbish, D. J.: Flow, sedimentation, and biomass production on a vegetated salt marsh in South Carolina: Toward a predictive model of marsh morphologic and ecologic evolution, Coastal and Estuarine Studies, 59, 165-188, 2004.
Mudd, S. M., Howell, S. M., and Morris, J. T.: Impact of dynamic feedbacks between sedimentation, sea-level rise, and biomass production on near-surface marsh stratigraphy and carbon accumulation, Estuarine, Coastal and Shelf Science, 82, 377-389, 2009.
Nolte, S., Koppenaal, E. C., Esselink, P., Dijkema, K. S., Schuerch, M., De Groot, A. V., Bakker, J. P., and Temmerman, S.: Measuring sedimentation in tidal marshes: a review on methods and their applicability in biogeomorphological studies, Journal of Coastal Conservation, 17, 301-325, 2013.
Nyman, J. A., Walters, R. J., Delaune, R. D., and Patrick Jr, W. H.: Marsh vertical accretion via vegetative growth, Estuarine, Coastal and Shelf Science, 69, 370-380, 2006.
Oenema, O. and DeLaune, R. D.: Accretion rates in salt marshes in the Eastern Scheldt, south-west Netherlands, Estuarine, Coastal and Shelf Science, 26, 379-394, 1988.
Ouyang, X. and Lee, S.: Updated estimates of carbon accumulation rates in coastal marsh sediments, Biogeosciences, 11, 5057-5071, 2014.
Ouyang, X. and Lee, S. Y.: Carbon accumulation rates in salt marsh sediments suggest high carbon storage capacity, Biogeosciences Discussions, 10, 19155-19188, 2013.
Phillips, D. L.: Converting isotope values to diet composition: the use of mixing models, Journal of Mammalogy, 93, 342-352, 2012.
Reddy, K. R. and DeLaune, R. D.: Biogeochemistry of wetlands: science and applications, Crc Press, 2008.
Reed, D. J.: Patterns of sediment deposition in subsiding coastal salt marshes, Terrebonne Bay, Louisiana: the role of winter storms, Estuaries, 12, 222-227, 1989.
Rogers, K. and Saintilan, N.: Relationships between surface elevation and groundwater in mangrove forests of southeast Australia, Journal of Coastal Research, 24, 63-69, 2008.
Rogers, K., Saintilan, N., and Copeland, C.: Managed Retreat of Saline Coastal Wetlands: Challenges and Opportunities Identified from the Hunter River Estuary, Australia, Estuaries and Coasts, 2013. 1-12, 2013.
Rogers, K., Saintilan, N., and Woodroffe, C. D.: Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: Implications for coastal wetland response to climate change, Estuarine, Coastal and Shelf Science, 149, 46-56, 2014.
Rogers, K., Wilton, K. M., and Saintilan, N.: Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia, Estuarine, Coastal and Shelf Science, 66, 559-569, 2006.
Rosencranz, J. A., Ganju, N. K., Ambrose, R. F., Brosnahan, S. M., Dickhudt, P. J., Guntenspergen, G. R., MacDonald, G. M., Takekawa, J. Y., and Thorne, K. M.: Balanced Sediment Fluxes in Southern California's Mediterranean-Climate Zone Salt Marshes, Estuaries and Coasts, 2015. 1-15, 2015.
Roy, P., Williams, R., Jones, A., Yassini, I., Gibbs, P., Coates, B., West, R., Scanes, P., Hudson, J., and Nichol, S.: Structure and function of south-east Australian estuaries, Estuarine, Coastal and Shelf Science, 53, 351-384, 2001.
Saintilan, N., Rogers, K., Mazumder, D., and Woodroffe, C.: Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands, Estuarine, Coastal and Shelf Science, 128, 84-92, 2013.
Skjemstad, J., Clarke, P., Taylor, J., Oades, J., and Newman, R.: The removal of magnetic materials from surface soils-a solid state 13C CP/MAS NMR study, Soil Research, 32, 1215-1229, 1994.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

Stapel, J. and Hemminga, M.: Nutrient resorption from seagrass leaves, Marine Biology, 128, 197-206, 1997.

Thomas, S. and Ridd, P. V.: Review of methods to measure short time scale sediment accumulation, Marine Geology, 207, 95-114, 2004.

van Proosdij, D., Davidson-Arnott, R. G. D., and Ollerhead, J.: Controls on spatial patterns of sediment deposition across a macro-tidal salt marsh surface over single tidal cycles, Estuarine, Coastal and Shelf Science, 69, 64-86, 2006.

Wang, X. C., Chen, R. F., and Berry, A.: Sources and preservation of organic matter in Plum Island salt marsh sediments (MA, USA): long-chain n-alkanes and stable carbon isotope compositions, Estuarine, Coastal and Shelf Science, 58, 917-928, 2003.

Zhou, J., Wu, Y., Kang, Q., and Zhang, J.: Spatial variations of carbon, nitrogen, phosphorous and sulfur in the salt marsh sediments of the Yangtze Estuary in China, Estuarine Coastal and Shelf Science, 71, 47-59, 2007.

Zhou, J., Wu, Y., Zhang, J., Kang, Q., and Liu, Z.: Carbon and nitrogen composition and stable isotope as potential indicators of source and fate of organic matter in the salt marsh of the Changjiang Estuary, China, Chemosphere, 65, 310-317, 2006.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

Table 1. Summary of sediment measure techniques; mean and standard error values for feldspar marker horizon (MH), vial and filter bulk sediment measures; mean and standard error of C deposition rates; and contributions of C3 and C4 vegetation to deposition among vegetation assemblages. Accretion rates slower than local sea level rise (1.15 mm y^{-1}) are in red. DN = December neap; DS = December spring; JN = January neap; JS = January spring.

Technique	Parameter *Measure* Temporal scale Biases/issues	Period	*SARCOCORNIA*		*SPOROBOLUS*		*JUNCUS*	
Feldspar MH								
	Bulk measure				**accretion rate (mm y^{-1})**			
	sediment accumulation		**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
	mid-term (days to years)	0-19 mo.	0.78	0.18	0.88	0.22	1.74	0.13
	MH may be lost through erosion or bioturbation	95% CI lower	0.42		0.44		1.48	
		95% CI upper	1.14		1.32		2.00	
			see also Figure 2					
Vial								
	Bulk measure				**bulk deposition rate (g cm^{-2} y^{-1})**			
	sediment deposition		**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
	short-term (hours to days)	DN	3.41	1.14	2.74	0.90	3.79	1.25
		DS	25.19	3.88	66.52	10.47	18.13	3.26
	Biased towards materials entrained by water. Biased against coarse litter larger than vial mouth	JN	38.67	9.20	18.84	5.49	4.99	1.33
		JS	100.78	32.73	80.94	8.92	14.92	2.14
Filter								
	Bulk measure				**bulk deposition rate (g cm^{-2} y^{-1})**			
	sediment deposition		**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
	short-term (hours to days)	DN	1.47	0.19	1.09	0.26	1.24	9.7E-04
		DS	2.18	0.35	1.31	0.10	2.37	2.5E-03
		JN	0.79	0.20	0.43	0.05	1.02	2.0E-03
		JS	3.04	0.79	2.50	0.46	2.55	2.8E-03
	Filter + material identification							
	composition of material deposited				*see Figure 3*			
	Filter + elemental analysis				**C deposition rate (g C cm^{-2} y^{-1}) [a]**			
	C deposition rate		**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
		DN	0.10	0.02	0.08	0.02	0.44	0.06
		DS	0.09	0.02	0.12	0.02	0.87	0.16
		JN	0.03	0.01	0.06	0.01	0.41	0.15
		JS	0.23	0.03	0.15	0.03	0.73	0.17
	Filter + isotopic analysis				**isotope mixing model - plant contribution (%)**			
	sources contributing to sediment residue		**C3**	**C4**	**C3**	**C4**	**C3**	**C4**
		DN	59.61	40.39	38.3	61.7	80.2	19.79
		DS	77.50	22.50	25.0	75.0	84.6	15.38
		JN	67.94	32.06	19.9	80.1	81.0	18.98
		JS	72.39	27.61	26.0	74.0	78.8	21.21
					see also Table 2			
	Filter + MIR & ^{13}C NMR							
	character of deposited materials				*see Figure 4 & Table 2*			

[a] Calculated by multiplying bulk accumulation for individual plots by %C values obtained for pooled litter and residue samples

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

Biogeosciences
Discussions
Open Access
EGU

Table 2. Results of ^{13}C NMR, $\delta^{13}C$ and elemental (C:N) analyses for each component of three saltmarsh plant assemblage, plus other potential sources. ^{13}C NMR outputs are the average of two samples for each of biomass and litter components (except *Sporobolus* litter, for which only one reliable spectrum was obtained). $\delta^{13}C$ and C:N values are the mean (±SE) of biomass (n=3) and litter (n=4) samples. Residue samples were pooled from 15 filters in each vegetation assemblage.

Community	Component	Tide	^{13}C NMR chemical assignment and region (ppm)							$\delta^{13}C$	C:N
			Alkyl (0 - 45)	N-Alkyl/Methoxyl (45 - 60)	O-Alkyl (60 - 95)	Di-O-Alkyl (95 - 110)	Aryl (110 - 145)	O-Aryl (145 - 165)	Amide/Carboxyl (165 - 190)	Ketone (190 - 215)	
Sarcocornia	biomass	n/a	14.4	6.6	45.0	10.6	10.5	4.4	7.1	1.4	-26.5 ± 0.5	38.0 ± 4.2
	litter	combined	10.2	5.1	34.0	9.0	16.3	8.6	13.2	3.6	-25.7 ± 0.1	33.0 ± 1.2
	residue	neap	23.1	8.2	33.7	7.3	11.3	4.3	11.0	1.1	-22.1 ± 0.3	14.2 ± 0.4
		spring	25.1	8.1	32.8	7.1	10.5	4.0	11.3	1.1	-23.3 ± 0.2	14.2 ± 0.7
Sporobolus	biomass	n/a	8.6	4.6	51.0	12.0	11.5	4.6	6.5	1.3	-14.9 ± 0.1	59.8 ± 6.3
	litter	spring	5.2	4.5	47.1	12.0	14.6	6.6	8.0	2.0	-15.8 ± 0.2	59.4 ± 5.2
	residue	neap	19.2	7.9	36.5	8.3	12.6	5.0	9.4	1.2	-18.7 ± 0.6	15.5 ± 0.5
		spring	18.5	7.3	36.6	8.4	13.0	5.2	9.5	1.4	-18.4 ± 0.0	16.3 ± 1.1
Juncus	biomass	n/a	8.6	5.4	51.8	12.2	11.2	4.6	5.2	1.1	-24.8 ± 0.3	61.3 ± 5.6
	litter	combined	5.6	5.4	52.2	12.8	11.9	5.4	5.4	1.3	-25.6 ± 0.1	89.9 ± 4.5
	residue	neap	*insufficient material available for ^{13}C NMR analysis*								-23.7 ± 0.0	19.6 ± 0.0
		spring	15.4	7.2	35.7	8.8	15.4	6.6	9.2	1.7	-23.8 ± 0.2	18.2 ± 0.4
Other sources	algal mat	n/a	14.3	5.6	37.5	8.7	11.5	4.9	14.8	2.6	-15.0 ± 0.4	13.2 ± 0.1
	mangrove leaf	n/a	16.4	6.4	40.6	9.1	12.8	4.8	8.7	1.1	-28.7 ± 0.3	24.8 ± 1.7
	seagrass wrack	spring	11.6	3.9	33.3	8.0	14.4	7.7	16.4	4.6	-12.3	29.2
	macroalga wrack	spring	6.0	2.6	52.5	14.0	5.5	6.6	11.5	1.3	-17.7	57.8

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

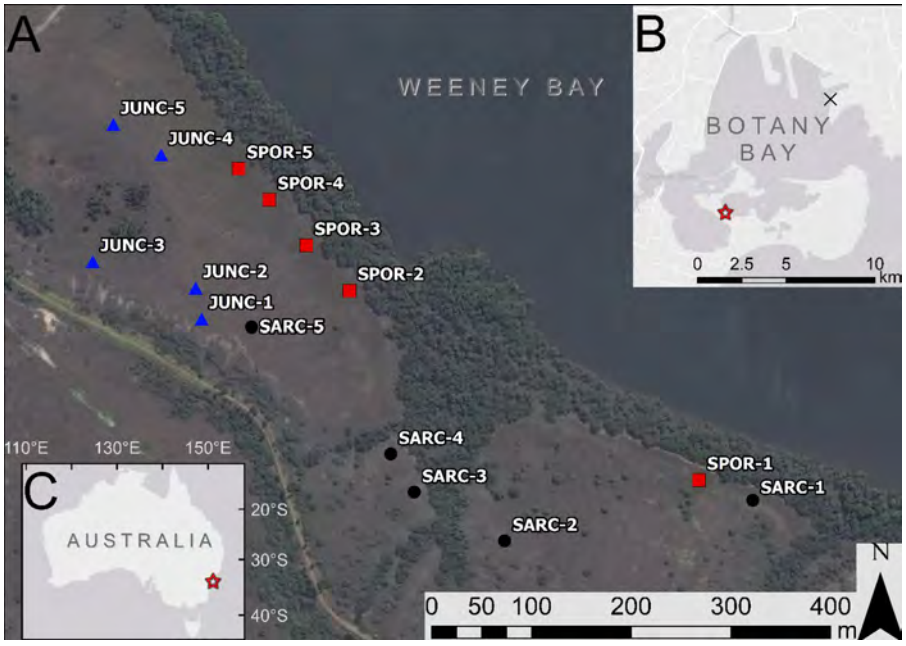


Fig 1. Location of experimental plots within Weeney Bay saltmarsh of Towra Point Nature Reserve (A), located along the southern shoreline of Botany Bay (B) in southeast Australia (C). Location of nearest tidal gauge is marked by an X in inset B. SARC = Sarcocornia quinqueflora assemblage; SPOR = Sporobolus virginicus assemblage; JUNC = Juncus kraussii assemblage.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

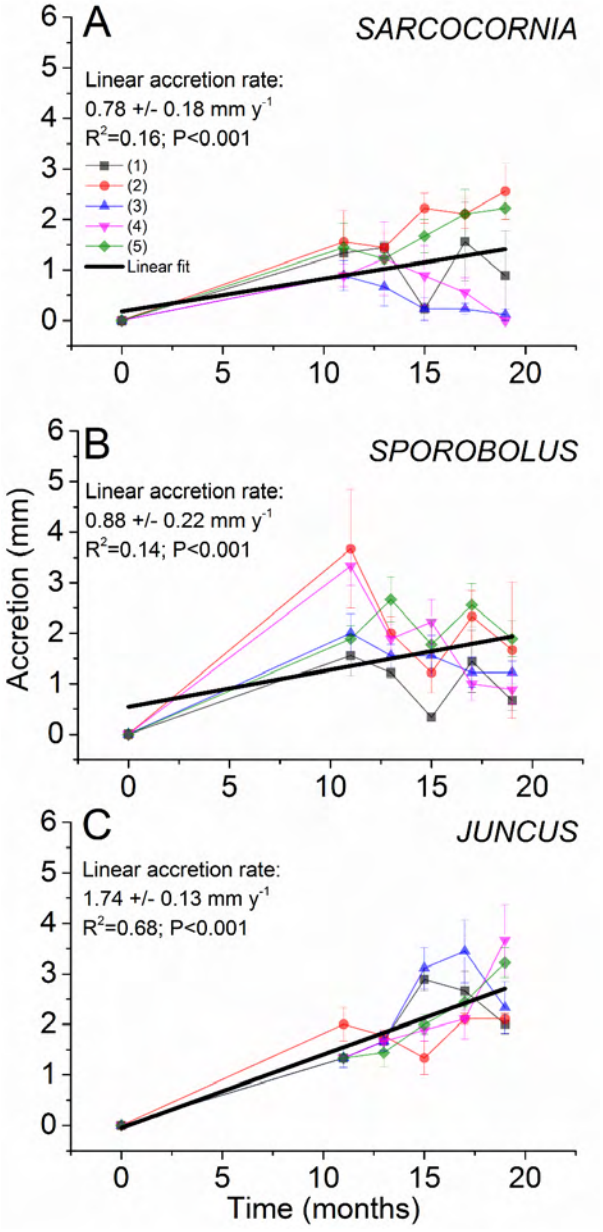


Fig 2. Surface accretion above feldspar marker horizons. Data are presented as the mean ± SE of three replicate plots in each of five locations for each vegetation assemblage. A linear fit was applied on the basis of all data points (n=90) for each vegetation assemblage.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

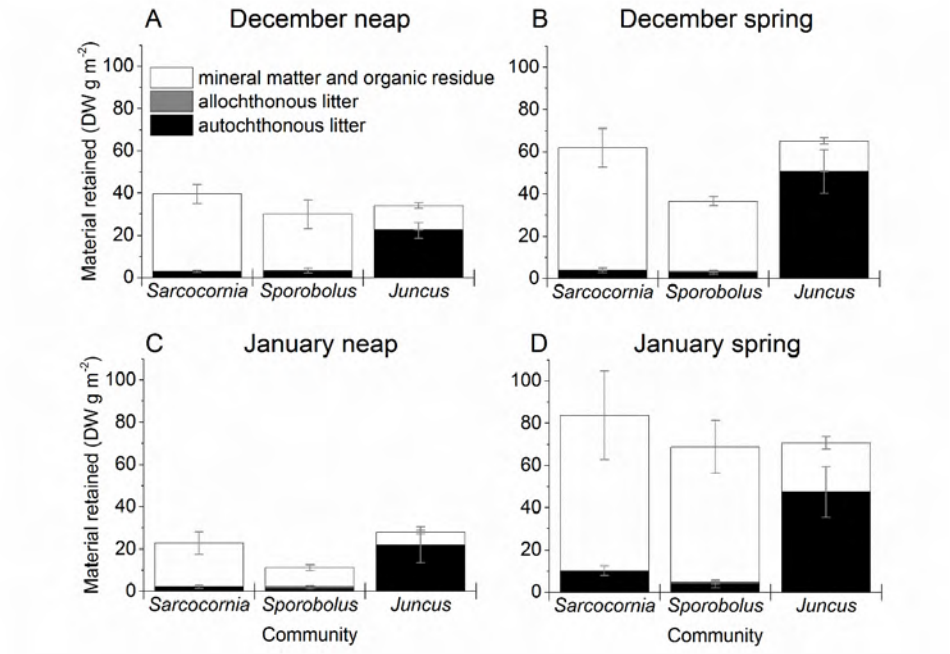


Fig 3. Mean mass of autochthonous litter, allochthonous litter and mineral matter / organic residue retained on filters at end of 6d deployment during December neap (A), December spring (B), January neap (C) and January spring (D) tidal periods. Error bars are presented for each component and represent 1 standard error each side of the mean.

Biogeosciences Discuss., doi:10.5194/bg-2017-15, 2017
Manuscript under review for journal Biogeosciences
Published: 3 February 2017
© Author(s) 2017. CC-BY 3.0 License.

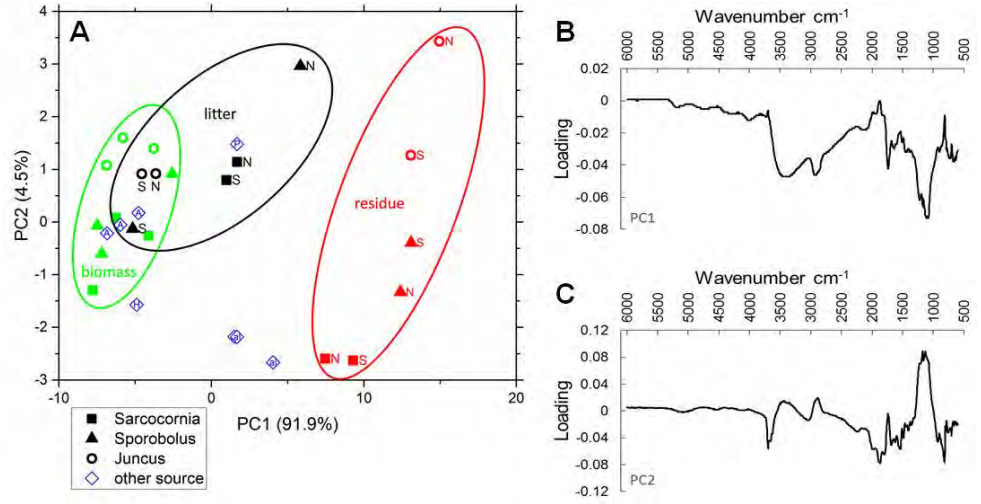


Fig 4. Principal component analysis of MIR spectra with the proportion of variance explained by each component is given in parentheses (A); spectral loading plots for PC1 (B) and PC2 (C). S = spring tide samples; N = neap tide samples; H = *Hormosira banksii* (macroalga) wrack; P = *Posidonia australis* (seagrass) wrack; A = *Avicennia marina* (mangrove) leaf; al = benthic algae mat.

Ecosystems (2016) 19: 865–880
DOI: 10.1007/s10021-016-9972-3

ECOSYSTEMS
© 2016 Springer Science+Business Media New York

Sedimentary Factors are Key Predictors of Carbon Storage in SE Australian Saltmarshes

Jeffrey J. Kelleway,[1,2]* Neil Saintilan,[2] Peter I. Macreadie,[1,3] and Peter J. Ralph[1]

[1]*Plant Functional Biology and Climate Change Cluster, School of Life Sciences, University of Technology Sydney, Ultimo, New South Wales 2007, Australia;* [2]*Present address: Department of Environmental Sciences, Macquarie University, Sydney, New South Wales 2109, Australia;* [3]*School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Burwood, Victoria 3125, Australia*

Abstract

Although coastal vegetated ecosystems are widely recognised as important sites of long-term carbon (C) storage, substantial spatial variability exists in quantifications of these 'blue C' stocks. To better understand the factors behind this variability we investigate the relative importance of geomorphic and vegetation attributes to variability in the belowground C stocks of saltmarshes in New South Wales (NSW), southeast Australia. Based on the analysis of over 140 sediment cores, we report mean C stocks in the surface metre of sediments (mean ± SE = 164.45 ± 8.74 Mg C ha^{-1}) comparable to global datasets. Depth-integrated stocks (0–100 cm) were more than two times higher in fluvial (226.09 ± 12.37 Mg C ha^{-1}) relative to marine (104.54 ± 7.11) geomorphic sites, but did not vary overall between rush and non-rush vegetation structures. More specifically, sediment grain size was a key predictor of C density, which we attribute to the enhanced C preservation capacity of fine sediments and/or the input of stable allochthonous C to predominantly fine-grained, fluvial sites. Although C density decreased significantly with sediment depth in both geomorphic settings, the importance of deep C varied substantially between study sites. Despite modest spatial coverage, NSW saltmarshes currently hold approximately 1.2 million tonnes of C in the surface metre of sediment, although more C may have been returned to the atmosphere through habitat loss over the past approximately 200 years. Our findings highlight the suitability of using sedimentary classification to predict blue C hotspots for targeted conservation and management activities to reverse this trend.

Key words: carbon sequestration; blue carbon; saltmarsh; salt marsh; spatial variability; geomorphic setting; ecosystem services; tidal marshes.

Introduction

Coastal vegetated ecosystems (saltmarshes, mangroves and seagrasses) contribute nearly 50% of the carbon (C) burial in marine sediments, despite occupying just 0.2% of the ocean surface (Chmura and others 2003; McLeod and others 2011; Duarte and others 2013). There are three main reasons for the disproportionate contribution of these 'blue C'

Received 11 September 2015; accepted 5 February 2016;
published online 24 March 2016
Electronic supplementary material: The online version of this article (doi:10.1007/s10021-016-9972-3) contains supplementary material, which is available to authorised users.
Author contributions All authors contributed to the design of the study and writing of the paper. JJK performed research and analysed data.
*Corresponding author; e-mail: jeffrey.kelleway@mq.edu.au

habitats—first, they are highly productive ecosystems converting CO_2 into plant biomass C (Nixon 1980; Alongi 2002). Second, they are depositional environments which trap particulate C from within the ecosystem (*autochthonous* C, including host plant litter or benthic algal biomass) and/or from external sources (*allochthonous* C, including particulate C derived from river catchment and/or marine sources) (Kennedy and others 2010). Third, low oxygen conditions within sediments slow the decay of belowground organic material and allow C to accumulate over centuries and millennia (Kristensen and others 2008; McLeod and others 2011; Fourqurean and others 2012).

Belowground C stocks (inclusive of belowground biomass) are the most significant C pool in coastal wetlands. Due to their potential for long-term storage of C—and conversely, the possibility of substantial C emissions if habitats are disturbed—belowground stocks are the primary interest in coastal C initiatives (Sutton-Grier and others 2014). Although global datasets indicate high C stocks in saltmarshes, mangroves and seagrasses, they also highlight the massive variability in C stocks from local through to global scales (Duarte and others 2013). An understanding of the factors behind this variability, as well as improved knowledge of the key processes mediating C sequestration in these habitats is therefore required to better inform regional and global C management.

Geomorphology-based assessments of blue C are increasingly being utilised to understand within and between estuary variations in sedimentation dynamics and C stocks (for example, Craft 2007; Adame and others 2010; Donato and others 2011; Saintilan and others 2013; Chen and others 2015a). This is because geomorphic setting (that is, the geographic location and depositional setting of a site) has an overarching influence on biological, physical and biogeochemical conditions within estuaries (Roy and others 2001), including parameters relevant to C storage. First, variations in salinity, nutrient and sediment supply influence rates of primary production and plant decomposition (Blum 1993; Craft 2007; Feller and others 2007; Lovelock and others 2007). Second, soil C density and character vary according to key physical parameters controlled by geomorphic setting, including soil type (Middelburg and others 1997; Kleber and others 2007; Serrano and others 2016), soil depth (Middelburg 1989; Choi and others 2001; Schmidt and others 2011) and depositional setting (Donato and others 2011; Doetterl and others 2012). Third, the long-term stability of C stocks is also likely to vary spatially across estuarine gradients, with allochthonous sources of marine C broadly considered to be more easily decomposed than terrestrial C sources (Burdige 2007 and references therein).

Vegetation-based assessments of C stock variability are widespread, ranging from within site to global comparisons (Elsey-Quirk and others 2011; Lavery and others 2013; Ouyang and Lee 2014; Chen and others 2015b; Kelleway and others 2015 among others). The general rationale for vegetation comparisons is that structural and productivity differences among plant species may influence their capacity to contribute or capture C inputs (Duarte and others 2010; Kennedy and others 2010), whereas the susceptibility of above and belowground tissues to decomposition may vary among taxa (Enriquez and others 1993; Trevathan-Tackett and others 2015).

In the southeast (SE) Australia, it has been estimated that up to 70% of the aerial extent of coastal wetlands has been lost since European settlement, primarily due to agricultural drainage and structural flood mitigation works (Zann 2000; Rogers and others 2015). The combination of such historic losses plus contemporary threats to remaining wetland extent is especially acute for saltmarshes, which are particularly subject to modification and destruction by human activity (Adam 2002). In the state of New South Wales (NSW), this has led to the listing of coastal saltmarshes under both state and federal threatened species legislation and sparked interest in management activities which might reverse the historic decline of saltmarsh extent and associated ecosystem services (Laegdsgaard and others 2009). An understanding of C storage is therefore particularly pertinent for NSW saltmarshes.

Despite their imperilled status, recent meta-analysis has placed Australian saltmarshes high among global C accumulation rates (Ouyang and Lee 2014). This however, is based upon a limited dataset of Australian saltmarsh C stocks and incomplete understanding of the processes driving spatial variability. Saintilan and others (2013) collated C stock data across five sites to complete the first regional assessment of saltmarsh C in southeast (SE) Australia. They found that soil C stock varied significantly between vegetation communities with rush (*Juncus kraussii*) saltmarshes containing higher stocks than non-rush saltmarshes vegetated by the grass *Sporobolus virginicus* and/or succulent *Sarcocornia quinqueflora*. They also identified the potential role of geomorphic setting, with C store generally higher in fluvial sites relative to marine

sites, although the relationship was weak ($P = 0.069$). Similarly, research in Moreton Bay, Queensland, found spatial differences in saltmarsh soil C density with *J. kraussii* saltmarshes containing higher soil C densities than *S. quinqueflora* saltmarshes (Lovelock and others 2013). In both these studies, however, attempts to ascertain C stock differences according to geomorphic setting may have been confounded by differences in the vegetation composition of sites in each setting. This highlights the need for an experimental design which differentiates the relative roles of both geomorphic setting and vegetation factors, as well as any interactions between the two.

In this study we undertake a broad scale survey of saltmarshes along the NSW coast of SE Australia, with the aim of identifying relationships between belowground C stocks and selected environmental variables. We use a factorial design to determine the influence of vegetation community (rush vs succulent/grass), geomorphic setting (fluvial delta vs marine tidal delta), and sediment depth (surface, mid-depth, and deep sediments) on C stocks. We hypothesise that C stocks will: (1) be higher in rush than non-rush vegetation communities, in line with previous research undertaken in the region; (2) be higher in fluvial delta than marine tidal delta, reflecting differences in sediment character and contributions from allochthonous C sources; and (3) decrease with sediment depth, reflecting decomposition of C over time. We then apply regression tree analysis and stable isotope analysis to identify ecosystem components and processes which may be most responsible for observed variability in saltmarsh C stocks.

Methods

Study Setting

The NSW coast is a moderate–high energy coastline with a maximum spring tidal range of 2.0 m and semi-diurnal tides. There are more than 150 estuaries and embayments, displaying a variety of sizes and forms. Barrier estuaries are the dominant form throughout the region. These estuaries have tidal inlets that are constricted by wave-deposited sands, and consequently tidal ranges within estuary basins are usually considerably less (~5–10%) than the ocean (Roy and others 2001). Intermittently open saline coastal lagoons occur in similar settings to barrier estuaries but have their entrances blocked part of the time by marine sands due to their low river discharge. In contrast, drowned valley estuaries typically occupy deeply incised bedrock valleys that open into semi-protected bays.

Regardless of estuary type, there are four sedimentary environments in estuaries (marine tidal delta, central mud basin, fluvial delta and riverine channel) which have characteristic water quality, nutrient cycling/primary productivity signatures and therefore characteristic ecosystems (Roy and others 2001). Two of these geomorphic zones—marine tidal delta and fluvial delta—represent depositional environments with distinctly different sedimentary sources and salinity regimes. According to the Roy and others (2001) classification, marine tidal delta sediments consist of moderately well-sorted quartzose sand derived from the open coast and subordinate amounts of mud. Open water salinities are similar to marine waters (~35) and are relatively constant compared to upstream zones influenced by freshwater inputs. A more complex association of physical settings are found in fluvial deltas with salinity, tidal exchange and temperatures fluctuating and sediment types ranging from poorly sorted mixtures of sand, mud and organics to muddy and organic-rich deposits.

Saltmarsh communities generally have low floral species richness, often being dominated by just one or two species (Adam and others 1988). Along the NSW coast, there are broad zonation patterns coinciding with surface elevation, whereby the majority of mid-intertidal marsh is considered a single association dominated by the low-growing chenopod *S. quinqueflora* and grass *S. virginicus* (Zedler and others 1995). Upper marsh communities are dominated by the rushes *J. kraussii* and *Baumea juncea* (Adam and others 1988). Although saltmarsh algae have not been well studied, they have been seen to colonise saltmarsh areas, particularly where the cover of higher plants is reduced (Adam, 1990). Data previously collected within the study region show a substantial difference in aboveground biomass of the rush community (*Juncus* mean = 1116 g m^{-2}), compared to that of the non-rush assemblages (*Sarcocornia* mean = 320 g m^{-2}; *Sporobolus* mean = 350 g m^{-2}), with distinct seasonal biomass patterns absent for all species (Clarke and Jacoby 1994). Throughout mainland Australia, saltmarshes are generally bordered downslope by mangroves (the species *Avicennia marina* is dominant throughout the region) and supratidal communities (*Casuarina glauca* and *Melaleuca ericifolia* trees and shrubs are common) to the higher, landward side. The saltmarsh grass *S. virginicus* is the only plant listed above with a C4 photosynthetic pathway.

Site Selection

Nine estuaries were selected for study on the basis of their saltmarsh aerial extent, distribution along the NSW coast and diversity of estuary structural type (Figure 1; Table 1). A factorial design was implemented to understand the effects of both geomorphic setting and vegetation structure upon soil C stocks. Within each estuary, two sites were chosen for field sampling—one site within the marine tidal delta geomorphic zone and another site further upstream subject to fluvial influence. Sites within each of these two zones were then selected based on the presence of both of the two most common saltmarsh vegetation communities of southeastern Australia: (i) a rush community dominated by *J. kraussii* and/or *B. juncea*; (ii) non-rush vegetation dominated by the grass *S. virginicus*, the succulent *S. quinqueflora* or a mosaic of the two. In some locations the rush community included the presence of non-rush species as sub-dominants—most notably *S. virginicus*, but occasionally *S. quinqueflora* and *Samolus repens*.

Field Collection and Measurement

A range of biological and physical field measurements were undertaken in concert with sediment core collection to assist in the identification of ecosystem components and processes responsible for variability in saltmarsh C stocks. A 0.5 m^2 plot was laid at each core location to take field measurements prior to sediment core insertion. Total plant cover was estimated visually to the nearest 5% using a gridded quadrat and canopy coverage comparison charts for reference. Where present, counts were made of crab burrows and mangrove pneumatophores using the same quadrat. Distance (m) to the nearest open water was later measured in ArcGIS 10.1 (Esri, Redlands, CA, USA) using field GPS co-ordinates of each plot.

A sediment core of 1 m depth was collected from four locations within each vegetation zone at each site, using a 5-cm diameter PVC pipe with sharpened edges to cut through root material. Compaction of sediments was evaluated by measuring the difference in elevation of the sediment surface

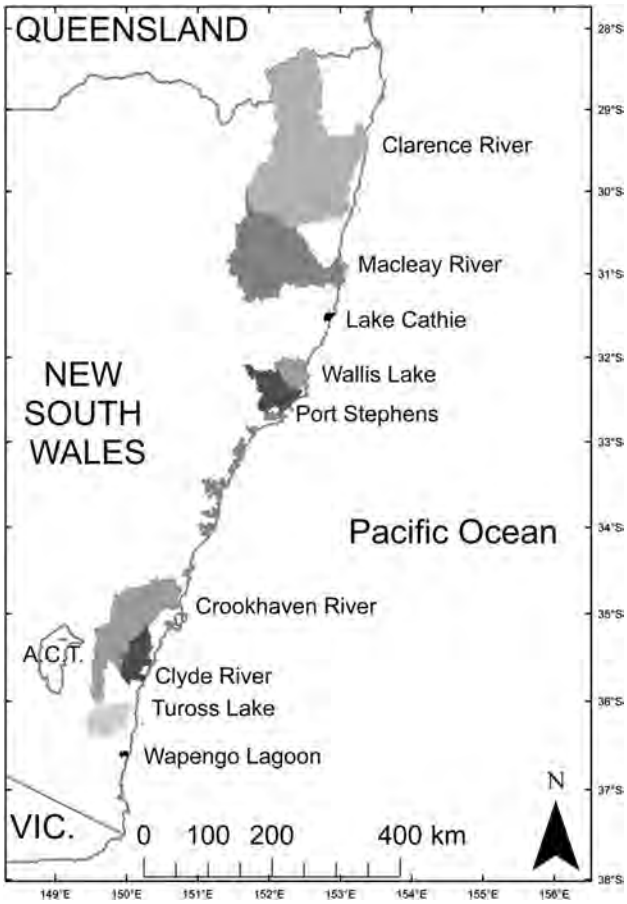


Figure 1. Location of the nine study estuaries along the New South Wales coast of southeast Australia. *Shaded areas* represent the catchments of each of the estuaries.

Table 1. Estuary and Study Site Information

Estuary	Entrance condition	Geomorphic type	Estuary area (km^2)	Catchment area (km^2)	Saltmarsh area (ha)	Site (M = marine; F = fluvial)	Latitude (°)	Longitude (°)	Distance from ocean (km)	Surface (0–20 cm) sediment classes[1]	Sub-surface (>20 cm) sediment classes[1]	Open water salinity
Clarence River	Open[2]	Barrier estuary	132	22,400	290	M	−29.434	153.356	3.0	Sand, mixed	Sand	35.3
						F	−29.379	153.352	7.6	Sand, mixed	Sand, mixed	32.2
Macleay River	Open[2]	Barrier estuary	32	11,385	425	M	−30.882	153.021	2.2	Fine, mixed	Fine, mixed, sand	36.5
						F	−30.894	152.999	5.9	Fine, mixed	Fine, mixed	34.7
Lake Cathie	Intermittent	Saline coastal lagoon	14	92	589	M	−31.549	152.850	1.0	Sand, mixed	Sand	37.7
						F	−31.551	152.845	1.6	Fine, mixed	Fine, mixed, sand	40.8
Wallis Lake	Open[2]	Barrier estuary	99	1420	590	M	−32.201	152.509	3.3	Mixed	Sand, mixed	34.5
						F	−32.335	152.487	18.2	Fine	Fine	37.7
Port Stephens	Open	Drowned valley estuary	134	4950	1063	M	−32.669	152.145	7.1	Sand, mixed	Sand	34.9
						F	−32.643	151.989	23.6	Fine	Fine	34.5
Crookhaven River[3]	Open[2]	Barrier estuary	32	7086	206	M	−34.909	150.741	2.7	Mixed, sand, fine	Mixed, sand	34.8
						F	−34.935	150.714	6.6	Fine	Mixed, fine	34.9
Clyde River	Open	Drowned valley estuary	18	1791	52	M	−35.710	150.172	2.8	Mixed, sand	Mixed	35.3
						F	−35.692	150.099	10.9	Fine	Fine	31.8
Tuross Lake	Open	Barrier estuary	15	1816	80	M	−36.077	150.123	1.7	Sand	Sand	34.3
						F	−36.055	150.063	7.5	Fine	Fine, mixed	33.9
Wapengo Lake	Open	Barrier estuary	4	73	51	M	−36.620	150.015	1.7	Sand, mixed	Sand, mixed	35.6
						F	−36.589	150.016	4.8	Fine	Mixed, fine	25.3

[1] *Sediment types listed in order of prevalence at each site.*
[2] *Entrance opening maintained by training wall(s).*
[3] *Estuary area data relate to broader Shoalhaven–Crookhaven estuary.*

within the core barrel and the outer sediment surface every 10 cm of core insertion. Mean compaction among all cores was 12.1 ± 0.8%. A compaction correction specific to each core was later applied (that is, prior to sectioning) at 10 cm intervals along the length of each core based on these measures.

After cores were extracted, multi-parameter water sensors (WTW GmbH; Germany) were inserted into the core hole to measure pH and salinity of 'seep' water, which were recorded once readings stabilised (generally <5 min). The average of three water measures was also recorded from the nearest open water area adjacent to each site at a depth of 0.5 m. Cores were transported under ice in large coolers to the laboratory, where they were stored at 4°C until sectioning and analysis.

Sediment Analysis

In the laboratory, cores were split open and sectioned for bulk density and chemical analysis. Previous research in saltmarshes has suggested that variations in C content are most significant in the upper 20–50 cm of soil (Johnson and others 2007). Therefore, we chose compaction-corrected depth intervals of 0–20, 20–50 and 50–100 cm to represent the surface rooting zone, mid and deep C stores, respectively. Sediment texture was categorised for each sample using a modified version of the texture-by-feel method of Thien (1979) and classified into one of the three broad groups: fine, mixed or sand-dominated sediments. For four cores (two from Wapengo fluvial site, and one each from Crookhaven fluvial and Clyde marine sites), sediment within the range 50–100 cm could not be retained. Subsequently these cores were excluded from overall C store calculations, although surface and mid intervals were retained for other analyses. Organic matter (including roots where it is present) was retained in the samples to allow measurement of bulk sediment characteristics.

Bulk sediment (inclusive of roots) was oven dried at 60°C for 72 h and measured to determine bulk density. Sediment was homogenised and ground into a fine powder using a ball mill. The 'Champagne test' (Jaschinski and others 2008) was used to determine whether samples contained inorganic C. Only 47 out of 428 aliquots contained sufficient inorganic C to cause bubbling upon acidification. Subsequently, those samples were subject to acid washing with 1 M HCl and shaken for 24 h prior to centrifugation, rinsing with MilliQ water and redrying.

Stable isotope approaches have been used extensively to distinguish between autochthonous and allochthonous sources of organic matter in estuarine wetlands, including in SE Australia (Connolly and others 2005; Mazumder and Saintilan 2010; Bouillon and others 2011). Stable isotope (δ^{13}C and δ^{15}N) analysis was therefore undertaken to elicit likely sources of organic matter to sediment stocks and allow comparison of inputs among wetland settings. Source materials measured include C3 intertidal species (comprising the saltmarsh species *S. quinqueflora* and *J. kraussii* and the mangrove *A. marina),* C3 supratidal species (comprising the tree species *C. glauca* and *M. ericifolia*), C4 saltmarsh (*S. virginicus*) and saltmarsh algal mat. Sediment and source materials were analysed for organic %C, %N, δ^{13}C and δ^{15}N using an Isotope Ratio Mass Spectrometry–Elemental Analyser (Thermo DeltaV) at University of Hawaii (HILO). Elemental and isotopic values for N were obtained from analysis of non-acidified aliquots. Organic C density (g C cm^{-3}) was determined by multiplying %C by bulk density of each sediment depth interval. Total organic C stock (Mg C ha^{-1}) was calculated as the C contained within the entire 0–100 cm depth range.

Data Analysis

A generalised linear model (Nelder and Baker 1972) was used for primary statistical analysis as C density data did not meet classical linear model assumptions, including normal distribution. Variation in C density (g C cm^{-3}) was assessed among the fixed factors of geomorphic setting (marine; fluvial), vegetation structure (rush; succulent/grass) and sampling depth (0–20; 20–50; 50–100 cm). A generalised linear model was also used to assess the role of geomorphic setting and vegetation structure factors on depth-integrated C stocks (that is, Mg C ha^{-1}). In both models, all main and interaction effects were included and estuary was included as a random factor.

Regression tree analysis (Breiman and others 1984) was used to further explore spatial patterns in the C density data. This was done for three purposes—(1) to assist in interpretation of interaction effects of the factorial design, (2) to identify which ecosystem components measured during the study are most responsible for C variability and (3) as a predictive model which might guide future research and land management priorities for C sequestration projects. Regression trees explain variation of a single dependent variable by repeatedly splitting the data into more homogeneous

groups, using combinations of independent variables (whether continuous, ordinal or categorical) (De'ath and Fabricius 2000). *Chi*-squared Automatic Interaction Detector (CHAID) was used at each step of tree creation to choose the independent variable with the strongest interaction with the dependent variable. Under this method, categories of each predictor are merged if they are not significantly different with respect to the dependent, with a significance level of 0.05 chosen for variable splitting. Bonferroni correction was made to P values to reduce the likelihood of obtaining type I errors when multiple pair-wise tests are performed on a single set of data. A minimum node size of 43 was set so that each node represented at least 10% of the 428 cases analysed. Independent variables included geomorphic setting (fluvial v marine); sediment depth; sediment type (fine, mixed, sand); vegetation structure (rush v succulent/grass); vegetation cover (%); dominant vegetation species; presence/absence of each of *S. virginicus, S. quinqueflora, J. kraussii, B. juncea* and seagrass wrack; crab hole density; seep water salinity and pH; and linear distance of the core from the nearest open water (m).

Results

Depth-integrated C stocks ranged from 17.89 Mg C ha to 448.20 Mg C ha^{-1} with a mean ± SE value of 164.45 ± 8.74 Mg C ha^{-1} across all cores. Overall, mean C stock was more than two times higher in fluvial settings (226.09 ± 12.37) than marine settings (104.54 ± 7.11; $F_{1,136} = 21.79$; $P < 0.001$), although differences between the two settings were not consistent across all estuaries (Figure 2). For example, Macleay River mean C stocks were higher in the marine setting (169.02 ± 10.05) than the fluvial setting (125.39 ± 8.29), whereas there was little difference between the two Port Stephens sites. Depth-integrated C stocks did not vary overall between the two vegetation communities assessed ($F_{1,136} = 0.03$; $P = 0.86$).

Assessment at the depth interval scale revealed sediment depth to be a significant factor ($F_{2,416} = 99.05$; $P < 0.001$), with pair-wise comparisons showing surface C densities (estimated marginal mean ± SE = 0.028 ± 0.002 g C cm^{-3}) significantly higher than both mid (0.016 ± 0.002; $P < 0.001$) and deep (0.013 ± 0.002; $P < 0.001$) intervals. There was, however, a significant interaction between sediment depth and geomorphic setting ($F_{2,416} = 18.025$; $P < 0.001$) with the magnitude of difference between geomorphic settings diminishing with sediment depth under both vegetation structures (Table 2). Nevertheless, mean C density remained significantly higher in fluvial settings relative to marine settings for all three depth intervals (except for the 50–100 cm interval of rushes).

Regression tree analysis revealed sediment grain type to be the most important explanatory factor ($F_{2,425} = 107.066$; $P < 0.001$) for variation in C density with C density significantly higher in fine sediments, followed by mixed sediments then sandy sediments (Figure 3). Secondary predictors of C density (in order of decreasing F value) were sediment depth among fine sediments only ($F_{2,157} = 30.148$; $P < 0.001$), vegetation cover among mixed sediments only ($F_{1,106} = 9.427$; $P = 0.030$) and surface vegetation structure among sand sediments only ($F_{1,157} = 5.598$; $P = 0.019$). Comparison of sediment grain types shows a trend of higher C densities in fine-grained sediments than mixed and sandy sediments both when geomorphic setting is made redundant (i.e. as is the case in the CART analysis; Figure 3) and when considered explicitly among geomorphic settings for each of the three depth intervals (Figure 4).

There were no clear relationships observed between C stocks and latitude, salinity or crab hole density (Figure S1). Salinity did vary between the two vegetation communities, however, in that 75% of grass/succulent community cores exceeded oceanic salinity, compared to 29% of rush measures (Figure S1C). There were significant but weak linear-log relationships between C stocks and distance to open water, with C decreasing with distance for both fluvial communities, but increasing slightly with distance in marine succulent/grass settings (Figure S1B). Plant cover was high (≥80%) in all rush plots, but varied across the succulent/grass community where there were weak positive relationships with C stocks in both marine and fluvial geomorphic settings (Figure S1E).

Like C density, there were significant differences in C:N ratios among sediment depths ($F_{2,416} = 34.786$; $P < 0.001$) and geomorphic setting ($F_{1,416} = 18.025$; $P = 0.005$), but not vegetation structure ($F_{1,416} = 0.428$; $P = 0.513$). There was also a significant interaction between geomorphic setting and depth ($F_{2,416} = 4.611$; $P = 0.010$). That is, C:N of surface sediments were similar among fluvial (estimated marginal mean ± SE = 16.4 ± 1.0) and marine (15.0 ± 1.0) settings, but were significantly higher in fluvial settings for both mid (22.2 ± 1.0 compared to 17.8 ± 1.0; $F_{1,416} = 8.982$; $P = 0.003$) and deep (22.9 ± 1.1 compared to 17.9 ± 1.0; $F_{1,416} = 11.210$; $P = 0.001$) sediment intervals.

Stable isotope analysis revealed diversity among sediment samples according to current vegetation

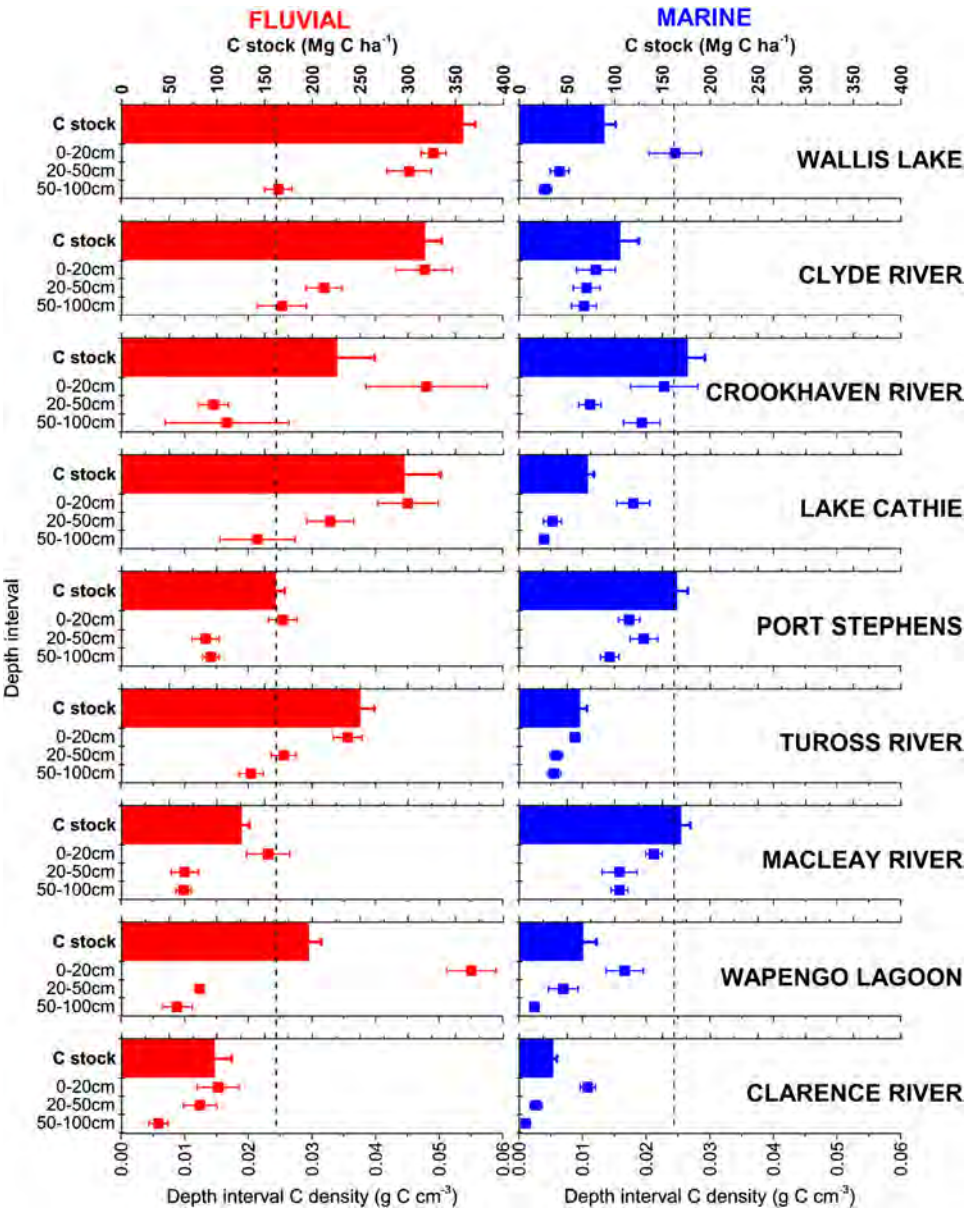


Figure 2. Mean depth-integrated (0–100 cm) carbon (C) stocks (*bars*) and mean C density of individual depth intervals (*squares*) for fluvial and marine sites of the nine study estuaries. *Error bars* represent one standard error either side of the mean. *Dashed line* at 162 Mg C ha^{-1} represents the mean C stock of saltmarshes globally (as reported by Duarte and others 2013).

composition and geomorphic setting (Figure 5). On the whole, surface sediments were more enriched in ^{13}C in marine sediments beneath *Sarcocornia* and *Sporobolus* than fluvial sediments vegetated by the same species. In contrast, sediments from rush communities (without C4) showed similarity in ^{13}C across both geomorphic settings with most values throughout surface and mid-depth intervals consistent with C3 vegetation values. There was increasing divergence from surface ^{13}C and ^{15}N values with depth in both settings, with divergence greatest in the 50–100 cm marine samples. A general trend of depletion in ^{15}N regardless of setting or vegetation, was also evident in sub-surface sediments.

Discussion

The mean belowground C stock of NSW saltmarshes as quantified in our study (164 Mg C ha^{-1}) is remarkably similar to the current global estimates of belowground saltmarsh stocks (162 Mg C ha^{-1}) (Duarte and others 2013). Our range of site estimates is also consistent with those made previously from other estuaries in the region—Livesley and Andrusiak (2012) report site means from 164.1 to 173.0 Mg C ha^{-1} within a single estuary, whilst all sites measured by Saintilan and others (2013) were within the range of our estimates. These similarities, however, belie the substantial variability in C stocks observed both in our regional assessment (where

Table 2. Estimated Marginal Means of Organic Carbon Density and C:N Calculated by Generalised Linear Models

Vegetation structure	Depth	C density						C:N					
		Fluvial		Marine				Fluvial		Marine			
		Mean	SE	Mean	SE	*F*	*P*	Mean	SE	Mean	SE	*F*	*P*
Depth intervals (g C cm^{-3})													
Rush	0–20 cm	0.037	0.003	0.021	0.003	14.544	**0.000**	17.340	1.476	16.272	1.476	0.262	0.609
	20–50 cm	0.022	0.003	0.010	0.003	8.967	**0.003**	21.969	1.476	18.439	1.476	2.859	0.092
	50–100 cm[1]	0.015	0.003	0.009	0.003	2.152	0.143	21.576	1.502	19.234	1.484	1.230	0.268
Succulent/grass	0–20 cm	0.039	0.003	0.013	0.003	41.489	**0.000**	15.541	1.476	13.719	1.476	0.762	0.383
	20–50 cm	0.022	0.003	0.009	0.003	9.558	**0.002**	22.483	1.476	17.165	1.476	6.491	**0.011**
	50–100 cm	0.018	0.003	0.008	0.003	5.487	**0.020**	24.227	1.476	16.628	1.476	13.253	**0.000**
Depth integrated (Mg C ha^{-1})													
Rush	0–100 cm[1]	215.835	25.697	118.022	25.585	7.276	**0.008**						
Succulent/grass	0–100 cm	232.919	25.545	91.803	25.545	15.258	**0.000**						

C density data are in the units of g C cm^{-3} for depth intervals and Mg C ha^{-1} for depth-integrated (0–100 cm) values. Effects statistically significant at $P < 0.05$ are in bold.
[1]sample n = 36 for all cases except fluvial rush (n = 35) and marine rush (n = 33) 50–100 cm and depth-integrated (0–100 cm) values.

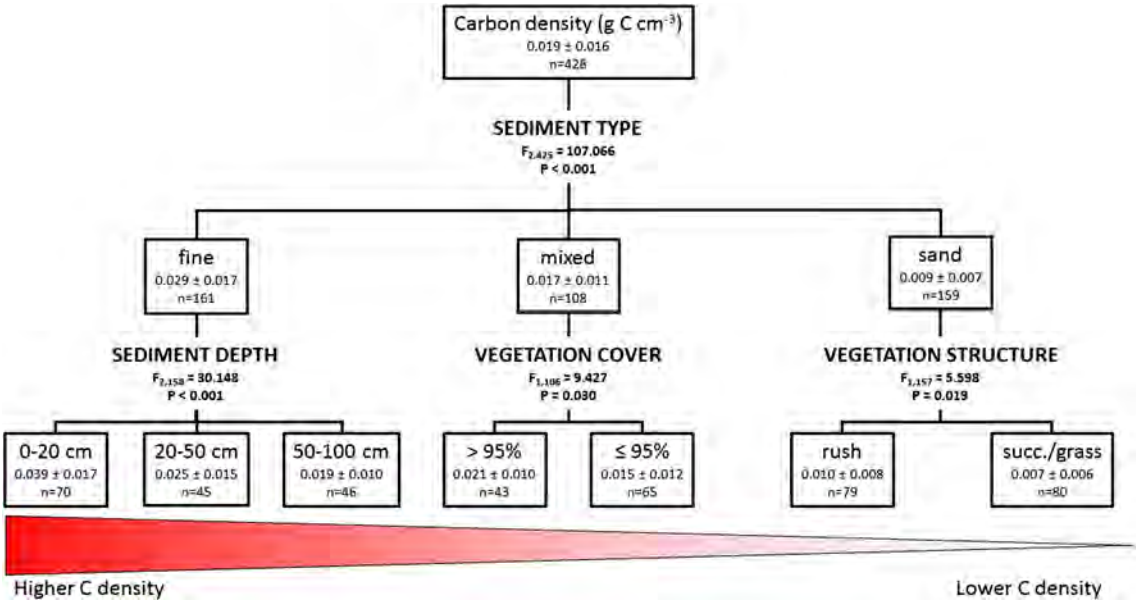


Figure 3. Classification and regression tree (CART) of carbon (C) density in New South Wales saltmarsh sediments. Mean ± standard deviation values and number of cases are presented for each node, with a minimum node size of 43 (>10% of all cases) and a 0.05 significance level selected.

core stocks ranged from 17.89 to 448.20 Mg C ha^{-1} with a coefficient of variation of 63%) and the larger variability at the broader, global scale (coefficient of variation = 160% (Duarte and others 2013)). Although some of the variability among global compilations may be due to methodological differences among contributing studies (for example, whether plant roots are retained or excluded from analysis), our results show that sedimentary setting within an estuary is key to understanding variability in salt-

marsh C stocks in SE Australia. This is reflected in both geomorphic setting differences in C stock and the subsidiary factor of sediment grain size.

C Stocks Vary According to Geomorphic Setting

Geomorphic setting was a significant factor explaining depth-integrated C stocks and C density across depth intervals, with mean stocks more than twice as high in fluvial settings, relative to marine sites. This finding contrasts with previous assessments in the region which have placed vegetation (rush versus succulent/grass) as the key predictor of saltmarsh C stocks (Lovelock and others 2013; Saintilan and others 2013). These previous efforts, however, have been limited in size (six sites and five sites, respectively), and confounded by different vegetation species inhabiting study sites in different estuarine settings. Consequently, analytical approaches appear to have apportioned variability to differences in vegetation structure over geomorphic differences. Using a factorial experimental design encompassing nine estuaries, we have been able to demonstrate an overarching role of geomorphic setting and sedimentary properties, rather than vegetation factors.

The processes responsible for a geomorphic distinction in C stocks may be diverse and complex, as fluvial and marine saltmarshes may vary in their hydrology, salinity, nutrient status, sediment type, and supply and character of allochthonous materials, among other factors (Roy and others 2001). Although our study was not designed to exhaustively test all such factors, our findings shed some light on important predictors of C stocks.

Sediment Grain Type is of Primary Importance

The Roy and others (2001) model identifies sediment texture as a key characteristic in the estuarine structure and function across geomorphic zones in SE Australia. Our simple categorisation of sediment samples as sand, fine or mixed sediment classes was sufficient to reveal broad differences in C stocks according to sediment type in both fluvial and marine geomorphic settings (Figure 4). In fact, CART analysis revealed sediment type to be the most important predictor of C density, of all variables tested, thereby making the broader classification of geomorphic setting redundant in the analysis (Figure 3). Sediment grain size may also explain the exceptional results of the Macleay estuary, which contained the only marine site with

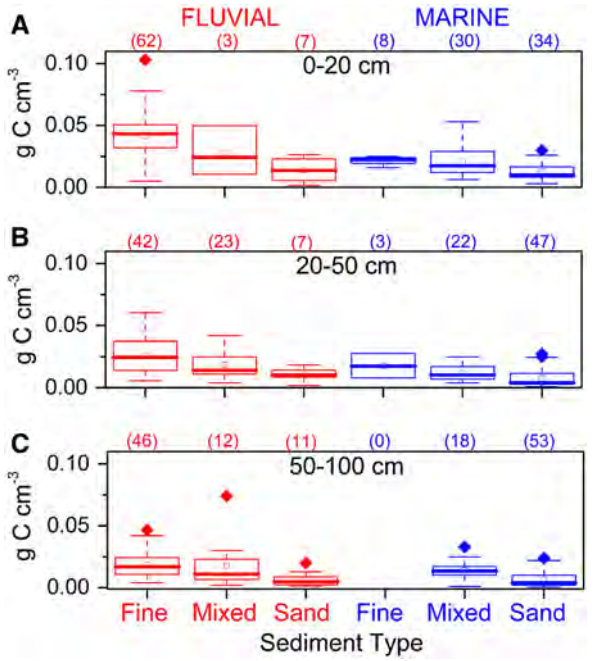


Figure 4. Boxplots of carbon density according to sediment grain type among surface (0–20 cm) (**A**), mid (20–50 cm) (**B**) and deep (50–100 cm) (**C**) sediments. *Dark horizontal lines* represent the median, *open squares* represent the mean, the *box* represents the 25th and 75th percentiles, the *whiskers* represent the maxima and minima, and outliers represented by *filled diamonds*. Samples numbers are presented in *parentheses* for each case.

(1) sediments dominated by fine grains, and (2) a distinctly higher C store than its fluvial counterpart. The dominance of fine grains here in a seaward setting is likely due to a combination of flood deposits in this mature infilled barrier estuary and extensive modifications around the site including levees which alter tidal energy and sedimentation dynamics. Our overall finding of higher C density in finer sediments is also consistent with observations in a variety of terrestrial and marine settings (Bock and Mayer 2000; Baldock and others 2004), including surface sediments of saltmarsh where correlation (R^2 = 0.77) between C content and clay content of sediments has been reported, with higher C content in fine-grained sediments (Zhou and others 2007).

There are multiple mechanisms which may explain the distinction in C storage among different sediment types. First, fine sediments have a greater specific surface area than coarser sediments, and as such have long been recognised for their greater potential for protection of C through organo-min-

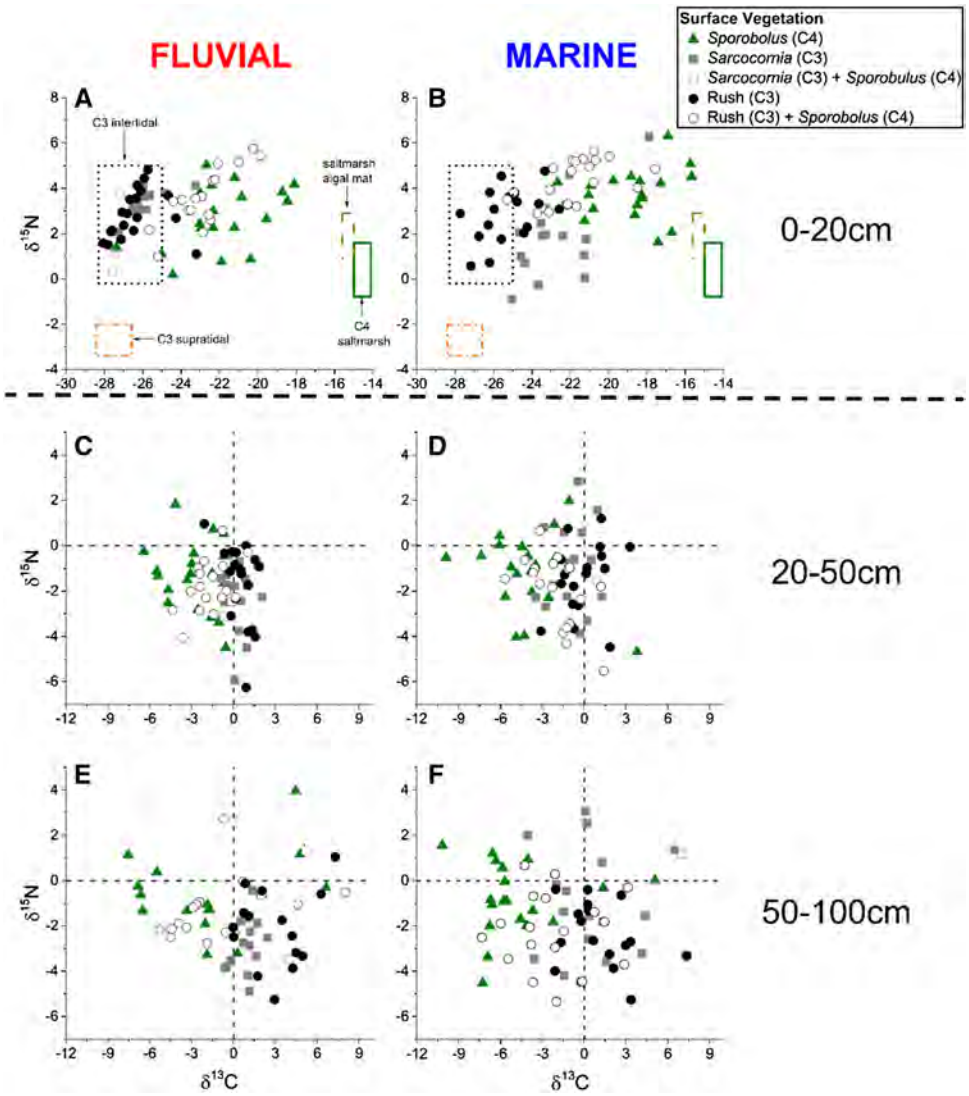


Figure 5. C and N isotope values for all sediment samples according to depositional setting (fluvial; marine) and sediment core depth (0–20 cm; 20–50 cm; 50–100 cm). Absolute values are presented for surface sediments whilst sub-surface data are presented as divergence from the corresponding surface sample from the same core. All data points are coded by the surface vegetation currently present within 0.5 m^2 plot around each core location. *Closed shapes* represent presence of C4 plant species (*Sporobolus virginicus*). Potential sources are indicated on each plot by the range of values for the functional groupings: C3 intertidal species (comprises the saltmarsh species *Sarcocornia quinqueflora* and *Juncus kraussii* and the mangrove *Avicennia marina*), C3 supratidal species (comprises the tree species *Casuarina glauca* and *Melaleuca ericifolia*), C4 saltmarsh (*Sporobolus virginicus*) and saltmarsh algal mat.

eral interaction (Bader and others 1960; Ransom and others 1998; Bock and Mayer 2000). Further, the cation exchange capacity of fine-grained minerals (including various oxides and hydroxides) (Baldock and others 2004) and greater capacity for protection within micro- or macro-aggregates (Baldock and Skjemstad 2000; De Gryze and others 2006) further enhance mineral protection in finer sediments. Whilst the contribution of mineral protection to saltmarsh C cannot be quantified with our current data, previous research has suggested that up to 90% of sedimentary OM from a broad range of marine depositional environments cannot be physically separated from its mineral matrix (Hedges and Keil 1995). We propose it is likely to be a key protective control in NSW saltmarshes, and deserving of further attention and quantification.

Oxygen exposure time (OET) is another important mechanism for C preservation in marine sediments (Hartnett and others 1998; Arnarson and Keil 2007), which may be of particular relevance in

intertidal ecosystems. Enhanced C preservation would be expected in fine sediments (as suggested in this study) due to lower porosity and oxygen exchange, resulting in lower sediment redox potentials and remineralization rates (Hedges and Keil 1995). In contrast, sandy saltmarshes—which have higher hydraulic conductivity and more rapid drainage (Crooks and others 2002)—would be expected to have higher OET and experience more rapid remineralisation of sediment C. We speculate that this mechanism may be at least partly responsible for the very low C preservation observed downcore in sandy marine sites at Wapengo, Tuross, Clarence and Lake Cathie. Detailed study of OET effects on C preservation in a range of intertidal sediments is required to confirm this.

Allochthonous C Inputs Vary Among Settings

Stable isotope and elemental ratios of C and nitrogen provide an insight into the character of OM preserved within the different saltmarsh settings. As there is little consensus on the effects of post-depositional decomposition on isotopic ratios in coastal habitats (Kennedy and others 2010) we limit interpretation to broad findings which are consistent with expected patterns of OM delivery and stability. On the basis of our data, we propose two important distinctions in OM character in our study. First, allochthonous inputs are of greater significance to C stocks in succulent/grass saltmarshes relative to rush saltmarshes. Second, OM preservation appears greater in fluvial relative to marine settings. Together, these distinctions have important implications for saltmarsh C storage.

The δ^{13}C values of surface sediments of succulent/grass saltmarshes in marine settings are indicative of ^{13}C-enriched sources. For cores collected from areas dominated by the C4 species *S. virginicus,* biomass from the host plant is the most likely explanation. For *S. quinqueflora*-dominated areas, however, significant OM contributions appear to be coming from sources more enriched than this host plant. These sources may include *S. virginicus* detritus washed in laterally from the same saltmarsh (though *S. virginicus* was uncommon or absent from some sites), saltmarsh benthic microalgae, or enriched allochthonous sources including seagrass wrack and marine plankton (Peterson and others 1986; Kennedy and others 2010). Surface sediments from marine succulent/grass cores also had the lowest mean C:N recorded in the study (Table 2), which is indicative of higher algal inputs relative to vascular plants or terrestrial OM inputs. Interestingly, these trends in δ^{13}C and C:N were less apparent in marine rush sediments, suggesting a greater proportion of autochthonous C in marine rushes relative to succulent/grass. This observation accords with both the high productivity and biomass of rushes (Clarke and Jacoby 1994) as well as their elevated position in the intertidal zone relative to succulent/grass saltmarshes (Adam and others 1988; Zedler and others 1995). At higher elevations, the inundation frequency of rushes is reduced and so is their access to tidal-borne materials. Additionally, low inundation frequency implies a lower capacity for tidal export of autochthonous C (that is, rush litter) in a community where biomass and litter production are both high (Clarke and Jacoby 1994). In a similar study, Adame and others (2010) found that allochthonous inputs were largely restricted to vegetation zones nearer the seaward fringe in tidal sites (that is, analogous to marine sites in our study), but were more uniformly distributed across river-dominated sites in southeast Queensland. Such geomorphic effects across the intertidal zone have implication for C stocks, with vegetation structure being a secondary predictor of C stock within sandy settings (that is, predominantly marine sites) but not fine sediment settings in our study (Figure 3). That is, higher biomass (Clarke and Jacoby 1994) and/or more stable OM inputs allow rush saltmarshes to have higher C stocks relative to succulent/grass saltmarshes in these settings.

More broadly, we would expect saltmarshes in fluvial and marine settings to be subject to different allochthonous inputs, which vary in both their quantity and stability. The higher C:N values of fluvial sediments over marine sediments for all depth intervals (Table 2) as well as the ^{13}C-depleted values in fluvial sediments relative to marine sediments (Figure 5) are indicative of this. These values suggest higher inputs of OM originating from C3 vascular plants, although it is not clear what proportion of this is from autochthonous (saltmarsh C3 plants) versus terrestrial sources. The fact that all fluvial surface sediments vegetated by *S. virginicus* (C4) are between 2 and 12% more depleted in ^{13}C than the host plant (Figure 5A) suggests that allochthonous input varies among core locations, but may also be substantial. Fluvial delta sites by their nature are likely to be depositional areas of terrestrially derived C, including stable sources such as lignin-rich plant detritus, charcoal from catchment fires and terrestrial soil C which has already undergone early diagenesis. Such inputs may also explain the high C:N ratios of fluvial saltmarsh sediments (Table 2). Finally, the

fact that there were contrasting relationships between C stocks and the distance of cores from open water (Figure S1B) suggests that tidal inundation patterns may also influence C supply and/or preservation differentially among estuarine settings.

Environmental Change and the Preservation of C

Deep C storage is becoming increasingly recognised for its importance to global soil and sediment C pools (McLeod and others 2011; Schmidt and others 2011). Although overall C densities decreased significantly with sediment depth on a cubic centimetre basis in our study, contributions of mid and deep interval sediments to total C stocks were high, with especially large contributions in some sites (Figure 2). Although variation in sediment grain size and/or preservation of stable allochthonous inputs may explain differences in deep C storage among sites, for some sites there is also evidence of historical environmental conditions which may influence C stocks. These range from very low C storage below the contemporary root zone in a young saltmarsh (Clarence marine <80 years old), through to deep C stocks concomitant with mangrove and saltmarsh root preservation (Port Stephens marine; but see also Saintilan and Hashimoto 1999) and deep C stocks in fluvial sites showing relics of past vegetation by the supratidal tree *Casuarina glauca* (Clyde fluvial and Tuross fluvial). Together, these observations highlight: (1) the dynamic nature of intertidal wetlands, (2) the site-specificity of C preservation and (3) the complexity which environmental history introduces to attempts to model blue C storage beyond the site scale. This also adds to growing literature on the influence of ecosystem change on blue C stocks (Choi and others 2001; Kelleway and others 2015; Kulawardhana and others 2015). Although such shifts in ecosystem structure may be caused through evolution (for example, infilling) of estuaries or alterations to entrance conditions, they are also likely to increase in coming decades due to changes in sea level and global climate (for example, Saintilan and others 2014). Broadly, our results show that C sequestered within estuarine ecosystems can be preserved under changing environmental conditions, however the influence of such change on long-term C stocks appears to be site specific. Further investigation of the molecular composition of C stocks downcore will provide insights regarding the sources and relative stabilities of deep C and the role of environmental history on regional blue C stocks.

Saltmarshes as Important C Stores

Our study adds to a growing compendium of regional quantifications of C storage in coastal wetlands. We have shown that on a per hectare basis, NSW saltmarshes contain similar C stocks to saltmarshes globally. The aerial extent of saltmarshes in NSW, however, is modest (72,589 ha; Creese and others 2009) when compared to many other temperate coastlines. This is due in part to the broader geomorphologic setting of NSW (with its relatively narrow coastal zone and the absence of broad intertidal zones in larger drowned valley estuaries) as well as significant human-induced declines in extent. Simple projection by multiplying mean C stock in our study (164.45 Mg C ha^{-1}) by statewide saltmarsh extent suggests NSW saltmarshes may hold 1.2 million tonnes (Mg) or more of C. Future efforts to delineate specific saltmarsh areas according to geomorphic zone and in particular, sediment types, will improve this statewide estimate.

It has been estimated that NSW has lost up to 70% of its coastal wetlands since European settlement (Zann 2000). Wetland draining through the construction of levees and floodgates would have been the major cause of saltmarsh loss during the 19th and early 20th centuries as floodplain agriculture expanded (especially along the northern NSW coast). The extent of this conversion is best highlighted by recent surface elevation modelling of the Hunter estuary on the mid-north coast of NSW. Here, it has been shown that 6970 ha of drained land occurs within elevation ranges suitable for estuarine wetlands (saltmarsh and mangrove), having been cut off from tidal flow by management structures (Rogers and others 2012). When considered in the context of remaining estuarine wetland extent in this estuary (2441 ha), this represents a 74% loss in area, which is in close agreement with the estimation of Zann (2000). Statewide projection (assuming a 70% reduction in saltmarsh extent and loss of 50% of C from the surface 1 m upon conversion) suggests 1.4 million tonnes of C may have been mobilised and potentially lost to the atmosphere. This suggests that more C may have been mobilised through historical habitat loss relative to C still retained within existing saltmarsh. Clearly, however, further research is needed regarding the proportion and fate of carbon lost after saltmarsh conversion.

Changes in saltmarsh extent and C storage are more complex over the past approximately 70 years. Although conversions through wetland drainage probably slowed, aerial photo analyses have shown losses during this period due to land claim/reclamation (ranging from 0 to 32% of original saltmarsh extent across nine sites), as well as conversion to terrestrial ecosystems (2–25%) (Wilton 2002). The fate of saltmarsh C under these new conditions, however, is unknown and potentially ranges from remineralisation (mediated by oxygenation of sediments during physical disturbance) to long-term preservation in deeper soil horizons. A more significant habitat change documented by Wilton (2002) is the replacement of saltmarshes by landward encroaching mangroves, which was responsible for the loss of 22–49% of original saltmarsh area across the same nine sites. Interestingly, this ecosystem shift has been shown to increase the overall C storage in estuarine wetland complexes (Doughty and others 2015; Kelleway and others 2015), suggesting saltmarsh changes in NSW over the past approximately 70 years is likely to have had a mixed impact on coastal C storage.

Managing Saltmarshes for C Storage

Our broad study along the NSW coastline shows that C storage is greatest in saltmarshes dominated by fine-grained sediments and subject to fluvial inputs. If avoiding C emission is an objective then conservation and management intervention should be prioritised for these saltmarsh types, as their loss or degradation is likely to lead to the most substantial losses of C. Maintaining or enhancing the conditions which have created these C hotspots—such as the continued delivery of fluvial sediments and stable, terrestrial OM inputs—will also promote future C sequestration. In other settings, namely sites with sediments comprising sands, our analysis suggests conservation of rush communities and maintaining high density vegetation cover may offer more substantial C gains. More broadly, our finding that sedimentary setting, rather than vegetation structure, is a key determinant of C storage represents a paradigm shift for saltmarsh C research in SE Australia. It also highlights the suitability of using sedimentary and geomorphic classification systems (such as Roy and others 2001) for upscaling field-based measurements to regional blue C inventories and for predicting blue C hotspots for targeted conservation and management activities.

ACKNOWLEDGEMENTS

Frederic Cadera is thanked for assistance with field sampling and sample preparation. Field collections were undertaken in accordance with NSW Office of Environment and Heritage scientific licence SL101217 and NSW Department of Primary Industries Scientific Permit P13/0058-1.0. We also thank NSW National Parks and Wildlife Service for supporting access to conservation reserves for fieldwork. This research was supported by the CSIRO Coastal Carbon Cluster and South East Local Land Services. PM was supported by an Australian Research Council DECRA Fellowship (DE13010 1084).

REFERENCES

Adam P. 1990. Saltmarsh ecology. Cambridge, UK.: Cambridge University Press.

Adam P. 2002. Saltmarshes in a time of change. Environ Conserv 29:39–61.

Adam P, Wilson N, Huntley B. 1988. The phytosociology of coastal saltmarsh vegetation in New South Wales. Wetlands (Australia) 7:35–85.

Adame MF, Neil D, Wright SF, Lovelock CE. 2010. Sedimentation within and among mangrove forests along a gradient of geomorphological settings. Estuar Coast Shelf Sci 86:21–30.

Alongi DM. 2002. Present state and future of the world's mangrove forests. Environ Conserv 29:331–49.

Arnarson TS, Keil RG. 2007. Changes in organic matter–mineral interactions for marine sediments with varying oxygen exposure times. Geochim Cosmochim Acta 71:3545–56.

Bader R, Hood D, Smith J. 1960. Recovery of dissolved organic matter in sea-water and organic sorption by particulate material. Geochim Cosmochim Acta 19:236–43.

Baldock JA, Masiello C, Gelinas Y, Hedges J. 2004. Cycling and composition of organic matter in terrestrial and marine ecosystems. Mar Chem 92:39–64.

Baldock JA, Skjemstad JO. 2000. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. Org Geochem 31:697–710.

Blum LK. 1993. Spartina alterniflora root dynamics in a Virginia marsh. Mar Ecol Prog Ser 102:697178.

Bock MJ, Mayer LM. 2000. Mesodensity organo–clay associations in a near-shore sediment. Mar Geol 163:65–75.

Bouillon S, Connolly R, Gillikin D. 2011. Use of stable isotopes to understand food webs and ecosystem functioning in estuaries. In: Wolanski E, McLusky DS, Eds. Treatise on estuarine and coastal science. Waltham: Academic Press. p 143–73.

Breiman L, Friedman JH, Olshen RA, Stone CJ. 1984. Classification and regression trees. Belmont, CA: Wadsworth.

Burdige DJ. 2007. Preservation of organic matter in marine sediments: controls, mechanisms, and an imbalance in sediment organic carbon budgets? Chem Rev 107:467–85.

Chen S, Torres R, Goñi MA. 2015a. The role of salt marsh structure in the distribution of surface sedimentary organic matter. Estuaries Coasts 39:108–22.

Chen Y, Chen G, Ye Y. 2015b. Coastal vegetation invasion increases greenhouse gas emission from wetland soils but also

increases soil carbon accumulation. Sci Total Environ 526:19–28.

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC. 2003. Global carbon sequestration in tidal, saline wetland soils. Global Biogeochem Cycles 17:22:21–22:12.

Choi Y, Wang Y, Hsieh Y-P, Robinson L. 2001. Vegetation succession and carbon sequestration in a coastal wetland in northwest Florida: Evidence from carbon isotopes. Global Biogeochem Cycles 15:311–19.

Clarke PJ, Jacoby CA. 1994. Biomass and above-ground productivity of salt-marsh plants in south-eastern Australia. Mar Freshw Res 45:1521–8.

Connolly RM, Gorman D, Guest MA. 2005. Movement of carbon among estuarine habitats and its assimilation by invertebrates. Oecologia 144:684–91.

Craft C. 2007. Freshwater input structures soil properties, vertical accretion, and nutrient accumulation of Georgia and US tidal marshes. Limnol Oceanogr 52:1220–30.

Creese R, Glasby T, West G, Gallen C. 2009. Mapping the habitats of NSW estuaries. NSW Fisheries Final Report Series 113. Port Stephens: Industry & Investment NSW, p 95.

Crooks S, Schutten J, Sheern GD, Pye K, Davy AJ. 2002. Drainage and elevation as factors in the restoration of salt marsh in Britain. Restor Ecol 10:591–602.

De'ath G, Fabricius KE. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–92.

De Gryze S, Jassogne L, Bossuyt H, Six J, Merckx R. 2006. Water repellence and soil aggregate dynamics in a loamy grassland soil as affected by texture. Eur J Soil Sci 57:235–46.

Doetterl S, Six J, Van Wesemael B, Van Oost K. 2012. Carbon cycling in eroding landscapes: geomorphic controls on soil organic C pool composition and C stabilization. Glob Change Biol 18:2218–32.

Donato DC, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M. 2011. Mangroves among the most carbon-rich forests in the tropics. Nat Geosci 4:293–7.

Doughty CL, Langley JA, Walker WS, Feller IC, Schaub R, Chapman SK. 2015. Mangrove range expansion rapidly increases coastal wetland carbon storage. Estuaries Coasts 39:385–96.

Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N. 2013. The role of coastal plant communities for climate change mitigation and adaptation. Nat Clim Change 3:961–8.

Duarte CM, Marbà N, Gacia E, Fourqurean JW, Beggins J, Barrón C, Apostolaki ET. 2010. Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. Global Biogeochemical Cycles 24.

Elsey-Quirk T, Seliskar DM, Sommerfield CK, Gallagher JL. 2011. Salt marsh carbon pool distribution in a mid-atlantic lagoon, USA: sea level rise implications. Wetlands 31:87–99.

Enriquez S, Duarte CM, Sand-Jensen K. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C: N: P content. Oecologia 94:457–71.

Feller IC, Lovelock CE, McKee KL. 2007. Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus phosphorus limited mangrove ecosystems. Ecosystems 10:347–59.

Fourqurean JW, Duarte CM, Kennedy H, Marbà N, Holmer M, Mateo MA, Apostolaki ET, Kendrick GA, Krause-Jensen D, McGlathery KJ. 2012. Seagrass ecosystems as a globally significant carbon stock. Nat Geosci 5:505–9.

Hartnett HE, Keil RG, Hedges JI, Devol AH. 1998. Influence of oxygen exposure time on organic carbon preservation in continental margin sediments. Nature 391:572–5.

Hedges JI, Keil RG. 1995. Sedimentary organic matter preservation: an assessment and speculative synthesis. Mar Chem 49:81–115.

Jaschinski S, Hansen T, Sommer U. 2008. Effects of acidification in multiple stable isotope analyses. Limnol Oceanogr 6:12–15.

Johnson BJ, Moore KA, Lehmann C, Bohlen C, Brown TA. 2007. Middle to late Holocene fluctuations of C3 and C4 vegetation in a Northern New England Salt Marsh, Sprague Marsh, Phippsburg Maine. Org Geochem 38:394–403.

Kelleway JJ, Saintilan N, Macreadie PI, Skilbeck CG, Zawadzki A, Ralph PJ. 2015. Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. Global Change Biol 22(3):1097–109.

Kennedy H, Beggins J, Duarte CM, Fourqurean JW, Holmer M, Marbà N, Middelburg JJ. 2010. Seagrass sediments as a global carbon sink: isotopic constraints. Global Biogeochem Cycles 24:GB4026.

Kleber M, Sollins P, Sutton R. 2007. A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. Biogeochemistry 85:9–24.

Kristensen E, Bouillon S, Dittmar T, Marchand C. 2008. Organic carbon dynamics in mangrove ecosystems: a review. Aquat Bot 89:201–19.

Kulawardhana RW, Feagin RA, Popescu SC, Boutton TW, Yeager KM, Bianchi TS. 2015. The role of elevation, relative sea-level history and vegetation transition in determining carbon distribution in *Spartina alterniflora* dominated salt marshes. Estuarine Coast Shelf Sci 154:48–57.

Laegdsgaard P, Kelleway J, Williams RJ, Harty C. 2009. Protection and management of coastal saltmarsh. Australian saltmarsh ecology. Collingwood: CSIRO Publishing. p 179–210.

Lavery PS, Mateo MA, Serrano O, Rozaimi M. 2013. Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. PLoS ONE 8:e73748.

Livesley SJ, Andrusiak SM. 2012. Temperate mangrove and salt marsh sediments are a small methane and nitrous oxide source but important carbon store. Estuar Coast Shelf Sci 97:19–27.

Lovelock CE, Adame MF, Bennion V, Hayes M, O'Mara J, Reef R, Santini NS. 2013. Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of South East Queensland, Australia. Estuaries Coasts 37:763–71.

Lovelock CE, Feller IC, Ellis J, Schwarz AM, Hancock N, Nichols P, Sorrell B. 2007. Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. Oecologia 153:633–41.

Mazumder D, Saintilan N. 2010. Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. Wetlands 30:375–80.

McLeod E, Chmura GL, Bouillon S, Salm R, Björk M, Duarte CM, Lovelock CE, Schlesinger WH, Silliman BR. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Front Ecol Environ 9:552–60.

Middelburg J, Nieuwenhuize J, Lubberts R, Van de Plassche O. 1997. Organic carbon isotope systematics of coastal marshes. Estuar Coast Shelf Sci 45:681–7.

Middelburg JJ. 1989. A simple rate model for organic matter decomposition in marine sediments. Geochim Cosmochim Acta 53:1577–81.

Nelder JA, Baker R. 1972. Generalized linear models. Encyclopedia Stat Sci 135:370–84.

Nixon SW. 1980. Between coastal marshes and coastal waters: a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry: URI, Marine Advisory Service, Publications Unit.

Ouyang X, Lee S. 2014. Updated estimates of carbon accumulation rates in coastal marsh sediments. Biogeosciences 11:5057–71.

Peterson BJ, Howarth RW, Garritt RH. 1986. Sulfur and carbon isotopes as tracers of salt-marsh organic-matter flow. Ecology 67:865–74.

Ransom B, Kim D, Kastner M, Wainwright S. 1998. Organic matter preservation on continental slopes: importance of mineralogy and surface area. Geochim Cosmochim Acta 62:1329–45.

Rogers K, Knoll EJ, Copeland C, Walsh S. 2015. Quantifying changes to historic fish habitat extent on north coast NSW floodplains, Australia. Reg Environ Change 1–11.

Rogers K, Saintilan N, Copeland C. 2012. Modelling wetland surface elevation dynamics and its application to forecasting the effects of sea-level rise on estuarine wetlands. Ecol Model 244:148–57.

Roy P, Williams R, Jones A, Yassini I, Gibbs P, Coates B, West R, Scanes P, Hudson J, Nichol S. 2001. Structure and function of south-east Australian estuaries. Estuar Coast Shelf Sci 53:351–84.

Saintilan N, Hashimoto T. 1999. Mangrove-saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia. Hydrobiologia 413:95–102.

Saintilan N, Rogers K, Mazumder D, Woodroffe C. 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuar Coast Shelf Sci 128:84–92.

Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW. 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob Change Biol 20:147–57.

Schmidt MW, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kogel-Knabner I, Lehmann J, Manning DA, Nannipieri P, Rasse DP, Weiner S, Trumbore SE. 2011. Persistence of soil organic matter as an ecosystem property. Nature 478:49–56.

Serrano O, Lavery PS, Duarte CM, Kendrick GA, Calafat A, York P, Steven A, Macreadie P. 2016. Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? Biogeosci Discuss 2016:1–24.

Sutton-Grier AE, Moore AK, Wiley PC, Edwards PET. 2014. Incorporating ecosystem services into the implementation of existing U.S. natural resource management regulations: operationalizing carbon sequestration and storage. Marine Policy 43:246–53.

Thien SJ. 1979. A flow diagram for teaching texture-by-feel analysis. J Agron Educ 8:54–5.

Trevathan-Tackett SM, Kelleway JJ, Macreadie PI, Beardall J, Ralph P, Bellgrove A. 2015. Comparison of marine macrophytes for their contributions to blue carbon sequestration. Ecology 96:3043–57.

Wilton KM. 2002. Coastal wetland habitat dynamics in selected New South Wales estuaries: Australian Catholic University Sydney, Australia.

Zann LP. 2000. The Eastern Australian Region: a dynamic tropical/temperate biotone. Mar Pollut Bull 41:188–203.

Zedler J, Nelson P, Adam P. 1995. Plant community organization in New South Wales saltmarshes: species mosaics and potential causes. Wetlands (Australia) 14:1–18.

Zhou J, Wu Y, Kang Q, Zhang J. 2007. Spatial variations of carbon, nitrogen, phosphorous and sulfur in the salt marsh sediments of the Yangtze Estuary in China. Estuar Coast Shelf Sci 71:47–59.

Global Change Biology

Global Change Biology (2016) **22**, 1097–1109, doi: 10.1111/gcb.13158

Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes

JEFFREY J. KELLEWAY[1], NEIL SAINTILAN[2], PETER I. MACREADIE[1,3], CHARLES G. SKILBECK[4], ATUN ZAWADZKI[5] and PETER J. RALPH[1]

[1]*Plant Functional Biology and Climate Change Cluster, School of Life Sciences, University of Technology Sydney, Ultimo, NSW 2007, Australia,* [2]*Department of Environmental Sciences, Macquarie University, Sydney, NSW 2109, Australia,* [3]*School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Burwood, Vic. 3125, Australia,* [4]*School of Life Sciences, University of Technology Sydney, Ultimo, NSW 2007, Australia,* [5]*Institute for Environmental Research, Australian Nuclear Science and Technology Organisation, Lucas Heights, NSW 2234, Australia*

Abstract

Shifts in ecosystem structure have been observed over recent decades as woody plants encroach upon grasslands and wetlands globally. The migration of mangrove forests into salt marsh ecosystems is one such shift which could have important implications for global 'blue carbon' stocks. To date, attempts to quantify changes in ecosystem function are essentially constrained to climate-mediated pulses (30 years or less) of encroachment occurring at the thermal limits of mangroves. In this study, we track the continuous, lateral encroachment of mangroves into two south-eastern Australian salt marshes over a period of 70 years and quantify corresponding changes in biomass and belowground C stores. Substantial increases in biomass and belowground C stores have resulted as mangroves replaced salt marsh at both marine and estuarine sites. After 30 years, aboveground biomass was significantly higher than salt marsh, with biomass continuing to increase with mangrove age. Biomass increased at the mesohaline river site by 130 ± 18 Mg biomass km^{-2} yr^{-1} (mean ± SE), a 2.5 times higher rate than the marine embayment site (52 ± 10 Mg biomass km^{-2} yr^{-1}), suggesting local constraints on biomass production. At both sites, and across all vegetation categories, belowground C considerably outweighed aboveground biomass stocks, with belowground C stocks increasing at up to 230 ± 62 Mg C km^{-2} yr^{-1} (± SE) as mangrove forests developed. Over the past 70 years, we estimate mangrove encroachment may have already enhanced intertidal biomass by up to 283 097 Mg and belowground C stocks by over 500 000 Mg in the state of New South Wales alone. Under changing climatic conditions and rising sea levels, global blue carbon storage may be enhanced as mangrove encroachment becomes more widespread, thereby countering global warming.

Keywords: biomass, blue carbon, carbon sequestration, climate change, ecosystem services, mangrove, mangrove encroachment, salt marsh, saltmarsh, sea level rise

Received 15 August 2015 and accepted 29 September 2015

Introduction

Shifts in ecosystem structure have been observed over recent decades as woody plants (shrubs and trees) encroach upon grasslands and wetlands globally (Saintilan & Rogers, 2015). A recent synthesis of shrub encroachment into terrestrial grasslands has shown that while structural change may have mixed effects on ecosystem functional traits, significant increases in aboveground and soil carbon (C) pools are common (Eldridge *et al.*, 2011). Such a change in 'blue carbon' habitats – that is, C-rich, marine habitats – could have significant implications for regional and global C pools, as mangroves (trees and shrubs) and salt marshes (communities of grasses, succulent herbs, rushes and low shrubs) are disproportionately important in sequestering C relative to their spatial extent (Duarte *et al.*, 2005; Mcleod *et al.*, 2011). This is due to (1) high productivity in both ecosystems (Nixon, 1980; Alongi, 2002) manifest in C bound within aboveground and belowground biomass; (2) effective trapping of particulate organic C originating from within the ecosystem (autochthonous) or external (allochthonous) riverine and oceanic sources (Mcleod *et al.*, 2011); and (3) anoxic, saline subsurface conditions which slow down the rate of decay of organic material (Magenheimer *et al.*, 1996; Duarte *et al.*, 2005; Mcleod *et al.*, 2011).

Mangroves and salt marshes are dynamic ecosystems found in a range of sedimentary settings along low-

Correspondence: Jeffrey J. Kelleway, tel. +61 423 361 821, fax: +61 2 9514 4079, e-mail: j.kelleway@gmail.com

© 2015 John Wiley & Sons Ltd

energy coastlines. They generally share a similar ecological niche in the intertidal zone and have different but overlapping latitudinal distributions. Globally, mangrove range is limited chiefly by physiological intolerance to subfreezing temperature, with most species confined to tropical or subtropical climes (Duke *et al*., 1998). In contrast, salt marshes appear to be less constrained by temperature, being found from tropical through to arctic zones, although extent and species diversity is greater in higher latitudes (Adam, 1993, Friess *et al*., 2012), where mangrove distributions decline. In temperate and subtropical zones, these two distributions often overlap, forming adjacent and/or ecotonal communities in the intertidal zone. In recent years, a poleward expansion of mangroves has been reported on each of the continents mangroves and salt marshes co-inhabit – Asia, Africa, North America, South America and Australasia (Saintilan *et al*., 2014 and references therein). To date, much of the research effort has focussed on encroachment by the species *Avicennia germinans* throughout the northern Gulf of Mexico (Stevens *et al*., 2006; Comeaux *et al*., 2012; Bianchi *et al*., 2013) and Atlantic coast (Cavanaugh *et al*., 2014) of the United States. Concurrent with this, poleward range expansion, however, is a lateral 'within-range' mangrove expansion into treeless salt marsh communities. This phenomenon is best documented throughout Australasia, where encroachment into salt marsh is a near-ubiquitous trend in south-eastern Australia and New Zealand (Burns & Ogden, 1985; Saintilan & Williams, 1999).

At a global scale, mangrove encroachment of salt marsh may be driven by a suite of changing environmental factors favouring mangrove, including rising sea level, elevated atmospheric CO_2 and higher temperatures (McKee *et al*., 2012; Saintilan *et al*., 2014). Among regions, however, the relative importance of specific drivers may vary. In south-eastern USA, for example, it has been well documented that mangrove abundance and coverage is winter temperature-sensitive with *A. germinans* strongly regulated by air temperatures of −4.0 to −8.9°C or less (Stevens *et al*., 2006; Osland *et al*., 2013; Cavanaugh *et al*., 2014). In the absence of extreme winter events, mangrove cover and abundance increases, with encroachment into salt marsh occurring, as has been observed across the region since extreme freezes in the 1980s (Stevens *et al*., 2006). Landward encroachment of mangroves has also been attributed to sea level rise and alteration of freshwater flow in this region (Krauss *et al*., 2011). Across Australasia, however, winter temperature extremes are not considered a primary control on mangrove encroachment. In this region, where encroachment has most commonly been reported as *A. marina* moving into *Sarcocornia–Sporobolus* salt marshes, numerous local and regional drivers have been proposed. These include increased rainfall in subtropical locations (Eslami-Andargoli *et al*., 2009), increases in sedimentation following catchment development in New Zealand (Lovelock *et al*., 2007), altered tidal regimes, enhanced nutrient concentrations and regional subsidence (Saintilan & Williams, 1999). It has also been demonstrated that mangroves have a higher capacity than salt marshes to respond to sea level rise through vertical sediment accretion throughout the region (Rogers *et al*., 2006).

Global estimates of mangrove biomass density and its associated C storage potential (237–563 tonnes CO_2 equivalent ha^{-1}) far outweigh those of salt marshes (12–60 tonnes CO_2 equivalent ha^{-1}) (Murray *et al*., 2011), suggesting that mangrove encroachment may cause a substantial increase in biomass C pools. Such a case has been highlighted recently, with Doughty *et al*. (2015) reporting large increases in C storage as a result of encroachment into a Florida salt marsh, with this increase driven by aboveground biomass, but not belowground biomass or non-biomass (soil) C pools.

Belowground C pools – inclusive of live and dead root biomass, accumulated litter and allochthonous organic matter – are by far the largest C store in coastal, intertidal wetlands. Higher sediment C densities have been reported in mangroves than salt marshes, globally, although density may be highly variable both within and between settings for both ecosystems (Chmura *et al*., 2003; Pendleton *et al*., 2012). While comparative data of mature ecosystems suggest belowground C storage should increase with mangrove encroachment of salt marsh, no measurement of the magnitude or temporal dynamics of such a C change has been examined in 'within-range' encroachment settings. By contrast, a number of studies have assessed belowground C responses to encroachment of *Spartina alterniflora* dominated salt marshes by *A. germinans* in the northern Gulf of Mexico, although to date, results have been mixed and are largely inconclusive. For example, in Fourchon, Louisiana, Perry & Mendelssohn (2009) reported similar sediment accretion, belowground production, decomposition, and C assimilation between salt marshes and areas encroached by *A. germinans,* proposing that the small stature and areal extent of mangroves after only 15 years of encroachment may have muted any significant effects. Similarly, no effects on bulk density or organic matter content were seen using sediment core depth as a 60-year temporal proxy in ecotones in the same locality (Henry & Twilley, 2013). In Texas, Comeaux *et al*. (2012) assessed, among other factors, the impact of encroachment on C sequestration and sediment geochemistry in back-barrier, sand-dominated wetlands. They found significant

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

increases in live root density in mangrove sediments at some locations, but did not report any higher organic matter densities associated with this – in fact, sediment organic matter density in new mangrove sediments was lower than in adjacent salt marsh cores. Based on the substantially higher sediment, C, and lignin accumulation rates, Bianchi *et al.* (2013) proposed that future mangrove encroachment of all Gulf of Mexico salt marsh could sequester 129 ± 45 Tg C belowground over 100 years.

A difficulty faced by these North American studies is the episodic nature of encroachment at the poleward limit of mangroves. Attempts to quantify changes in ecosystem function are essentially constrained to climate-mediated 'pulses' of encroachment; that is, mangrove expansion has historically been interrupted or set back every 30 years or less, rather than there being a continuous shift in ecosystem structure. In our study, we track continuous mangrove encroachment into two south-eastern Australian salt marshes over a 70-year period and undertake biomass and sediment core measurements at locations representing known encroachment timeframes. Using this approach, we aim to: (1) quantify changes in biomass and belowground C stores across the 70-year history of encroachment; (2) identify rates of change for aboveground and belowground stores between sites of contrasting salinity/geomorphic setting, and (3) investigate relationships between mangrove encroachment and surface elevation. The findings from our experimental setting will offer insights relevant into other regions, where changing climate is likely to shift encroachment from 'pulses' towards longer term ecosystem change.

Materials and methods

Sampling locations

The Georges River/Botany Bay estuary of south-eastern Australia (Fig. 1a) was chosen as a study estuary because its history of mangrove encroachment is well known from a long time series of aerial photograph coverage (Haworth, 2002). Georges River is a drowned-river valley estuary which flows into the oceanic embayment of Botany Bay. The estuary has a catchment of 930 km^2 comprising Triassic sandstone and shale. European settlement of the catchment from the early 1800s saw extensive clearing of the northern section of the catchment for farmland. More intensive disturbance to catchment soils occurred from the first half of the 20th century, as residential development began to dominate the northern catchment.

Two salt marsh-mangrove complexes within the system were chosen for analysis (Fig. 1b). An upstream site, referred to hereafter as 'Georges River', was chosen within the fluvial-influenced section of the river, located on a 'half-moon' embayment adjacent to the main river, ~ 14 km upstream of Botany Bay. A marine site was chosen at Towra Point – a sandy peninsula largely isolated from terrestrial influence on the southern shoreline of Botany Bay. Both sites are currently conservation reserves, with Towra Point also listed as a Ramsar Wetland of International Importance. Rainfall in the region is spread throughout the year, with annual rainfall of 1084 mm y^{-1} in Botany Bay (Sydney Airport weather station) and 1024 mm yr^{-1} near the Georges River site (Lucas Heights weather station). Mean ± SD salinity of open water is 32 ± 3 ppt and 15 ± 8 ppt near the Towra Point and Georges River sites, respectively (Geoscience Australia, 2015).

Avicennia marina is the dominant mangrove in the region. It is a cosmopolitan species with a wide latitudinal distribution ranging from the tropics to the southernmost location of mangroves in Australia (38°S). The root system is structurally complex, comprising cable roots, pneumatophores, fine feeding roots and anchor roots which grow from the trunk. Cable roots grow belowground to a depth of about one metre (Purnobasuki & Suzuki, 2005). The only other mangrove species present in the Sydney region is the river mangrove *Aegiceras corniculatum*, a species more commonly found in lower salinity settings. This species is uncommon at Towra Point, but forms an understorey along with low-statured *A. marina* in parts of the riverine fringe at the Georges River site.

Salt marsh vegetation at both sites is typical of New South Wales coast salt marshes, where the majority of mid-intertidal marsh is considered a single community complex dominated by the low-growing chenopod *Sarcocornia quinqueflora* and grass *Sporobulus virginicus* (Zedler *et al.*, 1995) and upper marsh communities dominated by the taller rush *Juncus kraussii* (Adam *et al.*, 1988). Salt marsh sampling was restricted to the *Sarcocornia* and *Sporobolus* complex at both sites, as this is the community most commonly encroached by mangroves in the region.

Experimental design

A chronosequence experimental design – that is, one which uses space as a substitute for time – was developed to explore the biomass and sediment C changes associated with mangrove encroachment into salt marsh at each of the two study sites. For the Georges River site, orthorectified aerial photographs taken in the years 1943, 1955, 1970, 1982, 1998 and 2013 were georeferenced and overlaid in ARCGIS 10.1 (Esri, Redlands, CA, USA). Overlaying of successive images allowed the identification of field sampling locations where mangrove encroached into salt marsh over the following time periods relative to 2013: 0–15 years; 31–43 years; 58–70 years (Fig. 1c). Mangrove and salt marsh vegetation were easily distinguished based on texture and colour differences in the aerial photographs. For Towra Point, maps of vegetation change created using historical aerial photography (1943, 1956, 1970, 1983, 1999) by Wilton (2002) were used to identify field sampling locations corresponding to the following past time intervals: 0–14 years, 30–43 years and 57–70 years (Fig. 1d). Interpretation of the 1943 images allowed the identification of mature mangrove stands >70 years old at each site. Locations

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

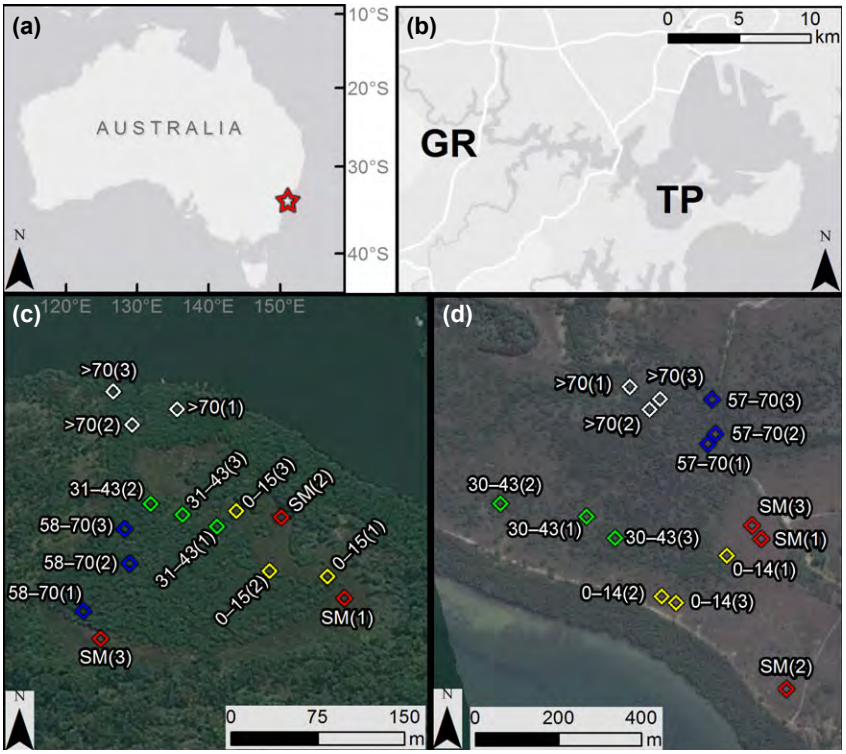


Fig. 1 Maps of the study region (starred) within Australia (a); the Georges River/Botany Bay estuary with Georges River National Park (GR) and Towra Point Nature Reserve (TP) study sites labelled (b); Georges River (c) and Towra Point (d) study sites with core locations labelled and marked by diamonds (white = ≥70 years mangroves; blue = 57/58–70 years mangroves; green = 30/31–43 years mangroves; yellow = 0–14/15 years mangroves; red = salt marsh (SM).

currently vegetated exclusively by salt marsh were identified in the field, with historic photographs/maps used to confirm the absence of mangrove at these sampling locations throughout the 70-year study period. Together, five distinct chronosequence zones were identified at each site: a mature mangrove community >70 years old, three zones where mangrove has replaced salt marsh within the past 0–70 years, and a salt marsh zone which has not been encroached. Three replicate sampling locations were identified for each age zone at each site (Table S1).

Field measurements

At each location, elevation was measured using a modified version of the tidal inundation method described by English *et al.* (1994), whereby three vertical rods marked with water-soluble dye were inserted within 2 m of each core location immediately prior to a summer Spring tide (Georges River: 06/12/2013 predicted tide 1.95 m above lowest astronomical tide (LAT) datum; Towra Point 04/12/2013 predicted tide 1.99 m above LAT). Depth of inundation was measured immediately after the tide receded and subtracted from the predicted tide height. English *et al.* (1994) report an accuracy of within 5 cm elevation for tidal inundation methods. Care was taken during the measurement procedure and in the selection of calm days (to minimize wind and waves effects) to minimize error among plots. Comparison of three replicate rods revealed a standard error of the mean ≤1 cm for each plot. Aboveground biomass measurements were undertaken from October 2013 through January 2014. At each location, mangrove aboveground biomass was determined using a 10 × 10 m plot centred at location coordinates. All mangrove trees >2 m height were measured for stem height (m) using extendable measuring sticks/tapes and diameter in cm at breast height (DBH; 1.3 m). In cases where *A. marina* had multiple stems branching from the same buttress, each of these stems was measured and treated as a separate tree (Clough *et al.*, 1997). In cases of leaning trees, DBH was measured at 1.3 m along the natural height of the trunk. Allometric equations specific to the species and region as modified by Saintilan (1997) were used to calculate aboveground biomass (W, in kg) of all trees >2 m height:

$$W = \frac{h[0.214(D_{\mathrm{BH}} \times \pi) - 0.113]^2}{10} \quad (1)$$

where, h = stem height (m); D_{BH} = diameter at breast height (cm).

Mangroves <2 m in height (which encompasses saplings and dwarf trees, hereafter referred to collectively as 'shrubs') were measured for height, crown depth, maximum crown width and crown length (perpendicular to the maximum width). All shrubs were measured within a 100-m^2 quadrat,

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

except where >100 shrubs were present and the shrub layer appeared uniform. In such instances, all shrubs were counted, with measurements restricted to the first 25 shrubs encountered in a clockwise direction from bearing 0°. Similarly, in a single Georges River >70 years quadrat where there were more than 400 small *Aegiceras corniculatum* trees (approximate height range 2.5–3.7 m), all trees were counted and the first 25 trees measured. The species *A. marina* and *A. corniculatum* have similar morphology in the height range 0–2.0 m. In the absence of allometric equations for *A. corniculatum* shrubs, shrub biomass was calculated for both species using allometric equations for *A. marina* developed by Woodroffe (1985):

$$W^{-1/3} = 0.489 + 0.100\,C \quad (2)$$

where W = total aboveground biomass (g) and C = average canopy width (cm) (calculated as the average of the greatest canopy width and the width of the canopy at right angles to the greatest width).

Salt marsh aboveground biomass was determined by cutting aboveground material from three 30 × 30 cm quadrats randomly located within 2 m of the plot centre. Material was transferred to the laboratory where it was rinsed to remove attached sediment, oven dried to constant mass (60 °C for 72 h) and then weighed. Previous research has suggested no seasonal trends occur in aboveground biomass of *S. quinqueflora* and *S. virginicus* (Clarke & Jacoby, 1994). Because the turnover times of aboveground biomass vary substantially between mangrove (years to decades or more) and salt marsh plants (annual to years), we chose to compare standing biomass stocks across the chronosequence, rather than rates of net primary production; that is, changes in aboveground biomass across the chronosequence are reported in terms of the total standing aboveground biomass (sum of mangrove tree + mangrove shrub + salt marsh biomass per unit of area).

Sediment cores

A sediment core of 1 m depth was collected from the centre of each 100-m^2 plot, using a piston coring device and a 5-cm-diameter PVC pipe with sharpened edges to cut through root material. Compaction of sediments was estimated by measuring the difference in elevation of the sediment surface within the core barrel and the outer sediment surface. A linear compaction correction factor was later applied along the length of each core based on this measure. Mean ± SD compaction was 14.9 ± 9.1% at Towra Point and 16.8 ± 6.4% at Georges River.

After extraction, cores were capped and transported to the laboratory, where they were kept at 4 °C until analysis. Magnetic susceptibility was measured downcore using a Bartington loop sensor (Model: MS2C) attached to a Multisensor Core Logger (MSCL; GeoTek, UK) to determine the downcore variability of magnetic mineral concentration. The ease with which sediments are magnetized is related to the concentration and composition of magnetisable material contained within the sample (Thompson *et al.*, 1975). In most recent sediment samples, magnetic susceptibility of sediments is a measure of the amount of the mineral magnetite (or its oxidized derivative, haematite) present by unit volume. In addition to mineralogic sources (mainly soils), human introduced magnetic materials and biogenic sources (including bacterially generated ferrimagnetic material) can also produce magnetic anomalies. 'Wiggle matching' of magnetic peaks among cores is commonly used to correlate stratigraphy among multiple cores (Buylaert *et al.*, 2008) and to correlate stratigraphy in undated cores to a dated reference core in order to verify the timing of sedimentation from catchment erosion (Dearing *et al.*, 1981).

^{210}Pb dating

^{210}Pb dating of Georges River 58–70 years core #3 was used to confirm the age of the magnetic susceptibility peaks present in Georges River cores. Ten dried and ground sediment aliquots from sediment core depth intervals (0–1; 10–11; 15–16; 20–21; 25–26; 30–31; 40–41; 50–51; 70–71 and 90–91 cm) were analysed by alpha spectrometry at the Australian Nuclear Science Technology Organisation.

A constant rate of supply (CRS) model (Appleby & Oldfield, 1978) using unsupported ^{210}Pb activities between 0 and 71 cm was used to calculate the sediment age and mass accumulation rate for each interval (Fig. S1). This type of model was chosen because we expect mass accumulation rates to vary throughout the core chronology, in accordance with changes in vegetation (from low accumulation under salt marsh to high accumulation under mangrove) and due to historic catchment disturbance.

Belowground C analysis

All cores were longitudinally split into half to provide one subsample for current analyses and another subsample for future analyses. Half-cores for this study were subsectioned for bulk density and chemical analysis. Compaction-corrected depth intervals of 0–5, 5–10, 10–15, 15–20, 20–30, 30–50 and 50–100 cm were sectioned for analysis. Bulk sediment was oven dried to constant mass (60 °C for 72 h), and measured to determine bulk density. Sediment was homogenized and ground into a fine powder using a ball mill (MM 301 Ball Mill, Retsch, Germany). The 'Champagne test' (Schlacher & Connolly, 2014) was used to determine whether samples contained inorganic C. Only six aliquots from Towra Point and none from Georges River contained sufficient carbonate to cause bubbling upon acidification. Subsequently, those samples were subject to acid washing with 1M HCl and shaken for 24 h prior to centrifugation, rinsing with Milli-Q (Merck Millipore, Darmstadt, Germany) water and re-drying. Elemental C (total organic C) content (%) was measured for all samples using a CN analyser (LECO TruSpec, LECO Corporation, St. Joseph, MI, USA). Organic C density (g cm^{-3}) was determined by multiplying %C by bulk density.

Statistical analyses

Generalized linear models (GzLMs) (Nelder & Baker, 1972) is a statistical approach applied extensively in ecological research because of their ability to deal with the multitude of

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

distributions that define ecological data (Guisan *et al.*, 2002; Venables & Dichmont, 2004). GzLMs are extensions of general linear models, but are more flexible to data with non-normal error distributions. This is because GzLMs enable analysis of data from a range of distribution types based on an assumed relationship (called a link function) between a linear predictor function of the explanatory variables and the mean of the response variable (Guisan *et al.*, 2002). Separate analyses were performed for each site to test for differences between salt marsh and each of the four ages of mangrove stand. Test variables were total aboveground biomass (mangrove tree + mangrove shrub + salt marsh) (kg m^{-2}), total belowground C store in the surface 1 m (kg C m^{-2}) and C density (g C cm^{-3}) in each of the seven sediment depth intervals.

Regression analyses were performed to assess rates of change in biomass and total belowground C across the chronosequence. Biomass and belowground C were regressed against the mid-point of each of the three transitional time periods. Contemporary salt marsh and >70 years mangroves were excluded because salt marsh to mangrove shift has not yet occurred (contemporary salt marsh), or a start point for the shift cannot be verified by aerial photographs (>70 years). Regressions performed for each site and with sites combined. Statistical analyses were performed using SPSS v19 (IBM Corp., Armonk, NY, USA).

Results

Biomass

Mean ± SE aboveground biomass in the contemporary salt marsh zone was 0.89 ± 0.09 kg m^{-2} at Towra Point and 0.71 ± 0.06 kg m^{-2} (Fig. 2). Biomass of 0–14/15 years mangroves was not significantly higher than salt marsh (Table S2; Table S3), and again, was similar between the two sites. After 30 years, however, biomass was significantly higher than salt marsh, with total aboveground biomass increasing with mangrove age at both sites (Fig. 2a, b; Table S2; Table S3).

A shrub layer of *A. marina* was present at both sites, although contributions to overall biomass varied. At Georges River, biomass change was primarily driven by mangroves >2 m in height (Fig. 2a), with saplings populating the <2 m layer. At this site, young trees reached nearly 4 m in the 0–15 years zone and maximum tree height (7.8 m) was reached within 31–43 years. At Towra Point, saplings <2 m were the major component of recent transition areas (52 of 54 individuals measured in 0–14 years zone), and dwarf trees (<2 m) were encountered throughout the older mangrove zones. The contribution of this layer to total biomass declined with age, however, and was negligible in >70 years quadrats (Fig. 2b). Although encountered in one 58–70 years location (nearest the riverine fringe) at Georges River, the smaller river mangrove *Aegiceras corniculatum* did not represent a large contribution, representing just 1.3% of the total biomass for this age zone.

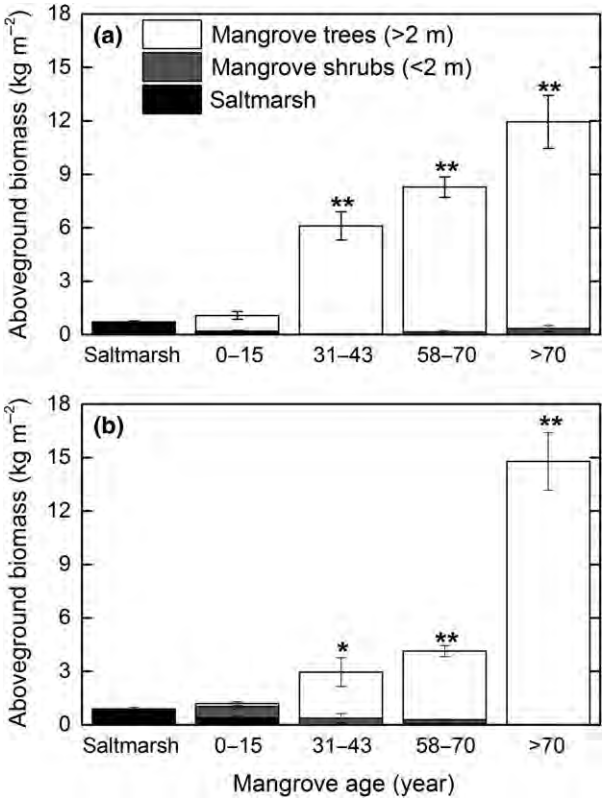


Fig. 2 Mean aboveground biomass by vegetation component across the chronosequence at Georges River (a) and Towra Point (b). Error bars represent 1 SE each side of the mean for each vegetation component. Significant difference from salt marsh value represented by asterisks for $P < 0.05$ (*) and $P < 0.01$ (**) where appropriate.

Belowground C

Total belowground C storage (0–100 cm) was higher at Georges River than Towra Point across all chronosequence zones (Fig. 3). The largest site difference was in salt marsh, where belowground C was 2.4 times higher in Georges River salt marsh (mean ± SE = 17.32 ± 1.71) relative to Towra Point salt marsh (7.18 ± 0.79), despite similar aboveground biomasses between sites (Figs 2, 3). Site differences in salt marsh belowground C were most pronounced below 15 cm of depth (i.e. below the live rooting zone of salt marsh), where C densities in Towra Point salt marsh were negligible (Fig. 4d–g). At Towra Point, total C storage increased with mangrove age and was significantly higher than salt marsh for 30–43 years and older zone classes relative to salt marsh, but was not significantly higher in 0–14 years mangroves ($P = 0.33$; Table S3).

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

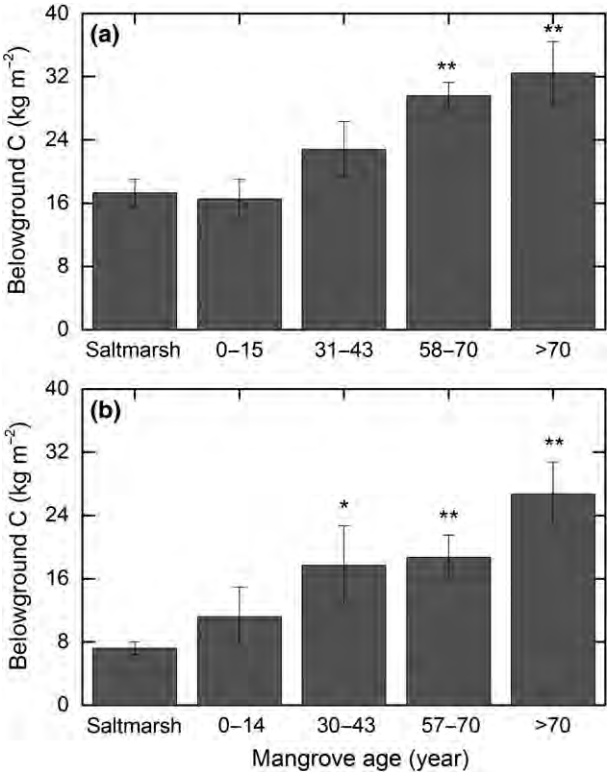


Fig. 3 Mean belowground carbon store (0–100 cm depth) within each vegetation community category at Georges River (a) and Towra Point (b). Error bars represent 1 SE each side of the mean. Significant difference from salt marsh value represented by asterisks for $P < 0.05$ (*) and $P < 0.01$ (**) where appropriate.

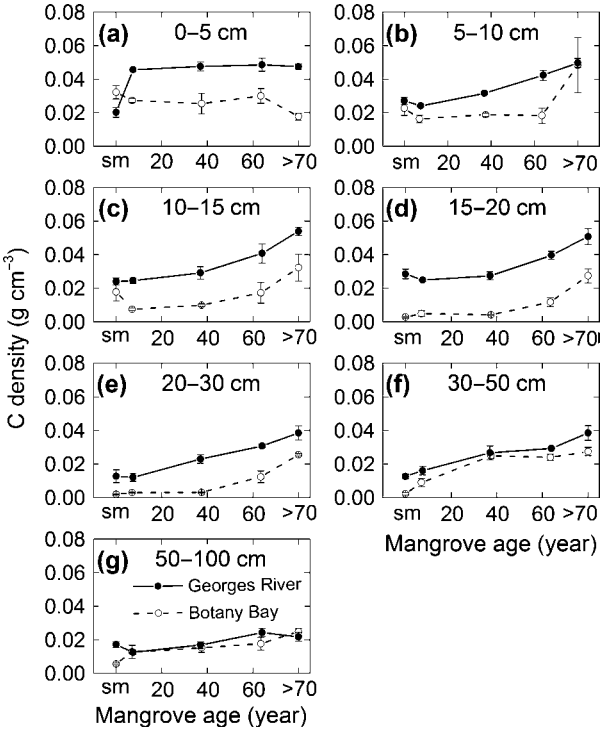


Fig. 4 Belowground carbon (C) density (g C cm^{-3}) for Georges River (closed circle) and Towra Point (open circle) for each sampled depth section across the >70 years chronosequence – (a) 0–5 cm; (b) 5–10 cm; (c) 10–15 cm; (d) 15–20 cm; (e) 20–30 cm; (f) 30–50 cm; (g) 50–100 cm. *X*-axis data are presented as the midpoint of each chronosequence period. SM = salt marsh.

There was also a trend of increasing C density at subsurface depths with mangrove stand age (Fig. 4d–g), reflected in depth interval ANOVAs where C density was significantly higher in older mangroves than salt marsh at depths >15 cm, but not within the surface 15 cm (Table S3).

At Georges River, an increasing trend in total belowground C is apparent from 31 to 43 years onward; however, stocks were only significantly higher than salt marsh in 58–70 and >70 years zones ($P < 0.05$) (Fig. 3a). Significant increases above salt marsh C densities were observed in surface depths (0–5 cm) for all mangrove ages with the peak C densities achieved within the first 15 years of encroachment (0.04–0.05 g cm^{-3}). By 58–70 years, C densities were significantly higher in 5–10 cm and 10–15 cm ($P < 0.05$), and to a lesser extent at 15–20 cm ($P = 0.06$) (Fig. 4a–d; Table S2). Like Towra Point, increases in belowground C density were apparent in the 15–50 cm depth range (Fig. 3d–f) with the increase becoming apparent across a broader depth range with increasing mangrove stand age (Table S2). Mangrove stands >70 years had significantly higher C concentrations than salt marsh across the top 50 cm, but not within 50–100 cm (Table S2).

Rates of change

A strong relationship exists between mangrove age and aboveground biomass at each site, although the rate of biomass increase is 2.5 times higher at Georges River than Towra Point (Table 1). The average rate of biomass increase when the two sites are combined was 91 Mg km^{-2} yr^{-1} ($R^2 = 0.58$; $P \leq 0.001$).

Belowground C store at Georges River increased by ~230 Mg km^{-2} yr^{-1}, representing an increase 1.7 times faster than aboveground biomass during the same period at this site. While belowground C was observed to increase throughout the chronosequence at Towra Point (Fig. 3b), the relationship with mangrove age over the period 0–70 years was not as strong as for Georges River.

An elevation gradient was apparent across the chronosequence at Towra Point, with more recent mangrove encroachment growing higher in the tidal frame than older mangrove zones, and salt marsh located at

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1 Summary of regression analyses for aboveground biomass and total belowground C store (0–100 cm). Adjusted R^2 values >0.5 as well as significant ($P < 0.05$) regression model P-values represented in bold, with rates of change presented for these cases only

Variable	Site	Slope coefficient ± SE	R^2	Adjusted R^2	P-value	Mg km^{-2} yr^{-1} ± SE
Elevation (cm)	Georges River	−0.015 ± 174.11	0.075	0.038	0.167	
	Towra Point	−0.132 ± 168.61	0.894	**0.890**	**<0.001**	
Aboveground	Georges River	0.130 ± 0.018	0.885	**0.868**	**0.000**	**130 ± 18**
biomass (Mg km^{-2})	Towra Point	0.052 ± 0.010	0.781	**0.750**	**0.002**	**52 ± 10**
	Sites combined	0.091 ± 0.019	0.603	**0.579**	**0.000**	**91 ± 19**
Belowground	Georges River	0.230 ± 0.062	0.662	**0.614**	**0.008**	**230 ± 62**
C store 0–100 cm	Towra Point	0.134 ± 0.094	0.226	0.116	0.196	
(Mg C km^{-2})	Sites combined	0.184 ± 0.066	0.326	0.284	**0.013**	

the highest elevation (Table S1). Regression analysis showed a strong linear relationship (adj. $R^2 = 0.89$) between elevation and mangrove age, suggesting an upslope mangrove encroachment rate of 0.132 cm yr^{-1} at this site. No such relationship was present at Georges River for contemporary surface elevation, where salt marshes and all mangroves zones younger than 70 years occur at a similar elevation, between 1.72 and 1.77 m above LAT. Peak magnetic susceptibility depth – a proxy for historical surface elevations – did vary among cores, with a broad trend of deeper peak depth in older mangrove zones and more shallow peaks in recent mangroves and salt marsh zones at Georges River (Fig. S2). No magnetic peaks were apparent in Towra Point cores.

The Georges River magnetic susceptibility peak was dated to 1958 (±7 years) based on ^{210}Pb dating of 58–70 years core #3, with an onset of increasing magnetic susceptibility from 1924 (±11 years) (Fig. 5), which accords well with timing of intensive development in the catchment. Mass accumulation rates obtained from the CRS model show a rapid increase in mass accumulation from this time, with a peak of 0.185 g cm^{-2} yr^{-1} around the time of mangrove expansion to this area (~70 years ago) (Fig. 5). These depths correspond with low belowground C concentrations, with C content increasing rapidly above 20 cm (39 ± 6 years), concurrent with decreases in both overall mass accumulation rates and magnetic susceptibility (Fig. 5).

Discussion

Intertidal wetlands are dynamic ecosystems that can respond quickly to natural or anthropogenic perturbations. This study tracked the shift from salt marsh to mangrove forest in two nearby, but geomorphically distinct, coastal wetlands over a period of 70 years. At both sites, a continuous landward migration of *Avicennia marina* into previously treeless salt marsh was apparent. As well as altering ecosystem structure, this vegetation shift brought about a significant change in ecosystem function as demonstrated by significant increases in aboveground biomass and belowground C stocks at both sites.

Biomass growth increases C storage

Aboveground biomass increase was seen at both study sites, as mangroves encroached areas previously vegetated by salt marsh species. This may not be surprising, considering the low biomass of salt marshes relative to mangroves, and in particular, the low aboveground biomass of the *Sarcocornia quinqueflora* and *Sporobolus virginicus* salt marsh community encroached in south-eastern Australia. Rates of aboveground biomass increase across the 70-year chronosequence (130 Mg km^{-2} yr^{-1} at Georges River and 52 Mg km^{-2} yr^{-1} at Towra Point) were modest when compared to biomass production rates of mature forests of *A. marina* (310 Mg km^{-2} yr^{-1}) and *Aegiceras corniculatum* (210 Mg km^{-2} yr^{-1}) reported in the same region (Clarke, 1994). Alongi *et al.* (2003) report C values of 43.7%, 45.2% and 44.9% for *A. marina* leaves, stems and branches, respectively. If the average C content among these tissues (44.6%) is multiplied by the rates of aboveground biomass increase reported in our study then increases in aboveground C storage under mangrove encroachment are estimated to be 58 ± 8 Mg C km^{-2} yr^{-1} for Georges River and 23 ± 4 Mg C km^{-2} yr^{-1} for Towra Point.

Although our study cannot identify with certainty which factors are responsible for the 2.5 fold difference in biomass response between sites, we propose that salinity, nutrient limitation and sedimentation are likely to be key determinants of biomass response. First, growth studies have shown increased growth of *A. marina* seedlings under lower salinities (20–80% seawater concentrations) (Clarke & Hannon, 1970) and, more specifically, declines in photosynthetic capacities of both *A. marina* and *A. corniculatum* with increasing

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

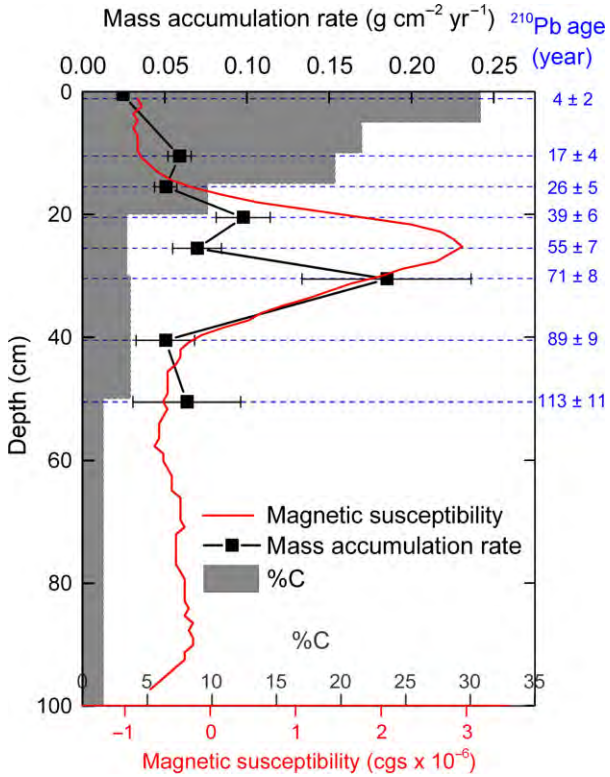


Fig. 5 Downcore profiles of sediment mass accumulation rate, magnetic susceptibility and carbon (C) content (%) of the core chosen for detailed analysis - GR 58–70 years core 3. Peaks in sediment mass accumulation rate and magnetic susceptibility occur at 30 cm (71 ± 8 years) and 25 cm (55 ± 7 years), respectively, within a zone of low carbon content, above which high carbon content corresponds with fine root-dominated peat development. Unsupported ^{210}Pb activities between 0 and 71 cm were used to calculate the sediment age (years before 2013) and mass accumulation rate at each interval. Neither sediment ages nor mass accumulation rates were calculated below 50 cm due to low activities of unsupported ^{210}Pb.

salinity (Ball & Farquhar, 1984), both of which are consistent with the more vigorous biomass response in the mesohaline site. Second, mangrove biomass and forest architecture are known to vary substantially according to nutrient status, ranging from growth of vigorous tall trees in nutrient-rich riverine settings down to dwarf trees in nutrient-poor areas near the coastal fringe (Feller *et al*., 2007) – a trend generally consistent with biomass differences in our study. Finally, differences in sedimentation among sites may alter the sensitivity of mangrove growth to nutrient enrichment and alter nutrient and carbon cycling (Lovelock *et al*., 2007). This is of relevance because our data suggest enhanced sedimentation may have been a precursor to mangrove encroachment at the Georges River site (discussed further below). Together, these findings suggest that the magnitude and rate of biomass change will vary among the range of settings in which mangrove encroachment of salt marsh is taking place, globally.

More broadly, biomass increases in our study were muted when compared to those measured for mangrove encroachment into salt marsh by Doughty *et al*. (2015) on the Atlantic coast of Florida. There, biomass increases were responsible for an overall C increase at the rate of 270 Mg C km^{-2} yr^{-1}. The reason for the sharp disparity in biomass accumulation between studies is likely related to the encroachment settings within each location. In the south-eastern USA, encroachment of salt marsh is most often explained in terms of extreme winter climate events (Cavanaugh *et al*., 2014) where severe freeze events cause an acute disturbance to mangrove survival and growth. In the absence of this disturbance, mangroves may outcompete local salt marsh species with few constraints on aboveground biomass growth. In south-eastern Australia, although the causes of mangrove encroachment are less understood, many of the leading theories – including sea level rise, increased atmospheric CO_2 and long-term changes in precipitation – may be considered more protracted changes; that is, we would expect: (i) a slow easing of the constraints which previously excluded mangroves from expanding into the areas that they now occupy, and (ii) such constraints may continue to operate, albeit to a lesser extent, across the encroachment front.

In this study, we have tracked increases in standing aboveground biomass as mangroves replace salt marshes and begin to develop into mature forests. A significant difference between the two vegetation types, however, is the turnover time of aboveground biomass between salt marshes (annual to years) and mangroves (years to decades or more). Studies which track the fate of aboveground biomass (and the C contained therein) over these timescales, and in relation to disturbances to biomass retention (e.g. storm damage to mangrove forests) will improve our understanding of the longer term C dynamics associated with salt marsh to mangrove transitions.

Importance of belowground C

Belowground stocks (inclusive of belowground biomass) are the most significant C pool in coastal wetlands and, due to their potential for long-term storage, are the primary reason for interest in coastal C initiatives (Sutton-Grier *et al*., 2014). At both sites, and across all vegetation categories in this study, belowground C (quantified in the surface 100 cm) considerably outweighed aboveground biomass stocks. Mean salt marsh belowground C stocks were within the low (Towra Point mean ± SE = 7.2 ± 0.8 kg C m^{-2}) and mid-

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

ranges (Georges River mean ± SE = 17.3 ± 1.7 kg C m^{-2}) of values reported both within south-eastern Australia (range = 6.1–34.3 kg C m^{-2}; mean = 19.1 kg C m^{-2}; Saintilan *et al*., 2013) and globally (mean = 16.2 kg C m^{-2}; Duarte *et al*., 2013). Mature (>70 years) mangrove stands at both sites were above average (Towra Point mean ± SE = 26.7 ± 4.1 kg C m^{-2}; Georges River mean ± SE = 32.5 ± 4.0 kg C m^{-2}) relative to global values (mean = 25.5 kg C m^{-2}; Siikamäki *et al*., 2012; Donato *et al*., 2011) and *A. marina*-dominated forests in south-eastern Australia (range = 2.5–34.3 kg C m^{-2}; mean = 23.1 kg C m^{-2}; Saintilan *et al*., 2013).

The increase in biomass measured aboveground as mangroves encroach salt marsh was also observed belowground in cores analysed for bulk C content. At Georges River, significant increases in belowground C coincided with fine root development of mangroves, with fine root biomass dominating sediment volume in surface layers of encroached areas. Here, both the density of C and depth of sediment in which fine root development was observed increased along the chronosequence. A similar phenomenon has been reported elsewhere, with Osland *et al*. (2012) observing upper sediment layer (0–10 cm) peat development (and associated sediment C accumulation) simultaneous with mangrove forest growth in restored wetlands. Such peat development not only increases belowground C stores, but also has implications for surface elevation dynamics and wetland response to sea level rise (McKee *et al*., 2007), and we propose that surface peat development has played an important role in altering surface dynamics as mangroves have encroached the Georges River site (discussed further below).

Surface peat development was less pronounced at Towra Point, where C storage in the surface 15 cm did not vary along the chronosequence. Below this, however, C content generally increased with mangrove age, where occasional *A. marina* cable roots and anchor roots were more commonly encountered. At Georges River, similar trends in subsurface (>15 cm) root presence and C density were also apparent across the chronosequence – although, C density differences did not extend to the 50–100 cm depth. This ability of mangrove roots to penetrate to greater depths in the sediment profile may have significant implications for blue C stocks under mangrove encroachment. First, root penetration to 50 cm or more may increase deep C storage, as is suggested by both sites in this study. In terrestrial studies, deep storage has been identified as a key trait in long-term preservation of sediment C, possibly due to suboptimal conditions for microbes or increased protection through organic matter-mineral interactions (Schmidt *et al*., 2011), although its importance in blue C ecosystems is not well understood. Second, mangrove root penetration may alter redox potential down core by introducing oxygen to previously anoxic depths (Comeaux *et al*., 2012). Third, root penetration may also stimulate microbial priming whereby the supply of fresh plant-derived C promotes the microbial mineralization of old, stored C. Such factors may be responsible for the lack of C increase in the 50–100 cm sections at Georges River (Fig. 4g), despite observations of considerable mangrove root biomass, and should certainly be considered in the broader global context of mangrove encroachment.

Timing of belowground C increases

At the higher C site, Georges River, belowground stocks were essentially unchanged in the first 15 years of encroachment despite the rapid change in aboveground vegetation structure (where almost half of all *A. marina* individuals had grown to a height >2 m). Similarly, increases over a similar period at Towra Point were insufficient to identify statistically significant change. These results mirror efforts from multiple authors in the C-rich deltaic wetlands of Louisiana, who have reported little change in belowground production and C assimilation after 15–20 years of *Avicennia germinans* expansion into *Spartina alterniflora* salt marsh (Perry & Mendelssohn, 2009; Henry & Twilley, 2013). Further, in their quantification of biomass change under recent (7 years) mangrove encroachment in Florida, Doughty *et al*. (2015) measured belowground biomass densities just 20% that of aboveground biomass, with belowground biomass C stocks subsequently playing just a small part in the overall C increase reported in that study. Interestingly, these authors proposed that if mangroves were to continue to grow and increase their structural complexity, then changes in sediment properties, including C content, may become apparent. The results of two contrasting wetland settings in our study show that in the absence of extreme winter events, and given sufficient time, significant increases in belowground C stocks do become apparent under mangrove encroachment (see also Lunstrum & Chen, 2014). Our results also have implications for mangrove restoration projects, as they suggest that demonstrating a carbon benefit may take time, and that it would be difficult to extrapolate from measures over just a few years.

Mangrove encroachment, sea level rise and surface elevation gain

The long-held model of estuarine vegetation zonation in south-eastern Australia places mangroves lower in

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

the tidal frame than the *Sarcocornia-Sporobolus* salt marsh association (Clarke & Hannon, 1967), which would suggest mangrove encroachment of salt marsh in this region involves an upslope migration. Regression analysis showed a negative, linear relationship (adj. $R^2 = 0.89$; $P < 0.001$) between elevation and mangrove age at Towra Point, with younger mangroves zones growing at higher elevations than older mangrove forest. This suggests agreement with this model under a rising sea level scenario; that is, if relative surface elevations across the Towra Point chronosequence are assumed to be static, mangroves would appear to be moving vertically upslope at a rate of 0.132 cm yr^{-1}. This is only slightly faster than sea level rise recorded at nearby Fort Denison (0.108 cm yr^{-1}) over the 1943–2013 study period and within Botany Bay itself (0.115 cm yr^{-1}) for the period of data availability (Fig. S3). We argue mangrove encroachment at this site has occurred simultaneously with sea level rise, with little evidence of surface elevation change (e.g. low peat development) resulting from the ecosystem change.

A different scenario, however, is observed across the Georges River chronosequence, where contemporary surface elevations are similar across the salt marsh, 0- to 15-years-, 31- to 43-years- and 58- to 70-years-old mangroves, with only the >70 years mangroves (located along the riverine fringe) at a lower elevation. Here, we argue that although sedimentation associated with historical catchment changes may have played a role in triggering mangrove expansion, mangrove development has promoted surface elevation growth and increases in belowground C storage. Firstly, a large increase in mass accumulation and magnetic susceptibility beginning at 89 ± 9 years pre-dates the change in vegetation by at least 10 years (Fig. 5), and accords well with the timing of intensive development in the catchment. Second, the presence of strong magnetic peaks in cores from the current salt marsh zone and more recent encroachment areas highlights that this sedimentation did not cause an immediate vegetation change across the entire site. Third, the low C content associated with periods of high mineral deposition suggests sedimentation did not directly enhance C stocks to any great extent, or at least was poorly preserved over time (Fig. 5). Instead, the greater depth of magnetic peaks under older mangroves relative to recent mangrove and salt marsh zones (Table S1) points to an historical elevation gradient at the time of peak magnetic susceptibility (dated to the year 1958 ± 7 years and coinciding with early mangrove expansion at the site). Since that time, it appears that enhanced vertical elevation gains have taken place in the older mangroves (58- to 70-years zone), relative to more recent mangrove and salt marsh zones, producing a contemporary surface which shows little to no elevation gradient across most of the site (Table S1). This enhanced elevation change in older mangroves is concomitant with both mangrove peat development and increasing belowground C storage, during a period in which sea level rise is known to occur in the region. It is also consistent with our growing understanding of the ability of mangroves to keep pace with changes in relative sea level rise through root contributions to soil volume and upward expansion of the soil surface (McKee *et al*., 2007; Krauss *et al*., 2014).

Mangrove encroachment may also alter surface elevation and C storage through access to new non-root materials (i.e. litterfall and downed wood from the developing mangrove canopy) and the enhanced capacity of mangrove pneumatophores to trap particulate organic carbon (POC) and mineral sediment from catchment sources. Such an enhanced sediment accretion capacity of mangroves over salt marshes has been described in south-eastern Australia (Rogers *et al*., 2006), and this phenomenon is likely to be part of the explanation for surface elevation change and C storage increase seen in this study. Whether enhanced trapping capacity allows for greater accumulation of refractory, allochthonous inputs such as terrestrial POC under mangrove encroachment is still largely unknown, however, and deserves further attention.

Estimates of C storage increases

The present study adds to a small body of literature regarding the temporal dynamics of C stocks in sites experiencing mangrove encroachment of salt marsh (Perry & Mendelssohn, 2009; Comeaux *et al*., 2012; Osland *et al*., 2012; Bianchi *et al*., 2013; Henry & Twilley, 2013; Doughty *et al*., 2015). To our knowledge, this is the first study to quantify C changes in the south-eastern Australian setting, where mangrove encroachment is a continuous, long-term and widespread phenomenon. While further research across larger spatial scales is necessary (especially across latitudinal gradients), projections based on current data suggest mangrove encroachment has initiated substantial gains in blue C storage in the region. Over the past ~70 years, mangrove encroachment has resulted in the conversion of ~30% or more of salt marsh to mangrove forest across south-eastern Australia (Straw & Saintilan, 2006). While the exact timing and rates of change of mangrove encroachment cannot be determined at a regional scale with current data, extrapolation of findings from the present study suggests a significant increase in blue C stocks has already occurred. Based on a 30% conversion of the current extent of salt marsh in New South Wales (72.6 km^2; Creese *et al*., 2009), biomass increases of 1618–4044 Mg yr^{-1} (113 239–

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

283 097 Mg over 70 years) and belowground C increases of up to 7155 Mg C yr^{-1} (500 864 Mg C over 70 years; extrapolated from Georges River rate only) may have already occurred over the past 70 years in New South Wales alone. If mangroves continue to further encroach salt marshes in the region, as is predicted to happen, annual additions to above and belowground C stores of the magnitude reported here may continue.

Under changing climatic conditions and rising sea levels, mangrove encroachment and forest development of the magnitude reported in this study is likely to become more widespread. The outcomes of the present study may have particular application for regions such as the Gulf of Mexico and Atlantic coast of the USA, where attempts to investigate C changes with encroachment of *A. germinans* have been limited to windows of <30 years (i.e. since freezes in 1983 and 1989 last 'reset' mangrove encroachment across much of that region). Recent research in that region suggests future expansion of *A. germinans* may be accelerated by increases in mangrove forest resistance and resilience to extreme winter events as forests mature in size (Osland *et al.*, 2015). In other words, a more continuous long-term encroachment, such as that seen in south-eastern Australia, is likely to occur if mangroves mature sufficiently before the next 'reset' event. Then, C increases of the magnitude seen in the present study – but largely eluding those of shorter term studies in the USA – might be seen in coming decades.

At present, global estimates of salt marsh extent vary markedly, from 22 000 to 400 000 km^2 (Mcleod *et al.*, 2011; Duarte *et al.*, 2013), and it is not currently known what proportion of global salt marsh extent is likely to be affected by mangrove expansion. Clearly, refinement of global salt marsh and mangrove encroachment extents are required. The C storage estimates provided in our study should encourage broader investigation of mangrove encroachment and long-term C dynamics associated with this important ecosystem change.

Acknowledgements

Charlie Hinchcliffe, Mikael Kim, Sarah Meoli and Frederic Cadera are thanked for assistance with field measurements and sample preparation. Field collections were undertaken in accordance with NSW Office of Environment and Heritage scientific licence SL101217 and NSW Department of Primary Industries Scientific Permit P13/0058-1.0. We also thank NSW National Parks and Wildlife Service for supporting access to conservation reserves for fieldwork. This research was supported by the CSIRO Coastal Climate Cluster and an Australian Institute of Nuclear Science and Engineering AINSE Grant (ALNGRA14004). PM was supported by an Australian Research Council DECRA Fellowship (DE130101084). We thank three anonymous reviewers for their comments, which have improved this manuscript.

References

Adam P (1993) *Saltmarsh Ecology*. Cambridge University Press, Cambridge.

Adam P, Wilson N, Huntley B (1988) The phytosociology of coastal saltmarsh vegetation in New South Wales. *Wetlands (Australia)*, **7**, 35–85.

Alongi DM (2002) Present state and future of the world's mangrove forests. *Environmental Conservation*, **29**, 331–349.

Alongi DM, Clough BF, Dixon P, Tirendi F (2003) Nutrient partitioning and storage in arid-zone forests of the mangroves Rhizophora stylosa and Avicennia marina. *Trees*, **17**, 51–60.

Appleby P, Oldfield F (1978) The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210 Pb to the sediment. *Catena*, **5**, 1–8.

Ball MC, Farquhar GD (1984) Photosynthetic and stomatal responses of the grey mangrove, Avicennia marina, to transient salinity conditions. *Plant Physiology*, **74**, 7–11.

Bianchi TS, Allison MA, Zhao J, Li X, Comeaux RS, Feagin RA, Kulawardhana RW (2013) Historical reconstruction of mangrove expansion in the Gulf of Mexico: linking climate change with carbon sequestration in coastal wetlands. *Estuarine, Coastal and Shelf Science*, **119**, 7–16.

Burns B, Ogden J (1985) The demography of the temperate mangrove [Avicennia marina (Forsk.) Vierh.] at its southern limit in New Zealand. *Australian Journal of Ecology*, **10**, 125–133.

Buylaert JP, Murray AS, Vandenberghe D, Vriend M, De Corte F, Van Den Haute P (2008) Optical dating of Chinese loess using sand-sized quartz: establishing a time frame for Late Pleistocene climate changes in the western part of the Chinese Loess Plateau. *Quaternary Geochronology*, **3**, 99–113.

Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W, Feller IC (2014) Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 723–727.

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles*, **17**, 22:1–22:12.

Clarke PJ (1994) Base-line studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. *Australian Journal of Botany*, **42**, 37–48.

Clarke LD, Hannon NJ (1967) The mangrove swamp and salt marsh communities of the Sydney district: I. Vegetation, soils and climate. *The Journal of Ecology*, **55**, 753–771.

Clarke LD, Hannon NJ (1970) The mangrove swamp and salt marsh communities of the Sydney district: III. Plant growth in relation to salinity and waterlogging. *The Journal of Ecology*, **58**, 351–369.

Clarke PJ, Jacoby CA (1994) Biomass and above-ground productivity of salt-marsh plants in south-eastern Australia. *Marine and Freshwater Research*, **45**, 1521–1528.

Clough BF, Dixon P, Dalhaus O (1997) Allometric relationships for estimating biomass in multi-stemmed mangrove trees. *Australian Journal of Botany*, **45**, 1023–1031.

Comeaux RS, Allison MA, Bianchi TS (2012) Mangrove expansion in the Gulf of Mexico with climate change: implications for wetland health and resistance to rising sea levels. *Estuarine, Coastal and Shelf Science*, **96**, 81–95.

Creese R, Glasby T, West G, Gallen C (2009) Mapping the habitats of NSW estuaries. In: *NSW Fisheries Final Report Series 113*. pp. 1–95. Industry & Investment NSW, Port Stephens, NSW, Australia.

Dearing JA, Elner JK, Happey-Wood CM (1981) Recent sediment flux and erosional processes in a Welsh upland lake-catchment based on magnetic susceptibility measurements. *Quaternary Research*, **16**, 356–372.

Donato DC, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, **4**, 293–297.

Doughty CL, Langley JA, Walker WS, Feller IC, Schaub R, Chapman SK (2015) Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuaries and Coasts*, doi:10.1007/s12237-015-9993-8.

Duarte CM, Middelburg J, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, **2**, 1–8.

Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N (2013) The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, **3**, 961–968.

Duke N, Ball M, Ellison J (1998) Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology & Biogeography Letters*, **7**, 27–47.

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, **14**, 709–722.

English SS, Wilkinson CC, Baker VV (1994) *Survey Manual for Tropical Marine Resources*. Australian Institute of Marine Science (AIMS), Townsville.

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Eslami-Andargoli L, Dale P, Sipe N, Chaseling J (2009) Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science*, **85**, 292–298.

Feller IC, Lovelock CE, McKee KL (2007) Nutrient addition differentially affects ecological processes of Avicennia germinans in nitrogen versus phosphorus limited mangrove ecosystems. *Ecosystems*, **10**, 347–359.

Friess DA, Krauss KW, Horstman EM, Balke T, Bouma TJ, Galli D, Webb EL (2012) Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biological Reviews*, **87**, 346–366.

Geoscience Australia (2015) Australian Online Coastal Information – Ozcoasts. www.ozcoasts.gov.au.

Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157**, 89–100.

Haworth R (2002) Changes in mangrove/saltmarsh distribution in the Georges River estuary, southern Sydney, 1930-1970. *Wetlands (Australia)*, **20**, 80–103.

Henry KM, Twilley RR (2013) Soil development in a coastal Louisiana wetland during a climate-induced vegetation shift from salt marsh to mangrove. *Journal of Coastal Research*, **29**, 1273–1283.

Krauss KW, From AS, Doyle TW, Doyle TJ, Barry MJ (2011) Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Islands region of Florida, USA. *Journal of Coastal Conservation*, **15**, 629–638.

Krauss KW, McKee KL, Lovelock CE, Cahoon DR, Saintilan N, Reef R, Chen L (2014) How mangrove forests adjust to rising sea level. *New Phytologist*, **202**, 19–34.

Lovelock CE, Feller IC, Ellis J, Schwarz AM, Hancock N, Nichols P, Sorrell B (2007) Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia*, **153**, 633–641.

Lunstrum A, Chen L (2014) Soil carbon stocks and accumulation in young mangrove forests. *Soil Biology and Biochemistry*, **75**, 223–232.

Magenheimer J, Moore T, Chmura G, Daoust R (1996) Methane and carbon dioxide flux from a macrotidal salt marsh, Bay of Fundy, New Brunswick. *Estuaries and Coasts*, **19**, 139–145.

McKee KL, Cahoon DR, Feller IC (2007) Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, **16**, 545–556.

McKee K, Rogers K, Saintilan N (2012) Response of saltmarsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In *Global Change and the Function and Distribution of Wetlands* (ed. Middleton BA), pp. 63–96. Springer, Dordrecht, the Netherlands.

Mcleod E, Chmura GL, Bouillon S *et al.* (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment*, **9**, 552–560.

Murray BC, Pendleton L, Jenkins WA, Sifleet S (2011) Green payments for blue carbon: Economic incentives for protecting threatened coastal habitats. Nicholas Institute for Environmental Policy Solutions, Report NI, 11.

Nelder JA, Baker R (1972) Generalized linear models. *Encyclopedia of Statistical Sciences*, **135**, 370–384.

Nixon SW (1980) *Between Coastal Marshes and Coastal Waters: A Review of Twenty Years of Speculation and Research on the Role of Salt Marshes in Estuarine Productivity and Water Chemistry*. Springer US, New York, NY.

Osland MJ, Spivak AC, Nestlerode JA *et al.* (2012) Ecosystem development after mangrove wetland creation: plant–soil change across a 20-year chronosequence. *Ecosystems*, **15**, 848–866.

Osland MJ, Enwright N, Day RH, Doyle TW (2013) Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology*, **19**, 1482–1494.

Osland MJ, Day RH, From AS, Mclemore ML, Mcleod JL, Kelleway JJ (2015) Life stage influences the resistance and resilience of black mangrove forests to winter climate extremes. *Ecosphere*, **6**, 1–15.

Pendleton L, Donato DC, Murray BC *et al.* (2012) Estimating global "Blue Carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS One*, **7**, e43542.

Perry CL, Mendelssohn IA (2009) Ecosystem effects of expanding populations of Avicennia germinans in a Louisiana salt marsh. *Wetlands*, **29**, 396–406.

Purnobasuki H, Suzuki M (2005) Functional anatomy of air conducting network on the pneumatophores of a mangrove plant, Avicennia marina (Forsk.) Vierh.

Rogers K, Wilton KM, Saintilan N (2006) Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science*, **66**, 559–569.

Saintilan N (1997) Above-and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Marine and Freshwater Research*, **48**, 147–152.

Saintilan N, Rogers K (2015) Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. *New Phytologist*, **205**, 1062–1070.

Saintilan N, Williams RJ (1999) Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography*, **8**, 117–124.

Saintilan N, Rogers K, Mazumder D, Woodroffe C (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. *Estuarine, Coastal and Shelf Science*, **128**, 84–92.

Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW (2014) Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*, **20**, 147–157.

Schlacher TA, Connolly RM (2014) Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: a review and synthesis. *Methods in Ecology and Evolution*, **5**, 541–550.

Siikamäki J, Sanchirico JN, Jardine SL (2012) Global economic potential for reducing carbon dioxide emissions from mangrove loss. *Proceedings of the National Academy of Sciences*, **109**, 14369–14374.

Schmidt MW, Torn MS, Abiven S *et al.* (2011) Persistence of soil organic matter as an ecosystem property. *Nature*, **478**, 49–56.

Stevens PW, Fox SL, Montague CL (2006) The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management*, **14**, 435–444.

Straw P, Saintilan N (2006) Loss of shorebird habitat as a result of mangrove incursion due to sea-level rise and urbanization. In: *Waterbirds Around the World* (eds Boere GC, Galbraith CA, Stroud DA), pp. 717–720. The Stationery Office, Edinburgh.

Sutton-Grier AE, Moore AK, Wiley PC, Edwards PET (2014) Incorporating ecosystem services into the implementation of existing U.S. natural resource management regulations: operationalizing carbon sequestration and storage. *Marine Policy*, **43**, 246–253.

Thompson R, Battarbee R, O'sullivan P, Oldfield F (1975) Magnetic susceptibility of lake sediments. *Limnology and Oceanography*, **20**, 687–698.

Venables WN, Dichmont CM (2004) GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries research*, **70**, 319–337.

Wilton KM (2002) *Coastal Wetland Habitat Dynamics in Selected New South Wales Estuaries*. Australian Catholic University Sydney, Australia.

Woodroffe CD (1985) Studies of a mangrove basin, Tuff Crater, New Zealand: I. Mangrove biomass and production of detritus. *Estuarine, Coastal and Shelf Science*, **20**, 265–280.

Zedler J, Nelson P, Adam P (1995) Plant community organization in New South Wales saltmarshes: species mosaics and potential causes. *Wetlands (Australia)*, **14**, 1–18.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of estimated elevation of field sampling locations and depth and intensity of magnetic susceptibility within sediment core.
Table S2. Summary of Generalised Linear Model results for Georges River aboveground biomass, total belowground C store (0–100 cm) and depth intervals.
Table S3. Summary of Generalised Linear Model results for Towra Point aboveground biomass, total belowground C store (0–100 cm) and depth intervals.
Fig. S1. Georges River core #3 unsupported 210Pb activity profile and calculated CRS model sediment ages.
Fig. S2. Magnetic susceptibility profiles for each sediment core collected at Georges River.
Fig. S3. Mean monthly sea level at nearby Fort Denison for the entire study period (1943–2013) and within Botany Bay (data available from 1981).

13652486, 2016, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.13158 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

BIOLOGY LETTERS

royalsocietypublishing.org/journal/rsbl

Research

Cite this article: Rogers K, Saintilan N, Mazumder D, Kelleway JJ. 2019 Mangrove dynamics and blue carbon sequestration. *Biol. Lett.* **15**: 20180471.
http://dx.doi.org/10.1098/rsbl.2018.0471

Received: 1 November 2018
Accepted: 7 February 2019

Subject Areas:
ecology, environmental science, plant science

Keywords:
sea-level rise, blue carbon, mangrove, saltmarsh, carbon accumulation

Author for correspondence:
Kerrylee Rogers
e-mail: kerrylee@uow.edu.au

A contribution to the special feature 'Blue Carbon' organized by Catherine Lovelock.

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4407674.

THE ROYAL SOCIETY PUBLISHING

Downloaded from https://royalsocietypublishing.org/ on 25 June 2024

Global change biology

Mangrove dynamics and blue carbon sequestration

Kerrylee Rogers[1], Neil Saintilan[2], Debashish Mazumder[1,3] and Jeffrey J. Kelleway[1,2]

[1]School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, New South Wales, Australia
[2]Department of Environmental Sciences, Macquarie University, Sydney, New South Wales, Australia
[3]Australian Nuclear Science and Technology Organisation, Sydney, New South Wales, Australia

KR, 0000-0003-1350-4737

We monitored coastal wetland vertical accretion, elevation gain and surface carbon (C) at Homebush Bay, Australia over 18 years (2000–2017) in three settings initially characterized by saltmarsh, mixed saltmarsh–mangrove ecotone and mangrove-dominated zones. During this time, the saltmarsh transitioned to mixed saltmarsh–mangrove ecotone, and the mixed saltmarsh–mangrove ecotone transitioned to mangrove, consistent with vegetation transitions observed across the east Australian continent in recent decades. In spite of mangrove recruitment and thickening in the former saltmarsh zone, and the dominance of mangrove root material as a contributing C source, the rate of C accumulation in the former saltmarsh zone did not change over the study period, and there was no significant increase in surface elevation. This contrasted with the response of sites with a longer history of mangrove colonization, which showed strong accretion and C accumulation over the period. The result suggests that the C accumulation and surface elevation gains made as a result of mangrove colonization may not be observable over initial decades, but will be significant in the longer term as forests reach maturity.

1. Introduction

Climate change is driving shifts in the distribution of vegetation communities across the globe [1], including the poleward movement of cold-intolerant species [2]. Along several sub-tropical and temperate coastlines where mangrove forests occur seaward of saltmarshes, mangroves have been observed replacing saltmarsh as the dominant vegetation community [3], a trend set to continue as temperatures warm and sea-level rises [4,5].

Appropriate management responses to these transitions depend on a clear understanding of the multiple and often related ecosystem services at the local scale. In southeastern Australia, where mangrove encroachment has been observed as a regional-scale trend extending more than half a century [6], experimental mangrove removal for the protection of bird habitat has become increasingly common. However, this might be detrimental to the long-term survival of the wetland if mangrove encroachment proves to be a mechanism for elevating the wetland surface. In this regard, mangrove replacement of saltmarsh may contribute towards building elevation by trapping sediment and sequestering atmospheric C into below-ground root matter, providing a negative feedback to relative sea-level rise. By sequestering atmospheric C at a rate higher than saltmarsh, mangrove may be more effective at providing the dual services of carbon mitigation coastal adaptation.

The effect of mangrove forest encroachment of saltmarsh on elevation gain and C sequestration has proved equivocal. Given the elevation building potential of mangrove root systems and generally higher root productivity [7,8], it would be

© 2019 The Author(s) Published by the Royal Society. All rights reserved.

Downloaded from https://royalsocietypublishing.org/ on 25 June 2024

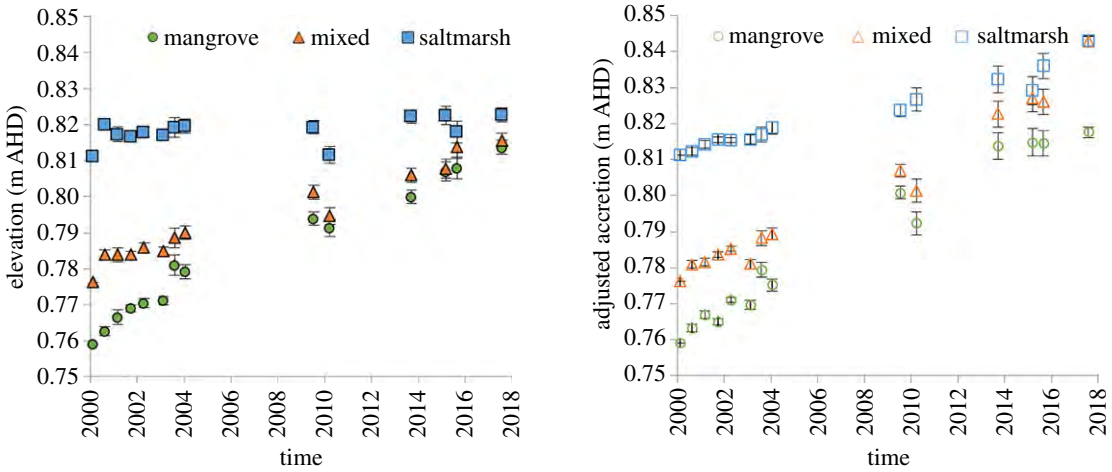


Figure 1. (*a*) Elevation changes of mangrove, mixed ecotone and former saltmarsh zones using SETs (standardized to m AHD), and (*b*) accretion trends in mangrove, mixed ecotone and former saltmarsh zones using MHs (standardized to m AHD). Data are provided in electronic supplementary material, S2. (Online version in colour.)

Table 1. Accretion rates above MH. Elevation (m above Australian Height Datum (AHD)) is reported as the mean of three SET-MH stations. Real-time kinematic (RTK) GPS measurement in 2015 corrected to the commencement of the experiment (2000).

zone	elevation (mean ± 1 s.d.) (m AHD)	accretion trend (mm y^{-1})	r^2	*p*-value
mangrove	0.76 ± 0.06	3.66	0.93	<0.001
mixed ecotone	0.78 ± 0.06	3.18	0.92	<0.001
former saltmarsh	0.81 ± 0.05	1.29	0.97	<0.001

Table 2. Density and rate of surface C accumulation above MH, derived from replicate cores taken from the mangrove forest and former saltmarsh zones, adjacent to SET-MHs. National estimates of surface C accumulation (mean ± 1 s.d.) from literature derived from SET-MH or radiometric dating.

ecosystem	surface C density (g C cm^{-3})	surface C accumulation rate (Mg C ha^{-1} y^{-1})	reference
mangrove 1	0.033	1.13	This study
mangrove 2	0.029	1.16	
former saltmarsh 1	0.029	0.30	
former saltmarsh 2	0.035	0.54	
mangrove (Australia)		1.3 ± 0.9	[22]
saltmarsh (Australia)		0.55 ± 0.34	[23]

reasonable to assume that mangrove forest encroachment of saltmarsh would encourage sediment trapping, C sequestration and hence elevation gain. However, comparisons of elevation gain in mangrove forests and saltmarshes produce contrasting findings. Studies in eastern Australia have pointed to the higher C sequestration rate in mangrove forests compared with saltmarshes [9,10], and a higher rate of surface elevation gain [11,12]. However, such comparisons are confounded by differences in elevation and hydroperiod between the two communities, with saltmarsh occurring in more landward, less frequently inundated locations. By contrast, on the US Gulf coast, mangrove forests often grow at similar or higher elevations than saltmarshes, and here analyses of accretion over short and longer time scales have suggested similar rates of accretion in both ecosystems [13–16], though mangrove forests may be lower [17] or higher [18] depending on climatic and geomorphic setting. Although similar rates of accretion were observed between mangrove forests and saltmarshes at restoration sites at Ten Thousand Islands National Wildlife Refuge, mangrove forest surface elevation decreased while saltmarsh remained steady [19].

A better test of the implications of mangrove–saltmarsh vegetation transition on accretion and elevation gain would require *in situ* observations over the period of encroachment, thereby removing the confounding effect of elevation in space-for-time substitutions. Here, we examine C accumulation and elevation gain at a site subject to considerable mangrove thickening and expansion over an 18-year period

Downloaded from https://royalsocietypublishing.org/ on 25 June 2024

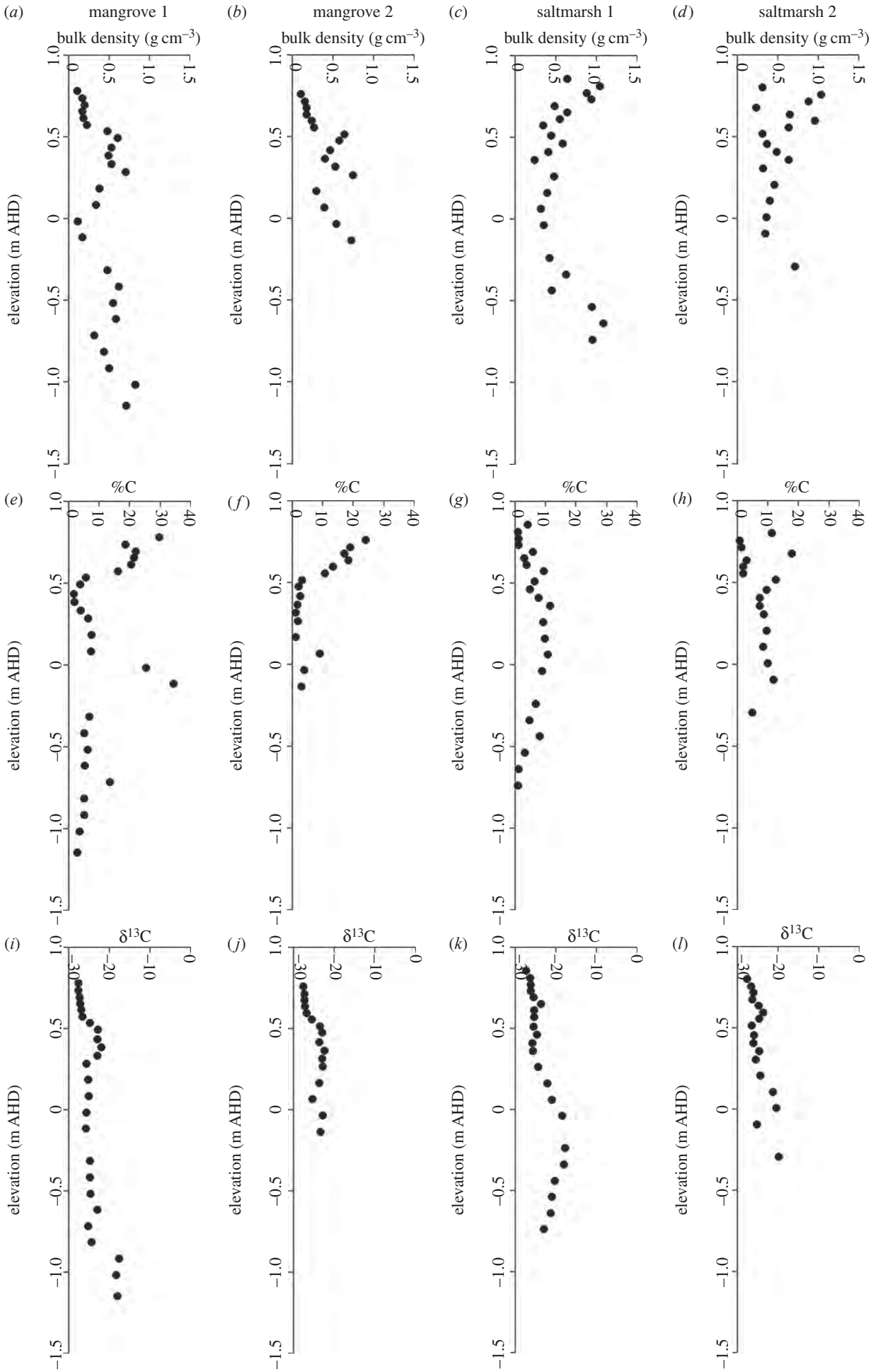


Figure 2. Bulk density (*a*–*d*), per cent organic C (*e*–*h*) and $\delta^{13}C$ (*i*–*l*) from mangrove and (former) saltmarsh zone core samples. Data are provided in electronic supplementary material, S3.

Downloaded from https://royalsocietypublishing.org/ on 25 June 2024

of observation. Our hypothesis was that the saltmarsh would transition to a mangrove forest and in doing so the rate of surface C accumulation and surface elevation gain would increase rapidly.

2. Material and methods

The Powells Creek wetlands are situated within Homebush Bay, Sydney Harbour, Australia (33°50′38″ S; 151°04′42″ E). The current mangrove forest appears to have been saltmarsh in photographs from the 1930s and 1950s, though became mangrove-dominated by the 1970s. During the 1980s, landward colonization of mangrove vegetation was disrupted by deposition of brick dust from an adjoining construction site, causing mangrove defoliation and the restoration of saltmarsh. Mangroves began to re-sprout and recolonize this area in the early 2000s [20]. In 2000, we installed surface elevation tables and feldspar marker horizons (SET-MHss) [21] in the saltmarsh, mixed saltmarsh–mangrove ecotone and mangrove zones of Powells Creek to determine trends in surface elevation change and vertical accretion. We took repeated measures over an 18-year period during which the saltmarsh zone transitioned to dense shrub-form mangrove, and the mixed saltmarsh–mangrove ecotone zone transitioned to tall mangrove of heights greater than 5 m (naming of vegetation zones henceforth follows original nomenclature). Towards the latter stages of the experiment, we took cores from the mangrove and (former) saltmarsh settings to document changes in C content and provenance (using $\delta^{13}C$ analyses), and sediment bulk density, and undertake radiocarbon dating. Detailed methods are provided in the electronic supplementary material, S1.

3. Results

All three zones showed linear trends in accretion over the 18-year record (table 1). The rate of accretion in the mangrove and mixed ecotone zones was twice that of the former saltmarsh zone, and the accretion rate in the former saltmarsh zone was not notably influenced by the thickening of mangrove vegetation (table 1, figure 1*a*).

Despite similarities in the density of C in surface sediments, accumulation above the MH suggests differing surficial rates of C accumulation between the mangrove and former saltmarsh zones (table 2). These estimates of C accumulation are likely to be particularly conservative in the mangrove zone, given the evidence of new root accumulation at depth.

The higher rate of accretion in the mangrove and mixed ecotone zones translated into an increase in surface elevation over time, and a gradual equilibration of surface elevation across the three zones (figure 1). The consistent low rate of accretion in the former saltmarsh zone did not translate into significant elevation gain, in spite of mangrove thickening.

Mangrove sediments have high %C and low bulk density throughout the surface 25 cm (figure 2). We interpret this as the modern mangrove rooting zone, reflected in the consistent $\delta^{13}C$ signature. A second C peak at approximately 0 m AHD, with similar C concentration and depleted $\delta^{13}C$ signatures as surface sediments, was regarded to be old, but also contained modern material, returning radiocarbon ages of 1200 years and 40 years.

Former saltmarsh-dominated sediments show higher bulk density relative to the mangrove sediments in the upper 40 cm (figure 2). Heterogeneous C concentrations in surface depths may correspond to contemporary mangrove roots in some locations, given the depleted $\delta^{13}C$, though the chenopod *Sarcocornia quinqueflora* may also contribute to the isotopic signature. Below 40 cm in both saltmarsh cores, the material becomes increasingly enriched in $\delta^{13}C$, associated with a higher %C (and lower bulk density).

4. Discussion

Most studies seeking to deduce the likely effects of mangrove forest encroachment on C storage and sequestration rates draw comparisons between mangroves and adjacent saltmarshes, showing higher C storage in the former [9,24]. Other studies are equivocal; Yando *et al*. [15] found differences in C storage to be significant only in drier locations, and Henry & Twilley [14] could find no difference in C storage within the sediments of mangroves and saltmarshes, an outcome attributed to the more oxidizing environment of the mangrove sediment in coastal Louisiana. Osland *et al*. [25] and Kelleway *et al*. [26] compared below-ground C across a chronosequence of encroachment dated from historical imagery, on the US Gulf coast and SE Australia, respectively, leading Kelleway *et al*. [26] to suggest that the identification of a significant contribution may take several decades.

Our study is the first to our knowledge to explore changes in C accumulation *in situ* as mangroves encroach and thicken within a saltmarsh. Our findings support that transitional zones do not quickly show increases in C storage [17,18]. After 18 years of mangrove forest development, the former saltmarsh zone showed little increment in %C or the rate of C accumulation within the soil, which is comparable to saltmarshes elsewhere in the region. Furthermore, what modest accretion occurred in the former saltmarsh zone failed to translate into vertical elevation gain. We therefore rejected our hypothesis that the rate of surface C accumulation and surface elevation gain would increase rapidly as mangrove encroached upon saltmarsh. Further work is required to determine whether this lack of change corresponds with a temporal lag in the proliferation of mangrove roots in the early stage of encroachment [27] or is related to the local hydrodynamic conditions in our study site. By contrast, areas that appeared as saltmarsh in early aerial photography (1930s–1950s) but were identified as mangrove forest or mixed mangrove–saltmarsh ecotone by 2000 showed rates of C sequestration consistent with other environments in the region, indicating that several decades are required before mangrove forest encroachment translates into increased C storage and surface elevation gain.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. N.S. and K.R. designed the experiment, collected and analysed data and wrote the manuscript. D.M. and J.J.K. analysed the data and contributed to the writing of the manuscript. All authors gave final approval for publication and agreed to be held accountable for the work described herein.

Competing interests. The authors declare no conflicts of interest.

Funding. Sydney Olympic Park Authority (SOPA) provided financial and logistic support for the installations of SET-MHs. Additional analyses were supported by the Australian Research Council (FT130100532).

Acknowledgements. We gratefully acknowledge the contribution of Dr Don Cahoon (USGS) to the establishment of the SET-MH network in SE Australia and ongoing support.

Downloaded from https://royalsocietypublishing.org/ on 25 June 2024

References

1. Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
2. Habary A, Johansen JL, Nay TJ, Steffensen JF, Rummer JL. 2017 Adapt, move or die – how will tropical coral reef fishes cope with ocean warming? *Glob. Change Biol.* **23**, 566–577. (doi:10.111/gcb.13488)
3. Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW. 2014 Mangrove expansion and salt marsh decline at mangrove poleward limits. *Glob. Change Biol.* **20**, 147–157. (doi:10.1111/gcb.12341)
4. Osland M, Enwright N, Day R, Doyle T. 2013 Winter climate change and coastal wetland foundation species: salt marshes versus mangrove forests in the southeastern U.S. *Glob. Change Biol.* **19**, 1482–1494. (doi:10.1111/gcb.12126)
5. Kelleway JJ, Cavanaugh K, Rogers K, Feller IC, Ens E, Doughty C, Saintilan N. 2017 Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Glob. Change Biol.* **23**, 3967–3983. (doi:10.111/gcb.13727)
6. Saintilan N, Williams RJ. 1999 Mangrove transgression into saltmarsh environments in south-east Australia. *Glob. Ecol. Biogeogr.* **8**, 117–124. (doi:10.1046/j.1365-2699.1999.00133.x)
7. Krauss KW, McKee KL, Lovelock CE, Cahoon DR, Saintilan N, Reef R, Chen L. 2014 How mangrove forests adjust to rising sea level. *New Phytol.* **202**, 19–34. (doi:10.1111/nph.12605)
8. Woodroffe CD, Rogers K, McKee KL, Lovelock CE, Mendelssohn I, Saintilan N. 2016 Mangrove sedimentation and response to relative sea-level rise. *Annu. Rev. Mar. Sci.* **8**, 243–266. (doi:10.1146/annurev-marina-122414-034025)
9. Saintilan N, Rogers K, Mazumder D, Woodroffe CD. 2013 Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. *Estuar. Coast. Shelf Sci.* **128**, 84–92. (doi:10.1016/j.ecss.2013.05.010)
10. Kelleway J, Saintilan N, Macreadie P, Baldock J, Heijnis H, Zawadzki A, Gadd P, Jacobsen G, Ralph P. 2017 Geochemical analyses reveal the importance of environmental history for blue carbon sequestration. *J. Geophys. Res. Biogeosci.* **122**, 1789–1805. (doi:10.1002/2017JG003775)
11. Rogers K, Wilton KM, Saintilan N. 2006 Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuar. Coast. Shelf Sci.* **66**, 559–569. (doi:10.1016/j.ecss.2005.11.004)
12. Rogers K, Saintilan N, Woodroffe CD. 2014 Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: implications for coastal wetland response to climate change. *Estuar. Coast. Shelf Sci.* **149**, 46–56. (doi:10.1016/j.ecss.2014.07.009).
13. Perry C, Mendelssohn I. 2009 Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. *Wetlands* **29**, 396–406. (doi:10.1672/08-100.1).
14. Henry KM, Twilley RR. 2013 Soil development in a coastal Louisiana wetland during a climate-induced vegetation shift from salt marsh to mangrove. *J. Coast. Res.* **29**, 1273–1283. (doi:10.2112/jcoastres-d-12-00184.1)
15. Yando ES, Osland MJ, Willis JM, Day RH, Krauss KW, Hester MW. 2016 Salt marsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. *J. Ecol.* **104**, 1020–1031. (doi:10.1111/1365-2745.12571)
16. McKee, KL, Vervaeke, WC. 2017 Will fluctuations in salt marsh–mangrove dominance alter vulnerability of a subtropical wetland to sea-level rise? *Glob. Change Biol.* **24**, 1224–1238. (doi:10.1111/gcb.13945)
17. Guo H *et al.* 2017 Coastal regime shifts: rapid responses of coastal wetlands to changes in mangrove cover. *Ecology* **98**, 762–772. (doi:10.1002/ecy.1698)
18. Doughty CL, Langley JA, Walker WS, Feller IC, Schaub R, Chapman SK. 2016 Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuar. Coasts* **39**, 385–396. (doi:10.1007/s12237-015-9993-8)
19. Howard RJ, Day RH, Krauss KW, From AS, Allain L, Cormier N. 2017 Hydrologic restoration in a dynamic subtropical mangrove-to-marsh ecotone. *Restor. Ecol.* **25**, 471–482. (doi:10.111/rec.12452)
20. Rogers K, Saintilan N, Cahoon D. 2005 Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetlands Ecol. Manage.* **13**, 587–598. (doi:10.1007/s11273-005-0003-3)
21. Webb EL, Friess DA, Krauss KW, Cahoon DR, Guntenspergen GR, Phelps J. 2013 A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. *Nat. Clim. Change* **3**, 458–465. (doi:10.1038/nclimate1756)
22. Serrano O, Lavery PS, Duarte CM, Kendrick GA, Calafat A, York PH, Steven A, Macreadie PI, Plus M. 2016 Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? *Biogeosciences* **13**, 4915–4926. (doi:10.5194/bg-13-4915-2016)
23. Macreadie PI *et al.* 2017 Carbon sequestration by Australian tidal marshes. *Sci. Rep.* **7**, 44071. (doi:10.1038/srep44071)
24. Bianchi TS, Allison MA, Zhao J, Li X, Comeaux RS, Feagin RA, Kulawardhana RW. 2013 Historical reconstruction of mangrove expansion in the Gulf of Mexico: linking climate change with carbon sequestration in coastal wetlands. *Estuar. Coast. Shelf Sci.* **119**, 7–16. (doi:10.1016/j.ecss.2012.12.007)
25. Osland M *et al.* 2012 Ecosystem development after mangrove wetland creation: plant–soil change across a 20-year chronosequence. *Ecosystems* **15**, 848–866. (doi:10.1007/s10021-012-9551-1).
26. Kelleway JJ, Saintilan N, Macreadie PI, Skilbeck CG, Zawadzki A, Ralph PJ. 2016 Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Glob. Change Biol.* **22**, 1097–1109. (doi:10-1111.gcb.13158)
27. Barreto CR, Morrissey E, Wykoff D, Chapman S. 2018 Co-occurring mangroves and salt marshes differ in microbial community composition. *Wetlands* **38**, 497–508. (doi:10.1007/s13157-018-0994-9)

LETTER

https://doi.org/10.1038/s41586-019-0951-7

Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise

Kerrylee Rogers[1]*, Jeffrey J. Kelleway[2], Neil Saintilan[2], J. Patrick Megonigal[3], Janine B. Adams[4], James R. Holmquist[3], Meng Lu[3,5], Lisa Schile-Beers[3], Atun Zawadzki[6], Debashish Mazumder[6] & Colin D. Woodroffe[1]

Coastal wetlands (mangrove, tidal marsh and seagrass) sustain the highest rates of carbon sequestration per unit area of all natural systems[1,2], primarily because of their comparatively high productivity and preservation of organic carbon within sedimentary substrates[3]. Climate change and associated relative sea-level rise (RSLR) have been proposed to increase the rate of organic-carbon burial in coastal wetlands in the first half of the twenty-first century[4], but these carbon–climate feedback effects have been modelled to diminish over time as wetlands are increasingly submerged and carbon stores become compromised by erosion[4,5]. Here we show that tidal marshes on coastlines that experienced rapid RSLR over the past few millennia (in the late Holocene, from about 4,200 years ago to the present) have on average 1.7 to 3.7 times higher soil carbon concentrations within 20 centimetres of the surface than those subject to a long period of sea-level stability. This disparity increases with depth, with soil carbon concentrations reduced by a factor of 4.9 to 9.1 at depths of 50 to 100 centimetres. We analyse the response of a wetland exposed to recent rapid RSLR following subsidence associated with pillar collapse in an underlying mine and demonstrate that the gain in carbon accumulation and elevation is proportional to the accommodation space (that is, the space available for mineral and organic material accumulation) created by RSLR. Our results suggest that coastal wetlands characteristic of tectonically stable coastlines have lower carbon storage owing to a lack of accommodation space and that carbon sequestration increases according to the vertical and lateral accommodation space[6] created by RSLR. Such wetlands will provide long-term mitigating feedback effects that are relevant to global climate–carbon modelling.

Broad biogeographic drivers, such as vegetation, climate, topography or water chemistry, are often emphasized as important global-scale controls on organic matter accumulation, decomposition and carbon stocks within tidal wetlands[7]. However, relative sea-level trends over the Holocene varied across the globe, principally on the basis of distance from maximal ice-sheet extent during the last glacial period, and have a profound influence on the contemporary character of coastal wetlands[8,9]. In Europe and North America, where studies of coastal wetland sea-level rise (SLR) impacts are concentrated, sea levels have been rising over the past few millennia at a decelerating rate up to the present (Fig. 1a, b). Tidal marshes in these locations, particularly when sediment supply is low–moderate, are often characterized by deep sediments that are highly organic[4,10,11], in contrast to coastal wetlands in locations where the sea level has been stable for the past few millenia[12], in spite of similarities in floristics[13].

We review published data, contribute new observations on soil carbon concentrations (%C) in tidal-marsh sediments and compare %C values over the active root zone (0–20 cm) and sub-surface depths (20–50 cm, 50–100 cm and >1 m) for 345 locations that vary in rates of SLR over the late Holocene (Supplementary Information). We find that variation in RSLR over past millennia is a primary control on carbon storage. Overall %C varies consistently between RSLR zones (areas spatially differentiated on the basis of consistent patterns of RSLR, fall or stability over the past 6,000 years) with concentrations in the upper 1 m significantly higher ($P < 0.001$) in zones subject to high rates of RSLR over the late Holocene (that is, zones I–II and II in Fig. 1) compared with zones subject to relative sea-level stability over the same period (that is, zones IV and V; Fig. 2, Extended Data Tables 1, 2). The upper metre of soil is the standard endorsed by the Intergovernmental Panel on Climate Change (IPCC) for tidal-wetland carbon-stock estimation[14], and in stable-sea-level zones it integrates processes over several thousand years[15,16]. Where data at depths exceeding 1 m are available, we find that this pattern of high storage in zones exhibiting RSLR over the past few millennia persisted (Fig. 2). Furthermore, the decline in %C with depth was greater in zones where sea level was relatively stable (that is, IV and V), yet remained relatively high in zones where rates of RSLR were high (Fig. 2, Extended Data Table 3; $P < 0.001$ for all pairwise comparisons). Trends were consistent with these findings in zones I and III, as well as in transitional regions, although relatively few data were available from these locations (Extended Data Fig. 1, Extended Data Table 3).

Models emphasizing biotic controls over coastal wetland elevation response to SLR have been largely derived from coasts with ongoing long-term SLR[11,17], where the vertical space available for mineral and organic material accumulation (henceforth termed 'available accommodation space') continued to expand as the sea rose over the past few millennia (Fig. 1c). In these situations, high rates of RSLR had the combined effect of promoting accumulation of mineral and organic matter and slowing rates of decomposition. That is, because sedimentation is positively correlated with patterns of inundation frequency[18], rapid accumulation of mineral and organic material is an outcome of the effect of RSLR on increasing inundation. Material that accumulates under conditions of RSLR becomes progressively submerged, creating more anoxic conditions that inhibit more rapid aerobic pathways of organic-matter decomposition. A substantial proportion of the world's tidal marsh[19] occurs in locations regarded to be relatively tectonically and isostatically stable, and their capacity to respond to accelerated RSLR has received little attention. For these coastal wetlands, several millennia of sea-level stability (Fig. 1d) provided considerable time for decomposition of organic material; as organic material was progressively stored near the limit of tidal inundation, decomposition increased under comparatively aerobic conditions.

The available accommodation space is a useful framework for considering the response of tidal wetlands to SLR because it integrates the influence of both tide range and position within the tidal frame[20]. We describe the effective accommodation space within tidal coastal wetlands as being bounded by the bedrock basement, highest astronomical tides (HAT) and hydrodynamic conditions that favour vertical accretion or lateral progradation, rather than sediment entrainment (Fig. 1e). As mineral and organic sediments accumulate, the available accommodation space diminishes (that is, a portion of the effective accommodation space is converted from available to realized

[1]School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, New South Wales, Australia. [2]Department of Environmental Sciences, Macquarie University, Sydney, New South Wales, Australia. [3]Smithsonian Environmental Research Center, Edgewater, MD, USA. [4]Department of Botany, Nelson Mandela University, Port Elizabeth, South Africa. [5]School of Ecology and Environmental Sciences, Yunnan University, Kunming, China. [6]Australian Nuclear Science and Technology Organisation, Sydney, New South Wales, Australia. *e-mail: kerrylee@uow.edu.au

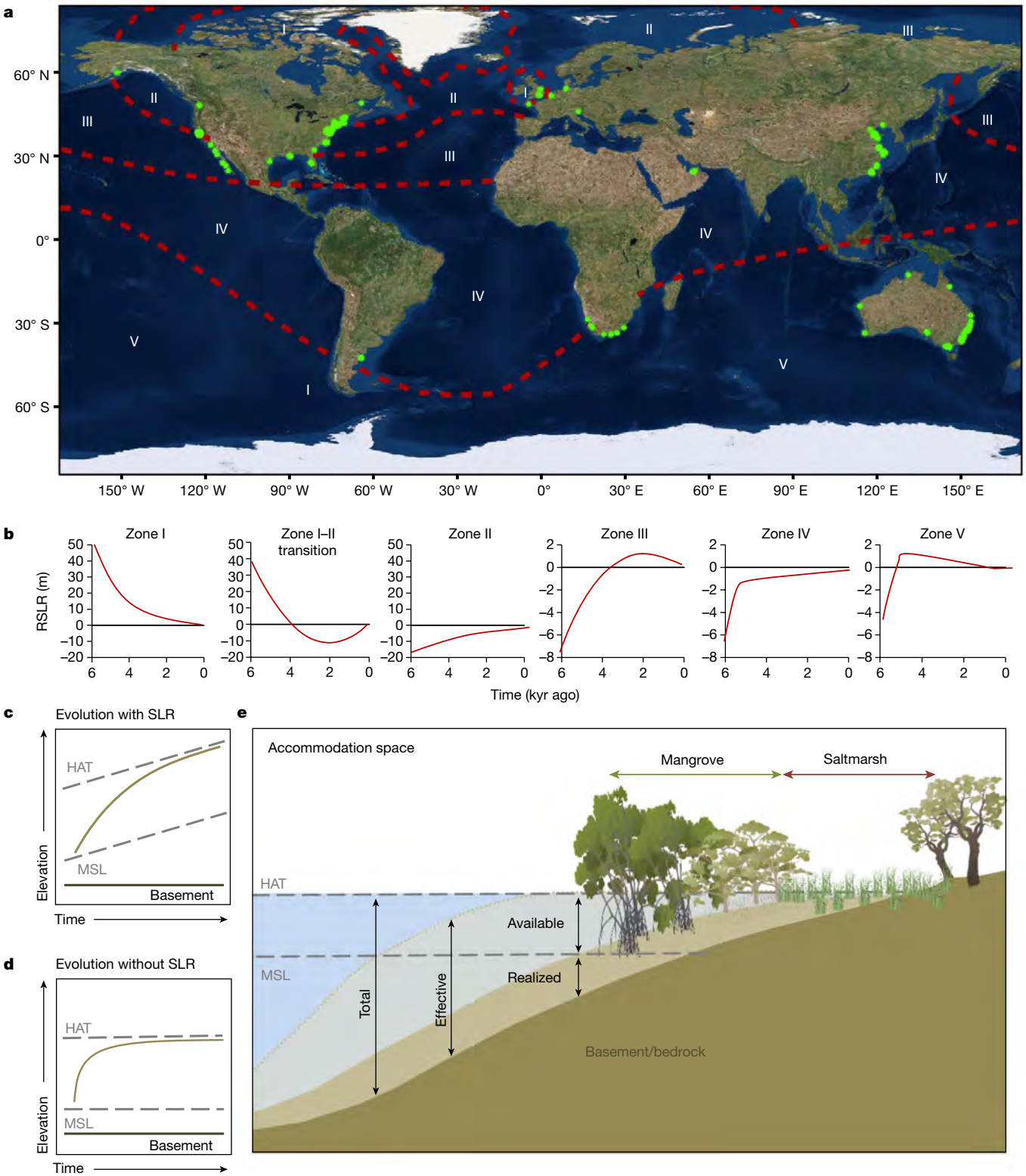


Fig. 1 | Millennial-scale influence of RSL on wetland evolution and accommodation space. a, Holocene RSLR zones and locations of carbon measurements. The figure shows generalized RSLR zones over the Holocene[9] and sample data used in this study, shown as green dots ($n = 345$ locations). Figure adapted with permission from ref. [9], Cambridge Univ. Press; map created with Esri software. **b**, Generalized Holocene relative sea-level history in zones I–V over the past six millennia[9]. Figure adapted with permission from ref. [9], Cambridge Univ. Press. **c**, Wetland surface evolution within an accommodation space defined by the highest astronomical tides (HAT) and mean sea level (MSL), which elevates as the sea rises. **d**, Wetland surface evolution within a stable accommodation space, as occurred in southeastern Australia over the late Holocene[17]. Figures **c** and **d** adapted with permission from ref. [17], Elsevier. **e**, Conceptualized wetland accommodation space, shown here in two dimensions.

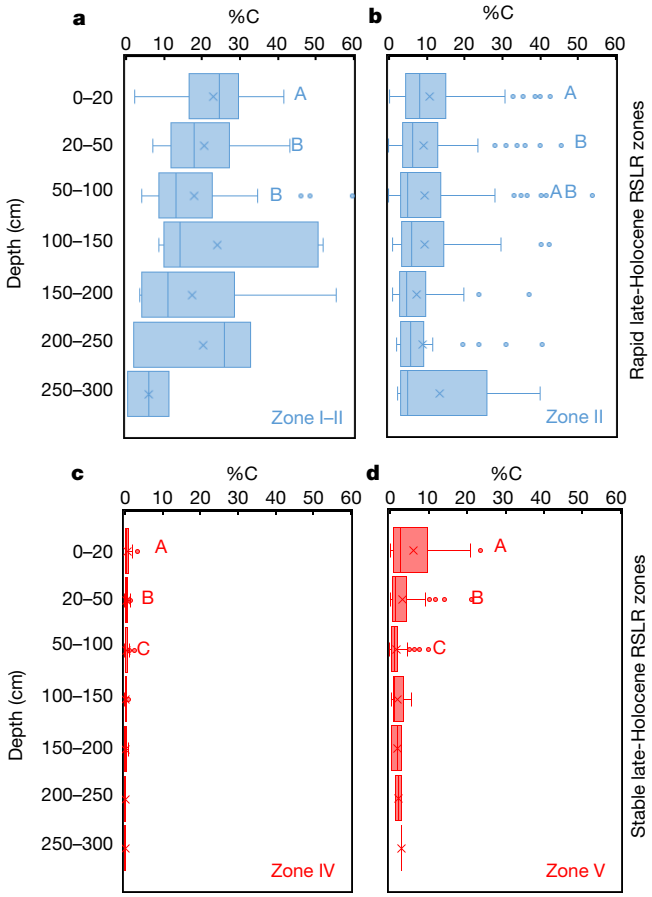


Fig. 2 | Influence of late-Holocene RSLR on carbon concentration. Tidal marshes located along coasts with rapid RSLR in the late Holocene contain higher %C than marshes along coasts with relatively stable sea level. **a**–**d**, Carbon concentration from late-Holocene RSLR over various depths in zone I–II (**a**; rapid RSLR), zone II (**b**; rapid RSLR), zone IV (**c**; stable RSL) and zone V (**d**; stable RSL). Different letters represent significant differences ($P < 0.05$) in %C among depths in the 0–100 cm range within each RSLR zone (that is, depths with the same letter are not significantly different within a zone). Box plots for data-poor RSLR zones (including I and III) are presented in Extended Data Fig. 1.

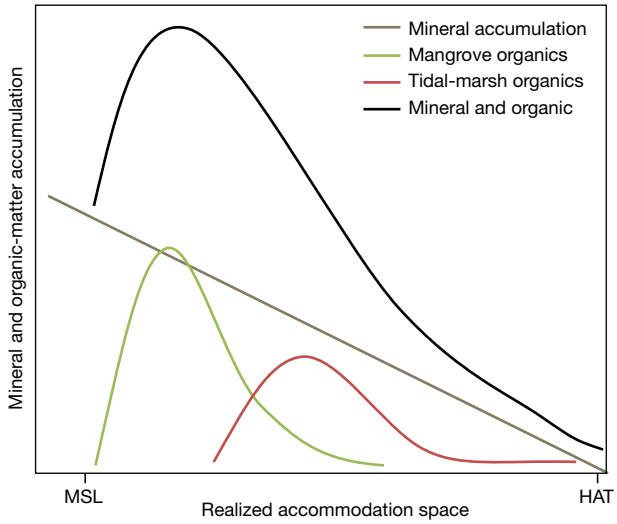


Fig. 3 | Conceptual links between mineral and organic-matter accumulation and realized accommodation space. Model of sediment characteristics with respect to realized accommodation space, here shown in two dimensions to represent the three-dimensional wetland accommodation space. Sedimentation may vary between sites according to mineral and organic sediment availability and to the addition of root material, which is a function of the productivity of vegetation. For simplicity, and following others[30], mineral sediment addition was conceptualized to increase linearly with accommodation space, but may diminish with decreasing accommodation space in an exponential or polynomial manner. Accommodation space varies because of mineral and organic sediment accumulation, SLR and autocompaction. Figure adapted with permission from ref. [30], Springer Nature.

accommodation space; Fig. 1e). This is only alleviated by RSLR, achieved either by subsidence associated with isostatic or tectonic processes, autocompaction of sediments associated with consolidation or decomposition of mineral and organic material, or eustatic SLR, which increases both vertical accommodation space for sediment accumulation and lateral accommodation space for landward encroachment[6]. Addition of bulk organic material from roots further acts to decrease the volume of available accommodation space[21,22].

The coastline of southeastern Australia is an ideal location to explore alterations to wetland accommodation space and SLR because the region is regarded to be relatively tectonically stable[23,24]. Geochronological analyses from a range of biological markers indicate that present sea level was attained approximately 7.8 thousand years (kyr) ago and continued to rise up to 1.5 m above present levels approximately 7.5 kyr ago, falling again to present levels approximately 2 kyr ago[23]. The relative sea-level stability over the past 2 kyr creates favourable conditions to decrease accommodation space and for progradation via accumulation of sediments, provided that sediment is available for deposition (that is, as in Fig. 1d, where elevations evolve without SLR).

Wetlands in this region range from primarily mineral-dominated tidal marshes at elevations high in the tidal frame near HAT to shoreline-fringing mangroves that are relatively lower in the tidal frame. Elevation of the wetland surface in the tidal frame is the relevant variable that indicates accommodation space. As such, low-elevation mangroves at this site are functionally equivalent to low-elevation tidal marshes in climatic regimes that do not support mangroves. Accordingly, mangroves, like lower tidal marsh elsewhere, have more available accommodation space than the adjacent tidal marsh (that is, as per Fig. 1e). In situ vegetation (mangrove and tidal-marsh species within this region) differentially modulates organic-matter additions with deeper root systems of mangrove that are able to add living biomass and organic matter to greater depths within substrates[25], but additions remain proportional to the available accommodation space, as conceptualized in Fig. 3. Under stable sea levels, we might expect organic-matter additions to decline as mineral sediment continues to be delivered by tides and is deposited on wetland surfaces, and the wetland surface approaches the upper limit of the available accommodation space, which is represented by HAT under most conditions, because periodic salt stress prevents encroachment of terrestrial vegetation. Increases in the contribution of organic material lower in the tidal frame would continue as long as accommodation space is available. Accordingly, as SLR increases the available accommodation space, we might expect to see an increase in both mineral additions and carbon storage through burial near wetland surfaces.

To test the effect of RSLR on the available accommodation space and soil organic-carbon accumulation in a zone V wetland, we selected a study site that experienced recent rapid RSLR following subsidence caused by the removal of pillars in an underlying coal mine (Chain Valley Bay, Lake Macquarie, Australia; 33° 10′ S, 151° 35′ E; Supplementary Information). Subsidence corresponded to high-end IPCC projections of SLR in 2100 (about 1 m) but occurred in the space of a few months in 1986. Following subsidence, tidal marsh and adjoining terrestrial vegetation rapidly transitioned to mangrove, and mangrove transitioned to subtidal wetland, over a 5–10 year period. We determined sediment chronologies from cores extracted from substrates that are currently mangrove and submerged.

Vertical accretion in both the mangrove and the submerged wetland increased following RSLR, with high proportional contribution

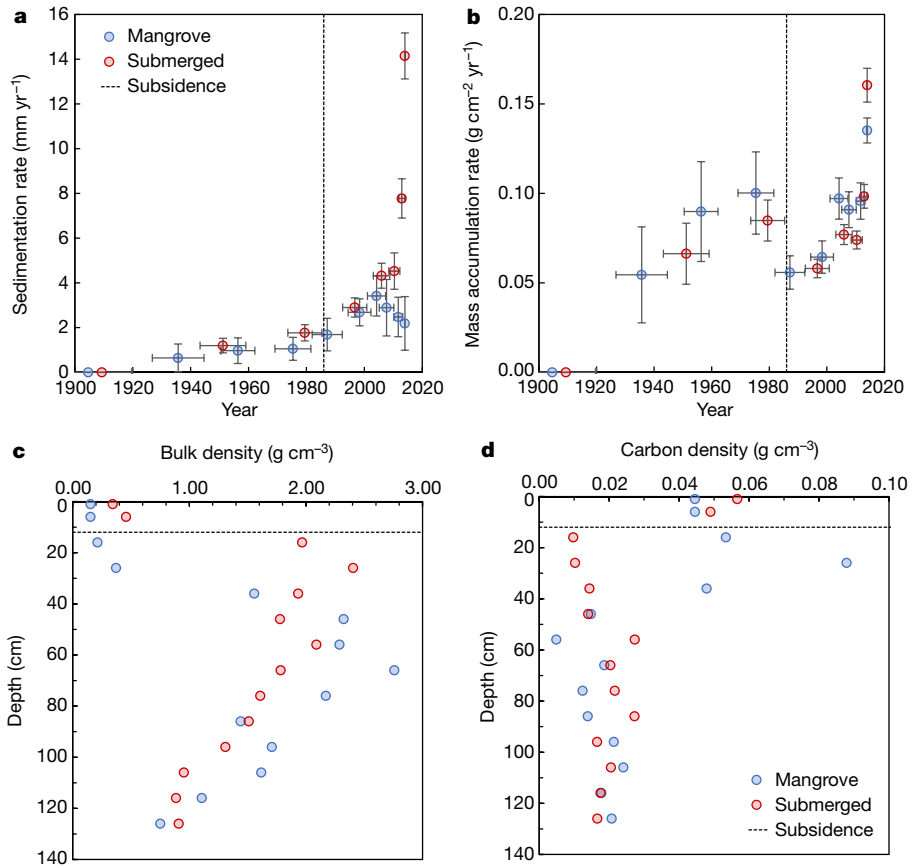


Fig. 4 | Sediment accumulation and character related to available accommodation space. a, **b**, Calculated sedimentation rate (**a**) and mass accumulation rate (**b**) derived from ^{210}Pb dating. Error bars show standard error. **c**, **d**, Bulk density (**c**) and carbon density (**d**) of mangrove (previously tidal marsh and terrestrial vegetation) and submerged (previously mangrove) sediments from Chain Valley Bay (outliers represent modern live root material at that depth). The depth and associated age of sediments at which the subsidence event is evident are indicated by dashed lines. ^{210}Pb activity for mangrove and submerged cores and ^{137}Cs validation of ^{210}Pb chronology are provided in Extended Data Fig. 2.

of carbon-dense organic matter in both settings (Fig. 4). Bulk density rapidly declined following RSLR despite the higher sediment accumulation rate. Sediment accumulation in the new mangrove post-subsidence was approximately double the pre-subsidence rate in the tidal marsh and mangrove, whereas organic-carbon accumulation increased by a factor of four. The sediment and organic-carbon accumulation rate within the newly created subtidal wetland, now a seagrass bed, was still accelerating 30 years after the subsidence event.

We argue that under relatively stable or slightly falling sea levels, as occurred in much of the Southern Hemisphere over the past few millennia, wetlands become increasingly mineral-dominated and favour carbon loss over accumulation as accommodation space diminishes. Our global analysis demonstrates the latent capacity of high organic-carbon accumulation contributing towards elevation gains under conditions in which the available accommodation space increases, as occurs under accelerated RSLR.

These results substantiate that carbon accumulation and storage is related to available accommodation space, which is influenced by rates of RSLR. They imply that SLR will lead to increases in carbon sequestration and storage in many places where vertical accommodation space has previously been constrained by stable or declining sea levels, including southern Africa, Australia, China and South America, which contain half of the global tidal marsh extent[19]. This feedback will be further enhanced where lateral expansion of wetlands in response to RSLR can occur, unless interrupted by storms or other perturbations. A doubling of carbon sequestration rates across wetlands along these coasts could potentially sequester an additional[19] 5 Tg C yr^{-1}, which might provide an important mitigating negative feedback on atmospheric carbon. Wetland loss to clearance[26,27] and impediments to tidal exchange continue to threaten the capacity of coastal wetlands to mitigate climate change[28] both now and in the future as seas continue to rise[29]. Reversing these trends will further improve the carbon sequestration value of coastal wetlands under future, more rapid SLR.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41586-019-0951-7.

Received: 19 December 2017; Accepted: 7 January 2019;
Published online 6 March 2019.

1. Donato, D. C. et al. Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* **4**, 293–297 (2011).
2. Mcleod, E. et al. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Front. Ecol. Environ.* **9**, 552–560 (2011).
3. Duarte, C. M., Middelburg, J. & Caraco, N. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* **2**, 1–8 (2005).
4. Kirwan, M. L. & Mudd, S. M. Response of salt-marsh carbon accumulation to climate change. *Nature* **489**, 550–553 (2012).
5. DeLaune, R. & White, J. Will coastal wetlands continue to sequester carbon in response to an increase in global sea level? A case study of the rapidly subsiding Mississippi river deltaic plain. *Clim. Change* **110**, 297–314 (2012).
6. Schuerch, M. et al. Future response of global coastal wetlands to sea-level rise. *Nature* **561**, 231–234 (2018).
7. Holmquist, J. R. et al. Accuracy and precision of tidal wetland soil carbon mapping in the conterminous United States. *Sci. Rep.* **8**, 9478 (2018); corrigendum **8**, 15219 (2018).
8. Murray-Wallace, C. V. & Woodroffe, C. D. *Quaternary Sea-Level Changes: A Global Perspective* (Cambridge Univ. Press, Cambridge, 2014).
9. Clark, J. A., Farrell, W. E. & Peltier, W. R. Global changes in postglacial sea level: a numerical calculation. *Quat. Res.* **9**, 265–287 (1978).
10. Redfield, A. C. Development of a New England salt marsh. *Ecol. Monogr.* **42**, 201–237 (1972).

11. Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B. & Cahoon, D. R. Responses of coastal wetlands to rising sea-levels. *Ecology* **83**, 2869–2877 (2002).
12. Lovelock, C. E. et al. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* **526**, 559–563 (2015).
13. Adam, P. *Saltmarsh Ecology* (Cambridge Univ. Press, Cambridge, 1990).
14. Hiraishi, T. et al. (eds) *2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands. Technical Report* (IPCC, 2014).
15. Saintilan, N. & Hashimoto, T. R. Mangrove-saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia. *Hydrobiologia* **413**, 95–102 (1999).
16. Woodroffe, C. D., Thom, B. G. & Chappell, J. Development of widespread mangrove swamps in mid-Holocene times in northern Australia. *Nature* **317**, 711–713 (1985).
17. Allen, J. R. L. Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. *Quat. Sci. Rev.* **19**, 1155–1231 (2000).
18. Pethick, J. S. Long-term accretion rates on tidal salt marshes. *J. Sediment. Res.* **51**, 571–577 (1981).
19. Ouyang, X. & Lee, S. Updated estimates of carbon accumulation rates in coastal marsh sediments. *Biogeosciences* **11**, 5057–5071 (2014).
20. Kirwan, M. L. & Guntenspergen, G. R. Influence of tidal range on the stability of coastal marshland. *J. Geophys. Res.* **115**, F02009 (2010).
21. Krauss, K. W. et al. How mangrove forests adjust to rising sea level. *New Phytol.* **202**, 19–34 (2014).
22. Langley, J. A., McKee, K. L., Cahoon, D. R., Cherry, J. A. & Megonigal, J. P. Elevated CO_2 stimulates marsh elevation gain, counterbalancing sea-level rise. *Proc. Natl Acad. Sci. USA* **106**, 6182–6186 (2009).
23. Sloss, C. R., Murray-Wallace, C. V. & Jones, B. G. Holocene sea-level change on the southeast coast of Australia: a review. *Holocene* **17**, 999–1014 (2007).
24. Lambeck, K. & Nakada, M. Late Pleistocene and Holocene sea-level change along the Australian coast. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **89**, 143–176 (1990).
25. Kelleway, J. J. et al. Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Glob. Change Biol.* **22**, 1097–1109 (2016).
26. Duke, N. C. et al. A world without mangroves? *Science* **317**, 41–42 (2007).
27. Duarte, C., Dennison, W., Orth, R. & Carruthers, T. The charisma of coastal ecosystems: addressing the imbalance. *Estuaries Coasts* **31**, 233–238 (2008).
28. Crooks, S., Herr, D., Tamelander, J., Laffoley, D. & Vandever, J. *Mitigating Climate Change through Restoration and Management of Coastal Wetlands and Near-Shore Marine Ecosystems: Challenges and Opportunities* (World Bank Environment Department, Washington DC, 2011).
29. Pontee, N. Defining coastal squeeze: a discussion. *Ocean Coast. Manage.* **84**, 204–207 (2013).
30. Kirwan, M. L. & Megonigal, J. P. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* **504**, 53–60 (2013).

Acknowledgements This research was supported by the Australian Research Council (FT130100532), AINSE (ALNGRA13046) and the UOW Global Challenges Program. The Smithsonian Environmental Research Center supported J.P.M., J.R.H, M.L. and L.S.-B. The data curation efforts of J.R.H. and data collection and synthesis efforts of J.P.M. were supported by United States National Science Foundation grants to the Coastal Carbon Research Coordination Network (DEB-1655622) and the Global Change Research Wetland (DEB-0950080, DEB-1457100 and DEB-1557009) and by a NASA Carbon Monitoring System programme grant (NNH14AY67I). L.S.-B. was supported by a Smithsonian Institution MarineGEO Postdoctoral Fellowship. This is contribution number 32 of the Smithsonian's MarineGEO Network. The authors acknowledge J. Curran for assistance with sample preparation, S. Rasel, S. Oyston and M. Rupic for assistance with data collation and the students who undertook fieldwork as part of this research.

Reviewer information *Nature* thanks Andrew Ashton and the other anonymous reviewer(s) for their contribution to the peer review of this work.

Author contributions K.R., N.S. and C.D.W. developed the premise of the study. J.J.K., N.S., J.P.M., J.B.A., J.R.H., M.L., L.S.-B. and K.R. gathered and produced input data for the global analysis. J.J.K. carried out global-scale statistical analyses. K.R., D.M. and A.Z. undertook local-study fieldwork, sample preparation, laboratory and statistical analyses. K.R., J.J.K., N.S. and C.D.W. wrote the paper. All authors contributed to editing and revising the paper.

Competing interests The authors declare no competing interests.

Additional information
Extended data is available for this paper at https://doi.org/10.1038/s41586-019-0951-7.
Supplementary information is available for this paper at https://doi.org/10.1038/s41586-019-0951-7.
Reprints and permissions information is available at http://www.nature.com/reprints.
Correspondence and requests for materials should be addressed to K.R.
Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2019

METHODS

Review of global tidal marsh carbon accumulation. Tidal marshes were the focus of our global analysis owing to their global distribution relative to other tidal wetlands (that is, mangroves). We collated published records of carbon concentration or organic matter concentration in tidal marshes because these are the two most widely reported measures related to carbon content and are less confounded by variation in mineral content and methodological error than values that incorporate bulk density (for example, grams of carbon per cubic centimetre or grams of organic matter per cubic centimetre). We tested the sensitivity of our results to the choice of carbon content and bulk density and confirmed that these two metrics produce similar patterns with respect to the role of RSLR variation on C sequestration (Supplementary Information, Extended Data Fig. 4, Extended Data Tables 4–6). This collation of records included research theses, national data collations, unpublished data and studies identified by previous reviews[19,31] and incorporated new literature identified using the same search terms as Ouyang and Lee[19] (Supplementary Information). We then identified records that contained data across the active root zone (0–20 cm), medium-depth (20–50 cm) and deeper (50–100 cm) depth intervals and beyond. This was undertaken to (i) compare the influence of the active root zone among RSLR zones and (ii) assess carbon accumulation across a period of centuries to millennia on the basis of global rates of tidal marsh accumulation[19] of <10 mm yr^{-1}. Organic-matter concentration data were converted[32] to %C. When multiple cores were available for a study location, we calculated mean %C values across replicate cores for each depth interval. Study locations with different geomorphic or floristic characteristics within a marsh were deemed to be different study locations for this purpose. The vast majority of studies retained live and dead roots in their analysis, although there were regional exceptions to this. For example, all Chinese records (zone IV) removed roots before %C analysis. To account for potential confounding effects of zones and methods, we recorded the aperture of the sieve and included it as a covariate in statistical analyses.

This approach resulted in a database comprising 1,266 depth-interval records across 345 locations (Supplementary Information). Data were assigned to RSLR zones on the basis of local or regional Holocene sea-level curves[24,33,34]. A linear mixed model[35] was used to assess the relationships between the dependent variable soil %C and the fixed factors of soil depth (three repeated measure levels: 0–20 cm, 20–50 cm and 50–100 cm) and RSLR zone (eight levels: zones I through V and transitional regions I–II, II–III and IV–V). The influence of climate and salinity was also tested using a linear mixed model (Supplementary Information). Climate was found to be insignificant (Extended Data Table 1a), whereas extremely weak linear-regression relationships between salinity and %C were identified over three depth intervals ($R^2 < 0.07$, $P < 0.001$; Extended Data Fig. 3), with little effect on the significance of RSLR zone on %C in the linear mixed model (Extended Data Table 1b).

To further assess variations in %C with soil depth, a separate repeated-measures analysis of variance (RM-ANOVA)[36] was completed for each RSLR zone. RM-ANOVA is a test to identify significant differences within related groups, in this case identifying differences in %C with soil depth down a core. Linear mixed-model pairwise comparisons and RM-ANOVA outcomes are reported for the data-rich RSLR zones II (156 locations), IV (68 locations), V (63 locations) and I–II transition (36 locations). Other RSLR zones (I and III) and transitional regions were considered data-poor and were excluded from these pairwise comparisons.

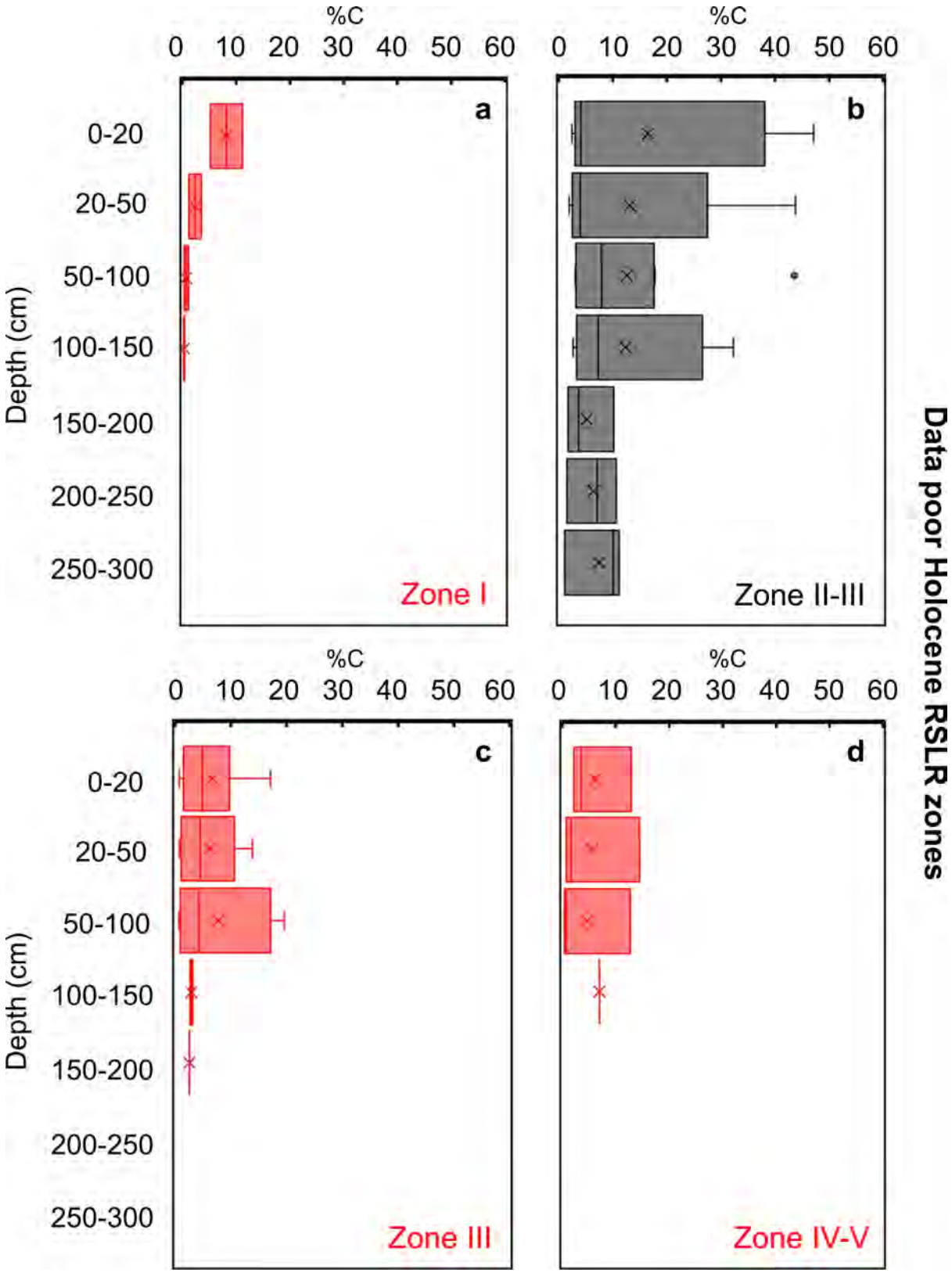
Core extraction and sediment characterization. Continuous cores of approximately 1.5–2 m length were extracted within vegetation zones along two transects that were normal to the vegetation zonation and the shoreline of Chain Valley Bay, Lake Macquarie (see detailed site description in the Supplementary Information). The sediment character of all cores was determined. Detailed analysis of bulk density, grain size and carbon and nitrogen content, as well as carbon and nitrogen stable-isotope analysis, were undertaken on selected cores. This paper presents information on the submerged wetland and mangrove core. Grainsize analysis was undertaken using a Malvern Mastersizer 2000 laser diffractometer. Elemental analysis and stable isotope analysis was undertaken using a continuous-flow isotope-ratio mass spectrometer (Delta V Plus, Thermo Scientific) interfaced with an elemental analyser (Thermo Fisher Flash 2000 HT EA, Thermo Electron).

Radiometric sediment dating. Sediment samples from cores that underwent detailed sediment characterization were also processed for ^{210}Pb and ^{137}Cs radiometric dating to determine rates of sediment accumulation. Sediment cores were sliced at 1-cm intervals and prepared for analysis of excess ^{210}Pb activities using α-particle spectrometry[37]. Bulk samples were prepared for ^{137}Cs activity analysis using γ-ray spectrometry. All analyses were undertaken at the Australian Nuclear Science and Technology Organisation (ANSTO). Recent sediment chronologies derived from analysis of excess ^{210}Pb activities were determined using the Constant Rate of Supply (CRS) model and validated using the presence of a subsurface peak in the ^{137}Cs activity concentration for each core, which marks the 1963 depth[38].

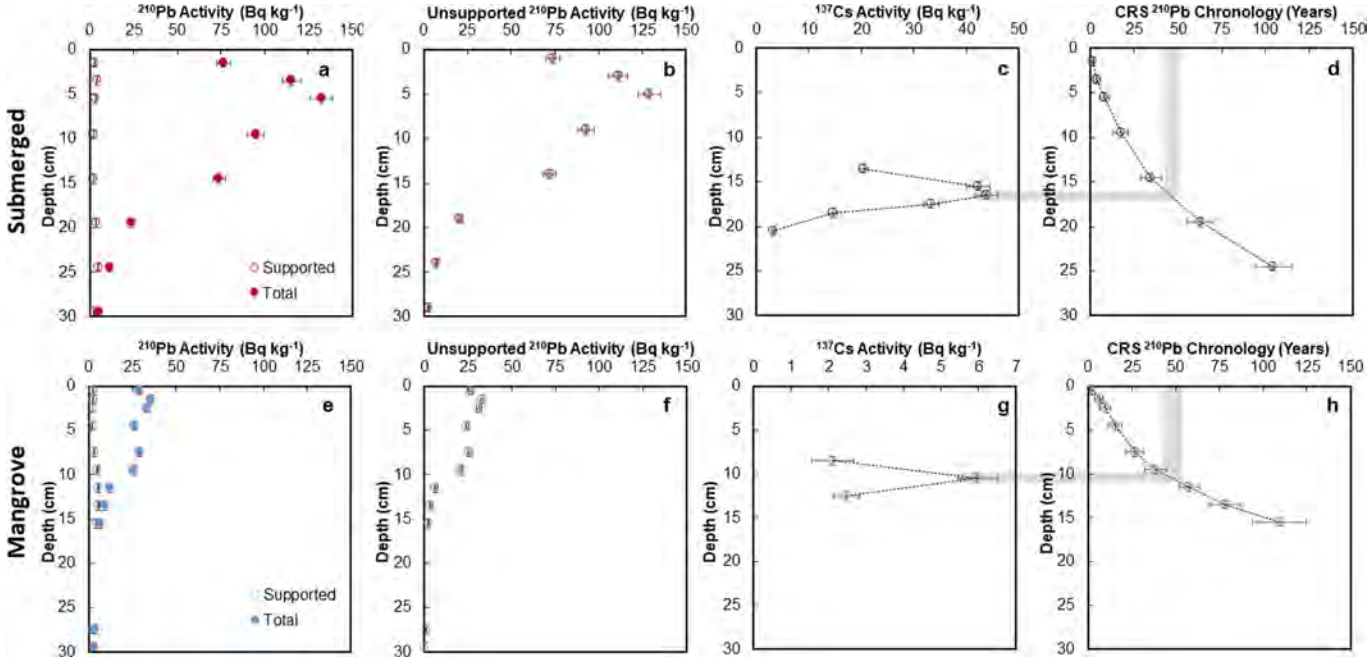
Data availability

The data used in the global analysis of carbon concentration with respect to Holocene RSLR are provided in the Supplementary Information. The data that support the Chain Valley Bay study site analysis are available from the corresponding author upon reasonable request.

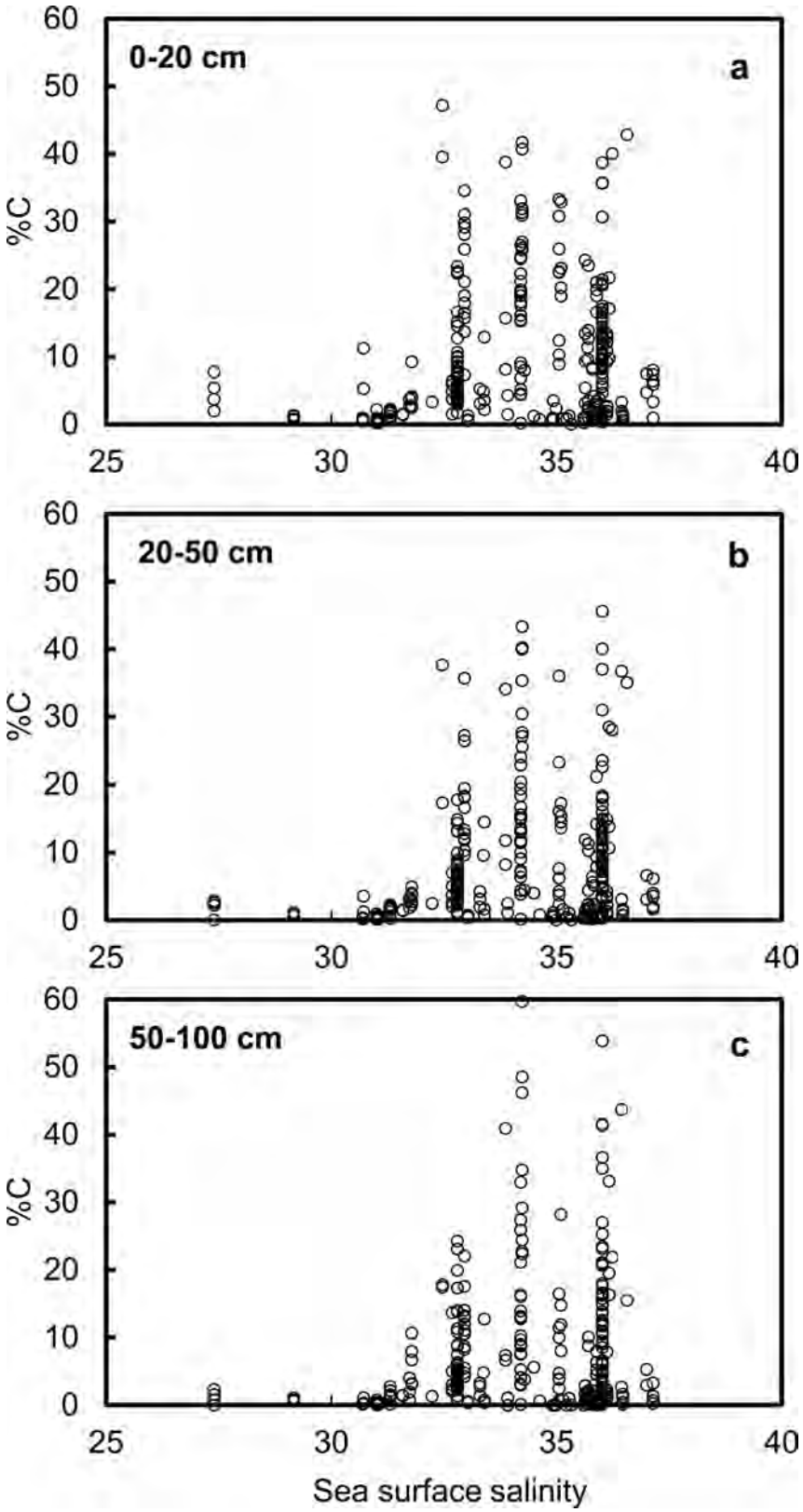
31. Chmura, G. L., Anisfeld, S. C., Cahoon, D. R. & Lynch, J. C. Global carbon sequestration in tidal, saline wetland soils. *Glob. Biogeochem. Cycles* **17**, 1111 (2003).
32. Craft, C., Seneca, E. & Broome, S. Loss on ignition and Kjeldahl digestion for estimating organic carbon and total nitrogen in estuarine marsh soils: calibration with dry combustion. *Estuaries Coasts* **14**, 175–179 (1991).
33. Shennan, I. & Horton, B. Holocene land- and sea-level changes in Great Britain. *J. Quaternary Sci.* **17**, 511–526 (2002).
34. Pluet, J. & Pirazzoli, P. *World Atlas of Holocene Sea-Level Changes* Vol. 58 (Elsevier, Amsterdam, 1991).
35. Verbeke, G. in *Linear Mixed Models in Practice* (eds Verbeke, G. & Molenberghs, G.) 63–153 (Springer, New York, 1997).
36. von Ende, C. N. in *Design and Analysis of Ecological Experiments* (eds Scheiner, S. M. & Gurevitch, J.) 134–157 (Oxford Univ. Press, New York, 2001).
37. Hollins, S. et al. Reconstructing recent sedimentation in two urbanised coastal lagoons (NSW, Australia) using radioisotopes and geochemistry. *J. Paleolimnol.* **46**, 579–596 (2011).
38. Appleby, P. in *Tracking Environmental Change Using Lake Sediments* (eds Smol, J. P. et al.) 171–203 (Kluwer, Dordrecht 2001).



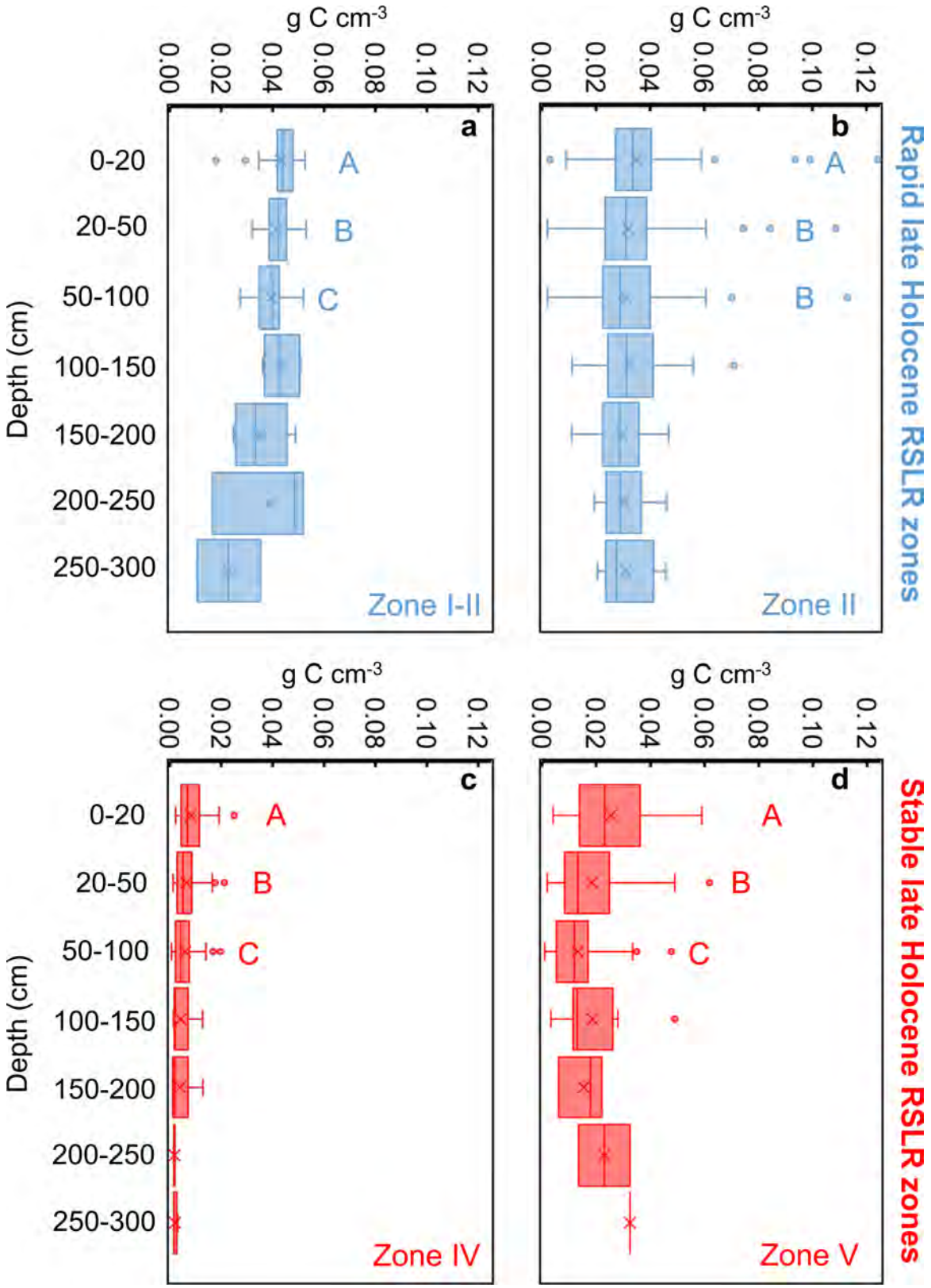
Extended Data Fig. 1 | Relationship between late-Holocene RSLR and carbon concentration for data-poor late-Holocene RSLR zones and transitional zones. a–d, Box plots of tidal-marsh soil C concentration for data-poor Holocene RSLR zones and transitional regions: zone I (**a**), zone II–III transition (**b**), zone III (**c**) and zone IV–V transition (**d**).



Extended Data Fig. 2 | ^{210}Pb and ^{137}Cs activity of submerged and mangrove sediments. a–d, Submerged-core supported and total (**a**) and unsupported (**b**) ^{210}Pb activity, ^{137}Cs activity (**c**) and CRS-based ^{210}Pb chronology (**d**). **e–h**, Mangrove-core supported and total (**e**) and unsupported (**f**) ^{210}Pb activity, ^{137}Cs activity (**g**) and CRS-based ^{210}Pb chronology (**h**). The grey validation lines confirm that the ^{137}Cs activity peak corresponds to a sediment date of 1963, in agreement with CRS-based ^{210}Pb chronology (core dating occurred in 2014).



Extended Data Fig. 3 | Relationship between sea-surface salinity and C concentration over three depth intervals. a–c, Regression analysis of C concentration and global-scale sea-surface salinity, derived from the NASA Aquarius Satellite Mission, exhibited extremely weak relationships over the depth intervals 0–20 cm (**a**; $R^2 = 0.07$, $P < 0.001$), 20–50 cm (**b**; $R^2 = 0.07$, $P < 0.01$) and 50–100 cm (**c**; $R^2 = 0.06$, $P < 0.001$). Soil %C values are low for zones I and IV in part owing to the removal of roots before analysis (see Supplementary Table 1).



Extended Data Fig. 4 | Relationship between late-Holocene RSLR and C density for data-rich late-Holocene RSLR zones and transitional zones. **a**–**d**, Box plots of tidal-marsh soil C density for data-rich Holocene RSLR zones and transitional regions: zone I–II transition (**a**), zone II (**b**), zone IV (**c**), and zone V (**d**).

Extended Data Table 1 | Results of the linear mixed model used for the dependent variable of tidal-marsh soil carbon concentration

a) Model with sieve size as a random factor covariate

Source	Numerator df	Denominator df	F-value	P-value
Intercept	1	328.9	28.134	**<0.001**
Soil Depth	2	330.5	3.922	**0.021**
RSLR Zone	6	297.2	31.464	**<0.001**
Köppen Climate Zone	2	326.4	1.657	0.192
Depth * RSLR Zone	14	333.0	1.847	**0.031**

b) Model with salinity as a random factor covariate

Source	Numerator df	Denominator df	F-value	P-value
Intercept	1	252.4	19.868	**<0.001**
Soil Depth	2	335.0	4.171	**0.016**
RSLR Zone	6	332.246	34.931	**<0.001**
Köppen Climate Zone	2	332.271	0.466	0.628
Depth * RSLR Zone	14	335.0	1.878	**0.028**

Analysis was restricted to the three soil depths for which %C data were most commonly available (0–20 cm, 20–50 cm and 50–100 cm). **a**, The sieve size was included in the model as a random factor covariate. **b**, The salinity was included in the model as a random factor covariate. 'Numerator df' refers to the degrees of freedom (df) of the regression; 'denominator df' refers to the degrees of freedom of the residuals; 'F-value' refers to the ratio of between-group variability to within-group variability.

Extended Data Table 2 | Results of linear-mixed-model pairwise comparisons among Holocene RSLR zones for the dependent variable of tidal-marsh soil carbon concentration

		RAPID HOLOCENE RSLR ZONES		STABLE HOLOCENE RSLR ZONES		
	RSLR zone	I-II transition (36)	II (156)	IV (68)	V (63)	
RAPID HOLOCENE RSLR ZONES	I-II transition (36)		**I-II > II**	**I-II > IV**	**I-II > V**	**COMPARISON DIRECTION**
	II (156)	**<0.001**		**II > IV**	**II > V**	
STABLE HOLOCENE RSLR ZONES	IV (68)	**<0.001**	**<0.001**		IV ≈ V	
	V (63)	**<0.001**	**<0.001**	1.0		
		P-VALUES				

The top right of the table shows the direction of pairwise comparisons and the bottom left of the table shows the corresponding *P* values, obtained using estimated marginal means with the Bonferroni adjustment. Pairwise comparisons that are significantly different at $P < 0.05$ are in bold. Values in parentheses indicate the number of soil cores included in the analysis from each sea-level zone.

Extended Data Table 3 | Results of global data compilation of tidal marsh soil carbon concentration and RM-ANOVA

Late-Holocene RSLR zone	Number of locations	%C by depth interval			RM-ANOVA		
		0-20cm	20-50cm	50-100cm	df	*F*-value	*P*-value
Rapid RSLR zones:							
I-II transition	36	23.6 ± 1.5^{A}	20.6 ± 1.7^{B}	18.1 ± 2.2^{B}	1.8, 60	7.771	**0.002**
II	156	10.9 ± 0.7^{A}	9.3 ± 0.7^{B}	9.5 ± 0.8^{AB}	1.5, 236	5.847	**0.007**
Stable RSLR zones:							
IV*	68	0.78 ± 0.07^{A}	0.62 ± 0.06^{B}	0.56 ± 0.07^{C}	1.4, 89	26.127	**<0.001**
V	63	6.8 ± 0.9^{A}	3.4 ± 0.6^{B}	2.0 ± 0.3^{C}	1.4, 77	32.311	**<0.001**
Data Poor zones:							
I*	2	8.2 ± 3.0	2.4 ± 1.2	0.7 ± 0.4		N/A	
II-III transition	9	16.6 ± 6.2	13.1 ± 5.5	12.6 ± 4.3		N/A	
III	7	4.5 ± 1.2	4.2 ± 1.4	3.1 ± 0.8		N/A	
IV-V transition	3	6.2 ± 3.4	5.6 ± 4.4	4.6 ± 4.1		N/A	

Values reported are the number of distinct study locations for which relevant data were available, as well as mean soil %C (± one standard error) for the most commonly reported depth intervals: 0–20 cm, 20–50 cm and 50–100 cm. A separate RM-ANOVA was conducted for each data-rich Holocene RSL zone to test for differences in tidal-marsh soil %C values among soil depth intervals. *P* values are based on estimated marginal means with the Bonferroni adjustment, with values significant at $P < 0.05$ in bold. Superscript letters denote significantly different depth intervals within each SLR zone.

Extended Data Table 4 | Results of the linear mixed model for the dependent variable of tidal marsh soil carbon density (in grams of carbon per cubic centimetre)

a) Model with sieve size as a random factor covariate

Source	Numerator df	Denominator df	F-value	P-value
Intercept	1	331.629	192.586	**<0.001**
Soil Depth	2	331.076	17.552	**<0.001**
RSLR Zone	6	333.036	62.070	**<0.001**
Köppen Climate Zone	2	332.151	1.084	0.339
Depth * RSLR Zone	14	348.530	3.822	**<0.001**

b) Model with salinity as a random factor covariate

Source	Numerator df	Denominator df	F-value	P-value
Intercept	1	285.765	14.538	**<0.001**
Soil Depth	2	330.326	17.553	**<0.001**
RSLR Zone	6	331.574	55.270	**<0.001**
Köppen Climate Zone	2	330.375	1.349	0.261
Depth * RSLR Zone	14	346.841	3.792	**<0.001**

Analysis was restricted to three soil depths: 0–20 cm, 20–50 cm and 50–100 cm. **a**, The sieve size (in millimetres) was included in the model as a random factor covariate. **b**, The salinity was included in the model as a random factor covariate.

Extended Data Table 5 | Results of linear-mixed-model pairwise comparisons among Holocene RSLR zones for the dependent variable of tidal-marsh soil carbon density (in grams of carbon per cubic centimetre)

		RAPID HOLOCENE RSLR ZONES		STABLE HOLOCENE RSLR ZONES		
	RSLR zone	I-II transition (36)	II (156)	IV (68)	V (63)	
RAPID HOLOCENE RSLR ZONES	I-II transition (36)		**I-II > II**	**I-II > IV**	**I-II > V**	**COMPARISON DIRECTION**
	II (156)	**0.006**		**II > IV**	**II > V**	
STABLE HOLOCENE RSLR ZONES	IV (68)	**<0.001**	**<0.001**		**IV < V**	
	V (63)	**<0.001**	**<0.001**	<0.001		
		P-VALUES				

The top right of the table shows the direction of pairwise comparisons and the bottom left of the table shows the corresponding *P* values, obtained using estimated marginal means with the Bonferroni adjustment. Pairwise comparisons that are significantly different at $P < 0.05$ are in bold. Values in parentheses indicate the number of soil cores included in the analysis from each sea-level zone.

Extended Data Table 6 | Results of global data compilation of tidal marsh soil carbon density and RM-ANOVA

Late-Holocene RSLR zone	Number of locations	g C cm^{-3} by depth interval			RM-ANOVA	
		0-20cm	20-50cm	50-100cm	df	*F*-value *P*-value
Rapid RSLR zones:						
I-II transition	36	0.044 ± 0.001 ^{A}	0.042 ± 0.001 ^{B}	0.039 ± 0.001 ^{C}	1.4, 49	13.079 **<0.001**
II	156	0.035 ± 0.001 ^{A}	0.032 ± 0.001 ^{B}	0.031 ± 0.001 ^{B}	1.5, 226	12.895 **<0.001**
Stable RSLR zones:						
IV*	68	0.008 ± 0.001 ^{A}	0.006 ± 0.001 ^{B}	0.006± 0.001 ^{C}	1.5, 95	35.457 **<0.001**
V	63	0.027 ± 0.002 ^{A}	0.018 ± 0.002 ^{B}	0.014 ± 0.001 ^{C}	1.6, 90	33.226 **<0.001**
Data Poor zones:						
I*	2	0.034 ± 0.004	0.020 ± 0.006	0.009 ± 0.004	N/A	
II-III transition	9	0.034 ± 0.005	0.035 ± 0.006	0.034 ± 0.004	N/A	
III	7	0.040 ± 0.013	0.035 ± 0.011	0.031 ± 0.009	N/A	
IV-V transition	3	0.025 ± 0.006	0.020 ± 0.009	0.016 ± 0.010	N/A	

Values reported are the number of distinct study locations for which relevant data were available, as well as the mean soil carbon density (in grams of carbon per cubic centimetre) (± one standard error) for the most commonly reported depth intervals: 0–20 cm, 20–50 cm and 50–100 cm. A separate RM-ANOVA was conducted for each data-rich Holocene RSLR zone to test for differences in tidal-marsh soil carbon density among soil depth intervals. *P* values are based on estimated marginal means with the Bonferroni adjustment, with values significant at $P < 0.05$ in bold. Superscript letters denote significantly different depth intervals within each SLR zone.

*Soil C density values are low for zones I and IV in part owing to the removal of roots before analysis (see Supplementary Table 1).

DYNAMIC SEDIMENTARY ENVIRONMENTS OF MANGROVE COASTS

Edited by
Frida Sidik | Daniel A. Friess

ELSEVIER

CHAPTER

9

Australian mangroves through the Holocene: interactions between sea level, mangrove extent, and carbon sequestration

Neil Saintilan[1], *Jeff Kelleway*[2], *Kerrylee Rogers*[2]

[1]Department of Environmental Sciences, Macquarie University, NSW, Australia; [2]School of Earth, Atmospheric and Life Sciences, University of Wollongong, NSW, Australia

OUTLINE

1. Introduction 218
2. Early phases of the postglacial marine transgression: 13,000–9000 BP 219
3. Late phases of the postglacial marine transgression: 9000–6000 BP 221
4. Estuary infill in the mid-late Holocene 224
5. Contemporary patterns of mangrove–saltmarsh interaction 226
6. 21st century sea-level rise acceleration and the challenges of coastal planning 227
7. Conclusions 230
References 230

Dynamic Sedimentary Environments of Mangrove Coasts
https://doi.org/10.1016/B978-0-12-816437-2.00009-4

Copyright © 2021 Elsevier Inc. All rights reserved.

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au)

Copyright Elsevier Inc.

1. Introduction

The Australian continent supports one-third of the world's mangroves (Spalding, 2010). Lying close to the centers of mangrove biodiversity in Southeast (SE) Asia, species diversity in the tropical north is high, with up to 28 species recorded in a single estuary, the Daintree (16° 16′S; 145° 24′E). Diversity and extent decrease along latitudinal and aridity gradients, with sporadic representation in the estuaries of south-west Western Australia and sympatric association on the SE coast with increasingly diverse saltmarsh south to Corner Inlet in Victoria (38° 54′S; 146° 18′E). Rhizophoraceae extend into northern New South Wales (NSW) to a latitudinal limit of *Rhizophora stylosa* at South West Rocks Creek (30° 53′S; 153° 02′E: (Wilson and Saintilan, 2012). *Aegiceras corniculatum* extends south to Lake Merimbula (36.88°S, 149.90°E), though is not as common SE Australia as *Avicennia marina*. Mangroves are not found in Tasmania (Rogers and Krauss, 2018).

Australian mangroves are largely protected from development by state government policy and legislation (Rogers et al., 2016) in place in most jurisdictions for three decades or more, though early losses to industrial, agricultural, and transport development were locally significant (Harty, 2004). Since the 1970s, legislative and policy direction has been influenced by research identifying links between mangrove habitat and fisheries productivity, including mud crab across the tropical north (Manson et al., 2005), wild prawn fisheries in the Gulf of Carpentaria (Staples et al., 1986) and SE Queensland (Skilleter et al., 2005), and crustacean and fin fish in NSW (Saintilan, 2004). The nursery role of mangrove and saltmarsh and their significance in providing a nutritional subsidy to estuarine fish has been supported by studies of trophic ecology (Guest and Connolly, 2005; Mazumder et al., 2006; Saintilan and Mazumder, 2017). More recently, the carbon sequestration capacity of tidal wetlands (termed "blue carbon") has generated interest in ecosystem service provision by mangrove and saltmarsh, while opening up new avenues for restoration and management (Kelleway et al., 2017a).

Sea-level rise is now recognized as the most significant emerging threat to Australian mangroves. Projections of sea-level rises of up to 80 cm by 2100 have prompted studies exploring physiological and landscape-scale responses of mangroves to sea-level rise. Rates of sedimentation and vertical accretion in mangroves have been informed by Surface Elevation Tables (SETs) installed in SE Australia from the early 2000s. These have allowed an assessment of relationships between sedimentation, autocompaction, and surface elevation gain in mangroves across a range of geomorphological settings, including estuarine embayments in Victoria (Rogers et al., 2005), drowned river valleys and barrier estuaries in NSW (Rogers et al. 2006, 2014), and back-barrier marine and coastal terrigenous settings in SE Queensland (Lovelock et al., 2014). Australian data have also contributed to regional assessments of drivers of mangrove vertical accretion and surface elevation gain in relation to sea-level rise (Lovelock et al., 2015; Rogers et al., 2006).

Data on rates of vertical accretion derived from the SET network have been important in informing models of mangrove response to sea-level rise projected to 2100 under a range of IPCC scenarios. Rogers et al. (2012) developed a dynamic elevation model relating intertidal wetland extent in the Hunter estuary to high- and low-range IPCC sea-level scenarios, based on SET data for the estuary. The model demonstrated the opportunities for mangrove expansion under low rates of relative sea-level rise, as well as the likely severe reductions in extent

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier 2021

under the higher end of sea-level rise to 2100 projected by the IPCC. Similarly, Traill et al. (2011) used the Sea Level Affecting Marshes Model (SLAMM) to explore the fate of wetlands under IPCC B1 and A1 scenarios, finding extensive opportunities for landward mangrove expansion. SET data have also been incorporated into efforts seeking to compare and validate models (Oliver et al., 2012; Mogensen and Rogers, 2018), and this work is likely to be ongoing, given the need to understand and project the response of mangrove to anticipated sea level rise.

Dynamic elevation models that incorporate feedback between accretion, surface elevation adjustment, and sea-level rise are becoming an important coastal planning tool as they can more effectively project the response of mangrove to sea-level rise than simpler bath fill approaches (Rogers et al., 2012). However, projections concerning the fate of mangroves under the higher range of projected sea-level rise are constrained by our understanding of the upper limits of mangrove vertical accretion that can be sustained under the pressure of rapid sea-level rise. Over the previous century, the rate of sea-level rise in eastern Australia has accelerated from ~2.0 mm yr^{-1} (averaged from 1966 to 2009) to ~3.4 mm yr^{-1} (averaged from 1990 to 2009: White et al., 2014). In most Australian settings for which SET data are available, mangrove vertical accretion has been equivalent to local sea-level trends, though falling short of projected rates of change over the coming century (e.g., Rogers et al., 2012). Higher rates of vertical accretion in mangrove have been recorded across SE Asia (Lovelock et al., 2015), but the limited duration of the record (often <5 years) gives limited insight into whether these rates can be sustained over decades. With high-emission IPCC scenarios suggesting rates of sea-level rise climbing to 10 mm yr^{-1} by the end of the century, an understanding of mangrove responses to sustained higher rates of sea-level rise are required.

In this chapter we explore mangrove responses to sea level on the Australian continent since the last glacial maxima (~22,000 calibrated years BP, henceforth BP). This period incorporates phases of very rapid sea-level rise in which mangroves over vast areas were unable to survive. In other periods, mangroves were able to sustain their position in situ for centuries while rates of sea-level rise were substantially higher than those encountered by the contemporary SET record. We review these data with a view to determine upper thresholds of mangrove survival and the possible biological and sedimentological controls influencing these observations. In particular, the role of mangrove root system production in mediating the response to sea-level rise is discussed in the context of carbon sequestration and the potential of negative feedback on radiative forcing.

2. Early phases of the postglacial marine transgression: 13,000–9000 BP

Glacial low sea-level deposits (14,000–21,000 calibrated years BP) on the Queensland east coast continental shelf (~17° S; 146° E) show very little mangrove development, and Amaranthaceae/Chenopodiaceae has the highest representation in a 60,000-year pollen record (Moss et al., 2017). The prevalence of saltmarsh on a coastline now dominated by tropical mangrove forest may suggest that the cooler, drier climatic conditions of the last glacial favored saltmarsh development over mangrove. The declining sea level prior to 17,000 years BP may also have restricted the habitat available to mangrove, increasing the proportion of estuarine habitat in the upper intertidal favored by saltmarsh (Fig. 9.1).

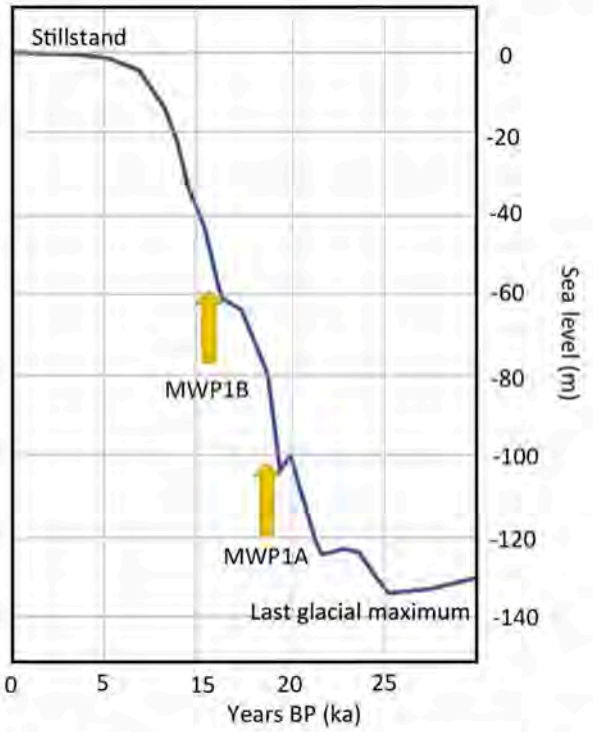


FIGURE 9.1 Postglacial eustatic sea-level reconstruction, indicating the timing of meltwater pulses 1A (MWP1A) and meltwater pulse 1B (MWP1B). *After Lambeck, K., Rouby, H., Purcell, A., Sun, Y., Sambridge, M., 2014. sea Level and global ice volumes from the last glacial maximum to the Holocene. Proc. Natl. Acad. Sci. U.S.A., 111 (43), 15296–15303.*

Following the end of the glacial maxima, mangroves began to expand with transgressing sea levels. Late Pleistocene mangrove sediments are preserved across large areas of the Timor Sea (Sahul Shelf) adjacent to the cost of North West Australia, dating to ~15,000–16,000 BP (Nicholas et al., 2014). Sea-level rise associated with the transition from glacial to interglacial conditions was nonlinear, punctuated with periods of rapid sea-level rise associated with ice-sheet failure. The first of these, meltwater pulse 1A (MWP1A), started no earlier than 14,650 BP and ended before 14,310 BP, rising most probably 14–18 m, a rate of 40 mm yr^{-1} on average, though this rate was probably temporally variable, with associated pulses of higher rates. This effectively drowned all mangroves in situ on the continental shelf. The paleochannels and floodplains associated with this early transgressive "big swamp" phase are largely preserved, the very rapid sea-level rise leaving their morphology in place (Fig. 9.2).

The flooding of the Queensland coastline during this early, rapid phase of marine transgression led ultimately to a sharp increase in the representation of mangrove pollen delivered to the shelf (Moss et al., 2017), particularly *Rhizophora* and *Ceriops/Bruguiera*, as these retreated into former Cyperaceae (freshwater) swamps. There is no evidence of rainfall having increased at this stage, and saltmarsh is still well represented to 13,000 BP.

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier 2018

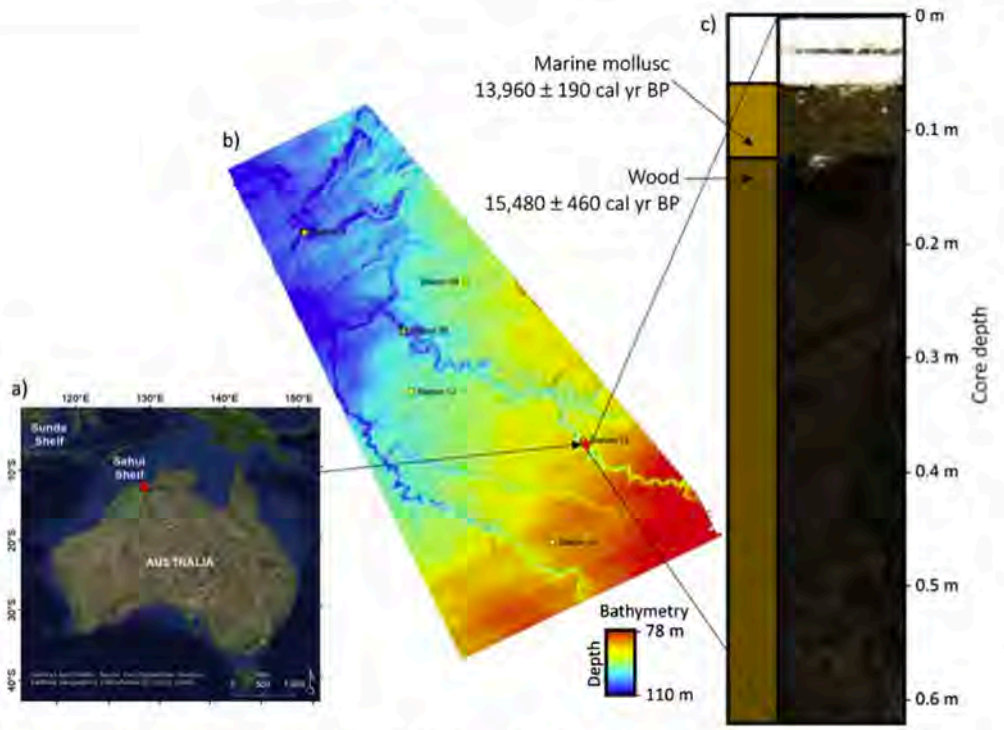


FIGURE 9.2 Abandoned estuarine habitats on the (A) Sahul Shelf, NW Australia, following marine transgression (B) now at bathymetric depths of 78–110 m, and (C) associated late-Pleistocene mangrove peats. *Adapted from Nicholas, W.A., Nichol, S.L., Howard, F.J.F., Picard, K., Dulfer, H., Radke, L.C., et al., 2014. Pockmark development in the Petrel sub-basin, Timor Sea, northern Australia: seabed habitat mapping in support of CO2 storage assessments. Continent. Shelf Res., 83, 129–142.*

The Arafura Sill was breached ~12,000 BP with full marine conditions attained in the former Lake Carpentaria 10,500 yr BP (Harris et al., 2008), and mangrove pollen dating to this time has been identified from cores extracted from the current Gulf of Carpentaria (Chivas et al., 2001). Sea level in the Gulf of Carpentaria coast reached current position around 8000 yr BP though continued to rise and may have reached a maxima of up to 2 m above current sea levels by 7400 BP, though there is regional variability and conflicting evidence regarding this highstand (Lewis et al., 2013). The stabilization of sea levels mid-Holocene set the scene for the development of the most extensive mangrove forests of the Holocene.

3. Late phases of the postglacial marine transgression: 9000–6000 BP

Holocene mangrove peat deposits have been dated to occur in many tropical localities between 10,000 and 7800 BP and their extent is pantropical (Saintilan et al., 2020). Radiocarbon basal dates from this period have been returned from thick mangrove organic soils far separated as the Ivory Coast of Africa (Tossou et al., 2008), Zanzibar (Punwong et al., 2018), the

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier 2022

Ganges delta (Hait and Behling, 2009), the Mekong delta (Tamura et al., 2009), Makassar Strait (Yulianto et al., 2004; Papua Ellison 2005), Belize (Monacci et al., 2011), and the delta of the Amazon (Cohen et al., 2012). The timing of the commencement of mangrove organic soil-building across the tropics corresponds to the slowing of sea-level rise at the concluding stages of the marine transgression. Mangroves had not been locally extirpated during rapid phases of Relative Sea Level Rise (RSLR), given their widespread expansion as sea levels stabilized. During very rapid rates of rise, mangroves can translate landwards by recruiting at high elevations in the intertidal and maintain their higher position with respect to sea level over sufficient time to grow to sexual maturity and deliver propagules to the new higher position of the tidal frame, before being drowned. Accordingly, there is, under this model, a successive role over of the next generation of mangrove to higher elevation.

By the time sea-level rise decelerated from 10 to 20 mm yr^{-1} to 5–7 mm yr^{-1}, mangroves were able to sustain their position in relation to mean sea level by increasing surface elevation in situ. Pollen from the genera *Rhizophora* and *Sonneratia* are particularly prevalent in transgressive sequences. Mangrove in situ adjustment was achieved by the trapping of sediment and the building of root mass, which, even in the absence of terrigenous input, can sustain mangrove elevation gain of up to 5 mm yr^{1} over centuries (McKee et al., 2007; Saintilan et al., 2020) on coral reefs in which mangroves grow thick peats subsidized by inputs of calcareous sediments. Decelerating sea-level rise occurred in most tropical localities circa 9000–8000 calibrated years BP, and extensive pantropical mangrove forest development coincides with this time, as the rate of sea-level rise declined below 7 mm yr^{-1} (Saintilan et al., 2020). In tropical northern Australia, black soil plains are drained by macrotidal rivers, flooded seasonally during the monsoon season (Woodroffe et al., 1989). Beneath the black soil plains lie extensive mangrove sediments several meters thick. These have been located in King Sound, the Fitzroy River (Jennings, 1975), the Ord River (Thom et al., 1975), and the Daly and Alligator Rivers (Woodroffe et al., 1985). Basal deposits date from ~8100 BP in the Mary River, Northern Territory (Woodroffe, 2018), 8000–7500 BP in the South Alligator River, Northern Territory (Woodroffe et al., 1987), 7500–8000 BP in the Fitzroy River (Jennings, 1975), and 7500 BP in the Ord River, Western Australia (Thom et al., 1975).

By 5000 yr BP these extensive mangrove forests had largely disappeared and the wide upper intertidal and supratidal flats were bare in lower rainfall areas or occupied by sparse grasses, sedges, and, in wetter areas, *Melaleuca* forest (Woodroffe et al., 1989). Mangroves are currently confined to active depositional environments, including channel banks, the edges of mid-channel islands, and prograding coastlines (Woodroffe et al., 1985). Jennings (1975) suggested rainfall as an explanation of the rise and fall of the great early-Holocene mangrove forests, with the Holocene climate optimum associated with higher rainfall across the region. Certainly, the proportion of mangrove and saltmarsh/hypersaline flats in northern Australian estuaries is associated with rainfall; more arid estuaries have lower proportional mangrove cover compared to humid estuaries (Bucher and Saenger, 1991). However, the confinement of mangroves to fringing environments is more likely to be related to geomorphological evolution of the estuaries through the Holocene, as proposed by Woodroffe et al. (1985). With the stabilization of sea level shortly after 8000 yr BP, sedimentation continued and led to the progressive shrinkage of accommodation space, the vertical space into which

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier 2021

mangroves can accrete in the intertidal. As estuaries infilled, the intertidal zone was replaced by supratidal flats inundated by seasonal monsoons and cyclonic storm surges. In dryer areas, mangroves gave way to hypersaline flats, while in wetter areas, upper intertidal and supratidal environments were colonized by salt-tolerant grasses and sedges.

On the east coast of tropical Queensland, extensive mangrove sediments dating to ~8000 yr BP have been found in Missionary Bay and Princess Charlotte Bay (Grindrod 1985, 1988), on the Mulgrave River near Innisfail (17° S; 146° E; Crowley et al., 1990), and in the nearby Russell River (Crowley and Gagan, 1995). These forests show a remarkable rate of vertical accretion (approximately 5–6 mm yr^{-1}) sustained for 800–900 years between 7900 and 7000 years BP. These forests were dominated by *Rhizophora*, though there is a noticeable shift to *Ceriops* and *Bruguiera* toward the end of the big swamp phase, indicating a transition toward conditions higher in the tidal frame prior to their replacement by terrestrial and freshwater swamp vegetation by the mid-Holocene.

The southernmost early-Holocene mangrove "big swamp" is situated several kilometers upstream of the current intertidal wetlands on the Richmond River, Northern NSW (29°S; 150.5°E: Hashimoto et al., 2006, Fig. 9.2). These organic silts extend to 3 m depth beneath the current floodplain, which is now used for agriculture. Between ~7800 and 7000 BP, the mangroves sustained a rate of in situ elevation gain of ~3 mm yr^{-1}, before being replaced by supratidal forests of *Casuarina* and *Melaleuca*. Pollen analysis suggests that the mangrove was dominated by Rhizophoraceae (*Rhizophora* and *Bruguiera*) in spite of the rarity of this family on the Richmond River today. Only a few individuals of either species can be found at the mouth of the estuary, among mangrove forests dominated by *Avicennia marina* and *Aegiceras corniculatum*.

It is interesting to speculate why the mid-Holocene mangrove assemblage on the Richmond River was dominated by Rhizophoraceae. Deep mangrove sediments across the globe are almost always associated with *Rhizophora*, suggesting that this genus may have significant capacity to increase elevation in situ and thereby dominate large transgressive forests under conditions of high relative sea-level rise. However, *Rhizophora* is a more prolific pollen producer than *Avicennia* (Crowley et al., 1994), and *Avicennia* pollen is not noted for its preservation, as wet–dry cycles in the upper intertidal can lead to oxidation and humic acids promote degradation, which may partly explain the rarity of *Avicennia* representation in transgressive mangrove facies. Temperatures may have been higher in the region during 8200–8000 BP, a time known as the "Holocene climatic optimum," facilitating the expansion of two species nearing their poleward limit. There is evidence of range expansion and strong population growth of *R. stylosa* over the past few decades in the northern rivers of NSW (Wilson, 2009) associated with higher temperatures.

In spite of extensive stratigraphic investigations across the temperate estuaries of SE Australia, no transgressive mangrove deposits have been discovered. Forests of *Avicennia marina* are well developed in tidal estuaries throughout NSW and Victoria, but estuarine facies dating to 7000–8000 BP are primarily subtidal (e.g., Umitsu et al., 2001), in common with the North Island of New Zealand (Woods, 2012). Several possibilities exist, including a late-Holocene expansion in the population of *Avicennia*, the presence of *Avicennia* though limited pollen and/or organic preservation, or a limited capacity of *Avicennia* to sustain position in situ under long-term transgressive phases.

4. Estuary infill in the mid-late Holocene

Sea-level stabilization has facilitated the infill of estuaries and recession of mangroves toward the present coastline. The extent to which this has occurred is a function of sediment yield, the size of the estuary accommodation space, and the retention of sediment within the estuary. In the relatively small catchments east of the Great Dividing Range, sediment yield varies in relation to catchment size and the resistance of soils to erosion and catchment geology to weathering. In catchments with low sediment yield, estuaries may still be in an "immature" phase of sediment infill to the present day (Roy et al., 2001), while others may be infilled, channelized to the mouth, and delivering sediment to the nearshore. Compared to the estuaries of West Coast USA, east coast Australian estuaries are skewed toward the immature stage of development, though estuaries with larger catchments are more likely to have evolved to maturity (Saintilan et al., 2016). Most estuaries have a predominance of open water habitat compared to lower intertidal unvegetated and upper intertidal vegetated habitat, which is a function of low sediment yield. In these estuaries, mangrove and saltmarsh is less represented, and extensive seagrass beds occur in shallow estuarine waters (Saintilan, 2004). Where estuary entrances close periodically, mangrove may be excluded. Mangroves are best represented in estuaries of intermediate to mature stages of infill and with open entrances (Saintilan, 2004).

The extent of mangrove development in mature estuaries is also a function of the relative importance of tides, river flow, and ocean waves in the formation of the estuary entrance conditions. In macrotidal estuaries, strong tidal currents create wide funnel-shaped estuarine mouths supporting extensive intertidal environments. In the high-wave energy coastlines characteristic of the southern half of the continent, sand barriers often restrict tidal exchange and truncate the development of flood-tidal estuarine deposits that create suitable conditions for intertidal vegetation, and where river flows are small, entrances may periodically close. As outlined above, the channelization of estuaries and gradual reduction in accommodation space has occurred to varying degrees.

These patterns of estuarine infill explain the historic and current development of mangroves. As suggested in Fig. 9.3, the progradational phase of estuary development leaves behind mangrove organic facies dating from the mid- to late Holocene, overlain by fluvial deltaic silts. Working in the middle reaches of the Hawkesbury River estuary in NSW (Fig. 9.4), Saintilan and Hashimoto (1999) found mangrove organic sediments 20–30 cm beneath the present-day wetland surface dating to 1200–1700 yr BP. These are approximately at the same elevation as contemporary mangrove root systems, implying that sea levels had stabilized by this time. The contemporary saltmarsh consisted of an assemblage of *Sporobolus virginicus*, *Juncus kraussii*, and *Casuarina glauca*. The stratigraphy suggests that infill has led to the gradual replacement of mangrove with saltmarsh as the river prograded within the sandstone bedrock valley (Saintilan, 1997). Further south, a similar pattern of mangrove replacement by saltmarsh over the late Holocene was identified for Currambene Creek and Cararma Inlet, small tributary creeks draining into Jervis Bay (Saintilan and Wilton, 2001). Within Currambene Creek, mangrove sediments dated to 1300 yr BP, while those in Carama Inlet dated to 1900 yr BP. Both were overlying subtidal sands. A similar scenario has also been observed further north in the drowned river valley of Port Stephens, where mangrove sediments below

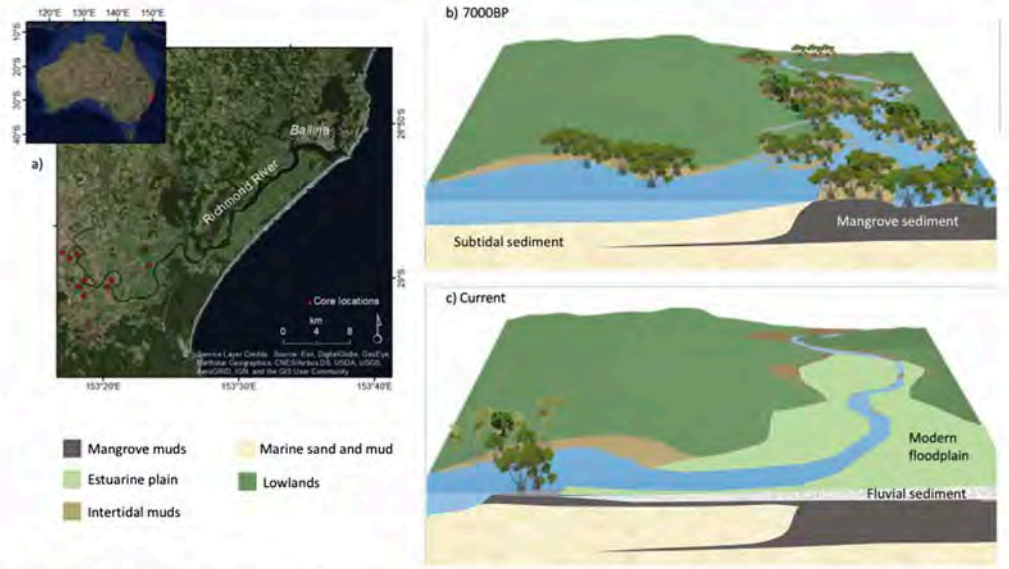


FIGURE 9.3 Widespread Rhizophoraceae mangrove cover identified on the (A) Richmond River at (B) ~7000 yr BP before (C) estuarine infill limited mangrove cover to the intertidal zone near the mouth of the estuary.

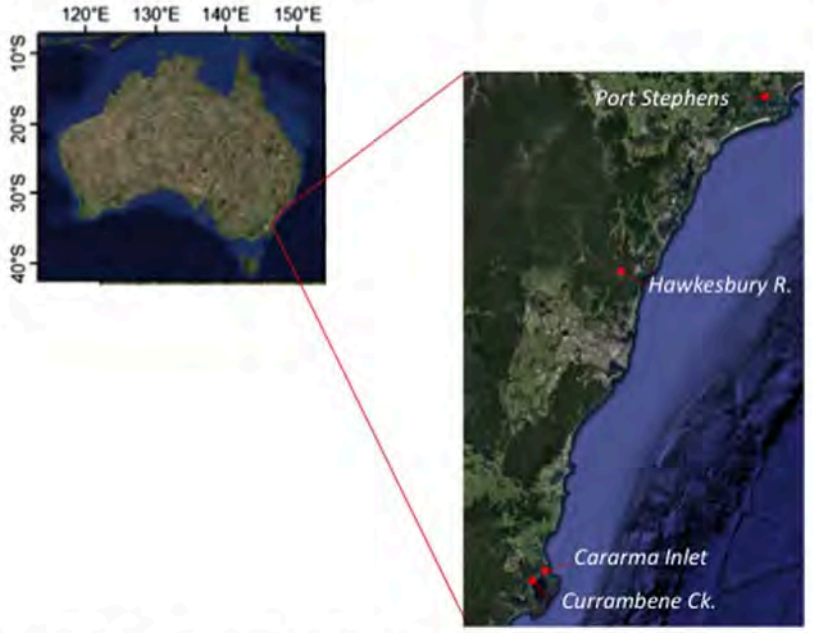


FIGURE 9.4 Location of SE Australian estuaries with mid- to late-Holocene mangrove facies overlain by saltmarsh.

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier 2024

saltmarsh were dated to 1800–1500 yr BP in a marine delta setting and 800 yr BP in a tidal creek network (Kelleway et al., 2017b).

5. Contemporary patterns of mangrove–saltmarsh interaction

Analyses of changes in mangrove and saltmarsh distribution over observational timescales indicate that a range of hydrological processes influence interactions between mangrove and saltmarsh, including changes associated with eustatic sea-level rise and sea-level change driven by climatic variability. Comparison of current mangrove distribution with earliest aerial photography (dating to the 1940s in some locations) has demonstrated widespread landward expansion of mangroves in most settings across the continent. Tidal creek expansion and landward mangrove expansion has been a notable feature on the estuarine plains of northern Australia (Winn et al., 2006; Knighton et al., 1991; Mulrennan and Woodroffe, 1998), spreading mangroves into upper intertidal environments previously free of mangrove since the mid-Holocene. On the East Alligator River, 64% of the *Melaleuca* forests had been lost by 2000 and 17,000 ha lost from the Mary River (Mulrennan and Woodroffe, 1998; Winn et al., 2006). These expansions coincided with sea-level fluctuations with a predominant rise (8–10 mm yr^{-1} 1990–2010: White et al., 2014; Asbridge and Lucas, 2016). Introduced buffalo and their effect on runnelling and tidal barrages may also be contributing to tidal reactivation (Knighton et al., 1991).

Expansion of mangrove across the tropical North occurred in association with relative sea-level rise enhanced by decadal-scale climate variability. The failure of monsoons in the summer of 2015/2016 led to a coincidence of lower relative sea level and lower rainfall, increasing salinity particularly in landward, recently colonized mangrove. The defoliation and dieback of mangrove observed in relation to this event affected an estimated 6% of mangroves in the Gulf of Carpentaria (Duke et al., 2017) and extended into Kakadu (Lucas et al., 2018) and NW Western Australia (Lovelock et al., 2017). Most affected were the landward forests (often dominated by *Avicennia marina*) many of which recruited over the past three decades (Asbridge et al., 2016). Recent estimates suggest that the extent of mangroves post-defoliation/dieback was still greater than a previous minimum (in 1991) because of the longer-term pattern of landward encroachment post 1991 and ongoing seaward expansion in some areas associated with estuary infill and sediment redistributions in a dynamic environment. Phases of contraction and subsequent expansion in extent and canopy cover have occurred previously (Lovelock et al., 2017). Based on 27-year time series (1987–2014) of mangrove dynamics and projected changes in inundation with sea-level rise to 2100, continued expansion of mangrove onto the broad lowland floodplains of northern Australia is probable, continuing the decline of freshwater wetland in the region (Asbridge et al., 2016).

The expansion of mangroves into the saltmarshes of SE Australia has been well-documented (Saintilan and Williams, 1999) and coincides with a pattern of mangrove proliferation at mangrove poleward limits across several continents (Saintilan et al., 2014). Estuarine foreshores have seen a transition from saltmarsh to mangrove dominance, as evidenced by early photography, historical drawings, and ground surveys (see Fig. 9.5 for one example). Saltmarsh loss has been documented in the range of geomorphological settings

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier 2021

FIGURE 9.5 The shoreline of the Cooks River, Sydney, at Tempe, mid-1940s (A) and 2020 (B). Note the occupation of *Avicennia marina* in previously saltmarsh foreshore vegetation.

occupied by subtropical and temperate mangroves in Australia, including back-barrier embayments in southern Queensland, large coastal rivers and drowned river valleys in northern and central NSW, smaller barrier estuaries on the NSW south coast, marine embayments of the Victorian Bass Strait coast, and the inverse estuaries of South Australia (reviewed in Saintilan et al., 2019).

In the estuaries of SE Australia, mangroves are delimited in their landward extent by desiccation of propagules (Clarke and Allaway, 1993; Saintilan, 2003). The landward encroachment of mangrove may therefore be attributed to changes to inundation frequency and water availability in the upper intertidal zone. It is difficult to disentangle the possible effects of rainfall and sea-level trends in driving these changes given their close correlation (Rogers et al., 2014a,b). In tropical and subtropical climates, the proportion of mangrove and saltmarsh in estuaries is correlated to annual rainfall (Bucher and Saenger, 1991; Duke et al., 2019). Where saltmarsh occurs, it often occupies a position in the tidal frame between seaward and landward mangrove zones. Increased rainfall in recent decades has been used to explain the encroachment of tall mangrove forest into saltpan in Hinchinbrook Channel (Duke, 1995). However, the correlation between rainfall and the proportion of mangrove and saltmarsh is not found in NSW (Saintilan, 2003), where the upslope limit of mangrove is more consistently related to frequency of tidal inundation, and there is no landward mangrove fringe. Saltmarsh in most settings has shown little increase in elevation in spite of sea-level rise of ~3.2 mm yr^{-1} over the 20-year measurement period of the SE Australian SETs network (Rogers et al., 2006, 2014), suggesting a vulnerability to encroachment. Saltmarsh survival is therefore contingent on opportunities for lateral expansion.

6. 21st century sea-level rise acceleration and the challenges of coastal planning

Global eustatic sea-level rise has accelerated through the past century, increasing from an average rise of 2.0 ± 0.3 mm yr^{-1} in the period 1966–2009 to 3.4 ± 0.4 mm yr^{-1} in the period 1990–2009 (White et al., 2014). This rate is likely to double by 2100 (Nerem et al., 2018). Based upon the SET and stratigraphic record, sea-level rise acceleration will have profound impacts on the distribution, structure, and carbon burial capacity of Australia's tidal wetlands.

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier 2021

The configuration of coastal lowlands is different today from that encountered by mangroves in the early Holocene. Nearly 7000 years of sea-level stability meant coastal valleys infilled and broad deltas could develop. Substrate compaction over time has provided a relatively stable platform for mangrove colonization, where permitted. Even in the most heavily developed of estuaries, such as the Cooks River in Sydney, opportunities for mangrove colonization under sea-level rise exist where there is a willingness to allow parkland to convert to coastal wetland (Rogers et al., 2019b). Modeling of coastal wetland responses to sea-level rise in the Hunter Estuary NSW has suggested a 20% increase in extent by 2100 under low sea-level rise scenario and 56% under a high sea-level rise scenario, if floodgates are opened (Rogers et al., 2014b). Factoring in both vertical elevation gain and lateral expansion Rogers et al. (2014a,b) estimated 775,000 tonnes of additional carbon burial by 2100. In other settings, such as the deeply incised Triassic sandstone drowned river valleys (for example, the Hawkesbury River and Clyde River in NSW), mangrove lateral expansion will be restricted by topographic impediments.

The expansion of mangrove into saltmarsh has been shown to increase soil carbon in the region. Unlike Gulf of Mexico settings where studies show an increase in soil carbon only in arid zone settings (Yando et al., 2016), mangrove root development in encroachment zones can exceed 600 Mg ha^{-1} (Lamont et al., 2020), among the highest ever recorded. Radiometric dating of a recently encroached wetland in the Sydney region shows an increase in the surface accumulation rate from <3 mm yr^{-1} during the prior saltmarsh phase, increasing up to 5–6 mm yr^{-1} during peak surface soil development by encroaching *Avicennia marina* (Fig. 9.6) in a time of relative sea-level rise. *Avicennia* is capable of keeping pace with current rates of sea-level rise (Rogers et al., 2013, 2014a), doing so partly through the accumulation of root mass (Rogers et al., 2019b).

There is an emerging understanding of the links between sea-level rise and blue carbon at local through to global spatial scales (Rogers et al., 2019a). As sea-level rise accelerates, it increases the vertical and horizontal accommodation space in which carbon-rich mangrove sediments can accumulate. For Australia, like much of the southern hemisphere which has experienced relatively stable sea level over recent millennia, an acceleration in sea-level rise is likely to shift tidal wetlands toward greater proportion of organic material within substrates as accommodation space infills, as seen in the North Atlantic (Rogers et al., 2019a,b) and observed already in Australian encroachment settings (Kelleway et al., 2016). This model of increasing organic carbon accumulation as relative sea-level rise increases available accommodation space has been confirmed at an intertidal wetland where rapid relative sea-level rise was imposed by collapse of an underlying coal mine that resulted in wetland subsidence (Rogers et al., 2019a).

The capacity of mangroves to build elevation while enhancing carbon burial under sea-level rise presents an opportunity to leverage the carbon sequestration benefits of tidal wetlands, while also promoting adaptation. As mangroves also buffer wave energy, bind sediments, and store floodwater, they are able to provide the dual benefits of climate mitigation through carbon sequestration and coastal adaptation to sea-level rise. Management interventions which (1) support the retention of mangrove carbon stocks and accumulation capacity in situ; (2) support the migration and development of new mangrove forests that would not otherwise occur (e.g., due to land use constraints or building of barriers), or (3) support biochemical changes avoiding greenhouse gas emission might be eligible to generate credits

This book belongs to Neil Saintilan (neilsaintilan@mac.com)

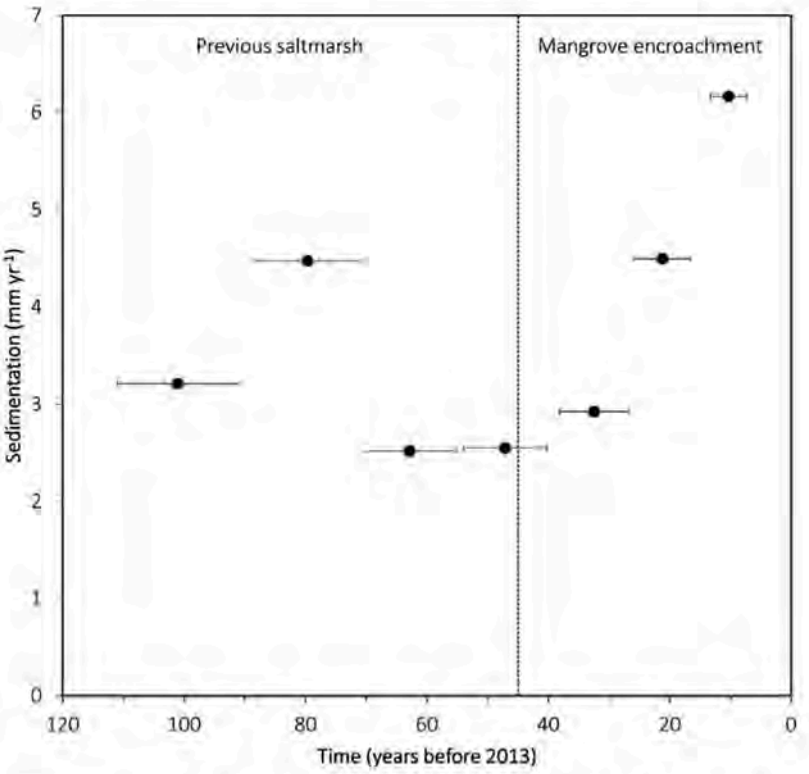


FIGURE 9.6 Sedimentation rate derived from ^{210}Pb dating of sediments that had accumulated in an intertidal wetland following mangrove encroachment of a previous saltmarsh in the Sydney region. Sedimentation rate accelerated after mangrove encroachment (onset indicated by dashed line) driven largely by root production (see Kelleway et al., 2016 for carbon data), reflecting a feedback between vertical accretion and increasing accommodation space that occurred synchronously with mangrove encroachment. The high sedimentation rate during the saltmarsh phase (at ~80 years) coincides with a period of catchment modification Kelleway et al. (2016).

under carbon mitigation schemes (e.g., Kelleway et al., 2017a). An additional benefit of tidal reinstatement in previously isolated wetlands is the effect of saline water in reducing methane gas emissions (Kroeger et al., 2017), though the extent to which these benefits are realized will depend on local groundwater and climatic conditions (Negandhi et al., 2019).

While the opportunities for market incentives in mangrove conservation and planning are exciting, the potential of carbon credits should be seen as one of the many reasons to conserve these important ecosystems, given their demonstrated importance for fisheries productivity, shoreline protection, and habitat provision (Kelleway et al., 2017a). However, current conservation mechanisms largely rely on fixed boundaries, either as habitat maps under State government planning policies or within the boundaries of protected areas. The speed with which climate change is altering the distribution of wetlands poses a challenge to planning instruments, and calls for the introduction of ambulatory boundaries, wider buffers, and other flexible planning provisions have been made (Rogers et al., 2016).

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier 2021

7. Conclusions

The extent of mangrove development within Australian estuaries has been strongly associated with sea-level trends since the last glacial maxima. Phases of rapid sea-level rise (>20 mm yr ^{1}) during at least two meltwater pulses were sufficient not only to drown mangroves over extensive areas but also to create opportunities for mangrove colonization of coastal lowlands newly exposed to the tide. As the rate of sea-level rise decelerated to below 5–7 mm yr^{-1}, mangrove forests dominated by Rhizophoraceae were able to keep pace with sea-level rise over millennial timescales and extensive mangrove forests formed across the tropical north, particularly in the period 8000–6000 BP.

There is growing consensus that biological processes in mangrove forests play a significant role in maintaining mangrove elevation in relation to sea-level rise (Krauss et al., 2014). Mangrove aerial roots promote the deposition of sediment to varying degrees depending on root architecture (Krauss et al., 2003). Fine mangrove roots on the surface of the forest assist in the binding and retention of sediment within the forest (McKee, 2011). Litterfall may contribute to the soil volume (Sukardjo et al., 2013), though this contribution is minor compared with the growth of root material. In Caribbean carbonate settings deprived of terrigenous input, mangrove root development has been sufficient to keep pace with sea-level rise of 3–5 mm yr^{-1} over several centuries (McKee et al., 2007).

The refractory nature of mangrove roots and the anaerobic, saline soil conditions of the mangrove provide an excellent environment for root preservation over extended time periods. These properties have not only facilitated their use in paleostratigraphic investigations but also promoted their value as "blue carbon" ecosystems. Their contribution to carbon sequestration and burial is likely to increase as sea levels rise (Kirwan et al., 2016; Rogers et al., 2019a,b), given the positive feedback between the rate of sea-level rise and carbon burial. An examination of accretion associated with the postglacial marine transgression would suggest that an upper threshold of mangrove vertical accretion might occur at ~5 mm yr^{-1} in carbonate settings (McKee et al., 2007) and 6–7 mm yr^{-1} in terrigenous settings (Crowley and Gagan, 1995). If this rate is exceeded, mangroves will seek to survive by retreating into new intertidal areas, as occurred following MWP1A and MWP1C. Their ability to do so will be subject to local planning decisions (Rogers et al., 2016).

References

Asbridge, E., Lucas, R., Ticehurst, C., Bunting, P., 2016. Mangrove response to environmental change in Australia's Gulf of Carpentaria. Ecol. Evol. 6 (11), 3523–3539.

Asbridge, E., Lucas, R., 2016. Mangrove response to environmental change in Kakadu National Park. IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens. 9 (12), 5612–5620.

Bucher, D., Saenger, P., 1991. An inventory of Australian estuaries and enclosed marine waters: an overview of results. Aust. Geogr Stud. 29, 370–381.

Chivas, A.R., Garcıa, A., van der Kaars, S., Couapel, M.J., Holt, S., Reeves, J.M., Wheeler, D.J., Switzer, A.D., Murray-Wallace, C.V., Banerjee, D., Price, D.M., Wang, S.W., Pearson, G., Edgar, N.T., Beaufort, L., De Deckker, P., Lawson, E., Cecil, C.B., 2001. Sea-level and environmental changes since the last interglacial in the Gulf of Carpentaria, Australia: an overview. Quat. Int. 83, 19–46.

Clarke, P.J., Allaway, W., 1993. The regeneration niche of the grey mangrove *Avicennia marina* – effects of salinity, light and sediment factors on establishment, growth and survival in the field. Oecologia 93, 548–556.

This book belongs to Neil Saintilan (neil.saintilan@mq.edu.au) Copyright Elsevier Inc.

Cohen, M.C.L., Pessenda, L.C.R., Behling, H., de Fátima Rossetti, D., França, M.C., Guimarães, J.T.F., et al., 2012. Holocene palaeoenvironmental history of the Amazonian mangrove belt. Quat. Sci. Rev. 55, 50–58.
Crowley, G.M., Gagan, M.K., 1995. Holocene evolution of coastal wetlands in wet-tropical northeastern Australia. Holocene 5 (4), 385–399.
Crowley, G.M., Grindrod, J., Kershaw, A.P., 1994. Modern pollen deposition in the tropical lowlands of northeast Queensland, Australia. Rev. Palaeobot. Palynol. 83, 299–327.
Crowley, G.M., Anderson, P., Kershaw, A.P., Grindrod, J., 1990. Palynology of a Holocene marine transgressive sequence, lower Mulgrave River valley, north-east Queensland. Aust. J. Ecol. 15 (2), 231–240.
Duke, N.C., 1995. Genetic diversity, distributional barriers and rafting continents – more thoughts on the evolution of mangroves. Hydrobiologia 295, 167–181.
Duke, N.C., Field, C., Mackenzie, J.R., Meynecke, J.O., Wood, A.L., 2019. Rainfall and its possible hysteresis effect on the proportional cover of tropical tidal-wetland mangroves and saltmarsh–saltpans. Mar. Freshw. Res. 70 (8), 1047–1055.
Duke, N.C., Kovacs, J.M., Griffiths, A.D., Preece, L., Hill, D.J., Van Oosterzee, P., et al., 2017. Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. Mar. Freshw. Res. 68 (10), 1816–1829.
Ellison, J., 2005. Holocene palynology and sea-level change in two estuaries in Southern Irian Jaya. Palaeogeogr. Palaeoclimatol. Palaeoecol. 220 (3–4), 291–309.
Grindrod, J., 1985. The palynology of mangroves on a prograded shore, Princess Charlotte Bay, North Queensland, Australia. J. Biogeogr. 323–348.
Grindrod, J., 1988. The palynology of Holocene mangrove and saltmarsh sediments, particularly in northern Australia. Rev. Palaeobot. Palynol. 55 (1–3), 229–245.
Guest, M.A., Connolly, R.M., 2005. Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. Aquat. Ecol. 38 (4), 599–609.
Hait, A.K., Behling, H., 2009. Holocene mangrove and coastal environmental changes in the western Ganga–Brahmaputra Delta, India. Veg. Hist. Archaeobotany 18 (2), 159–169.
Hashimoto, T.R., Saintilan, N., Haberle, S.G., 2006. Mid-holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond River estuary, New South Wales, Australia. Geogr. Res. 44 (1), 63–76.
Harris, P.T., Heap, A.D., Marshall, J.F., McCulloch, M., 2008. A new coral reef province in the Gulf of Carpentaria, Australia: colonisation, growth and submergence during the early Holocene. Mar. Geol. 251 (1–2), 85–97.
Harty, C., 2004. Planning strategies for mangrove and saltmarsh changes in Southeast Australia. Coast. Manag. 32 (4), 405–415.
Jennings, J.N., 1975. Desert dunes and estuarine fill in the Fitzroy estuary, north-western Australia. Catena 2, 215–262.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Skilbeck, C.G., Zawadzki, A., Ralph, P.J., 2016. Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. Global Change Biol. 22 (3), 1097–1109.
Kelleway, J.J., Serrano, O., Baldock, J., Cannard, T., Lavery, P., Lovelock, C.E., Macreadie, P., Masqué, P., Saintilan, N., Steven, A.D., 2017a. Technical Review of Opportunities for Including Blue Carbon in the Australian Government's Emissions Reduction Fund. ACT: CSIRO, Canberra.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Baldock, J.A., Heijnis, H., Zawadzki, A., Gadd, P., Jacobsen, G., Ralph, P.J., 2017b. Geochemical analyses reveal the importance of environmental history for blue carbon sequestration. J. Geophys. Res. Biogeosci. 122 (7), 1789–1805.
Kirwan, M.L., Temmerman, S., Skeehan, E.E., Guntenspergen, G.R., Fagherazzi, S., 2016. Overestimation of marsh vulnerability to sea level rise. Nat. Clim. Change 6 (3), 253.
Knighton, A.D., Mills, K., Woodroffe, C.D., 1991. Tidal-creek extension and saltwater intrusion in Northern Australia. Geology 19, 831–834.
Krauss, K.W., Allen, J.A., Cahoon, D.R., 2003. Differential rates of vertical accretion and elevation change among aerial root types in Micronesian mangrove forests. Estuar. Coast Shelf Sci. 56 (2), 251–259.
Krauss, K.W., McKee, K.L., Lovelock, C.E., Cahoon, D.R., Saintilan, N., Reef, R., Chen, L., 2014. How mangrove forests adjust to rising sea level. New Phytol. 202 (1), 19–34.

Kroeger, K.D., Crooks, S., Moseman-Valtierra, S., Tang, J., 2017. Restoring tides to reduce methane emission in impounded wetlands: A new and potent Blue Carbon climate change intervention. Sci. Rep. 7 (1), 1–12.
Lambeck, K., Rouby, H., Purcell, A., Sun, Y., Sambridge, M., 2014. sea Level and global ice volumes from the last glacial maximum to the Holocene. Proc. Natl. Acad. Sci. U.S.A. 111 (43), 15296–15303.
Lamont, K., Saintilan, N., Kelleway, J.J., Mazumder, D., Zawadzki, A., 2020. Thirty-year measures of mangrove above- and below-ground biomass reveals unexpectedly high carbon sequestration. Ecosystems 23 (2), 370–382 (in press).
Lewis, S.E., Sloss, C.R., Murray-Wallace, C.V., Woodroffe, C.D., Smithers, S.G., 2013. Post-glacial sea-level changes around the Australian margin: a review. Quat. Sci. Rev. 74, 115–138.
Lovelock, C.E., Adame, M.F., Bennion, V., Hayes, M., O'Mara, J., Reef, R., Santini, N.S., 2014. Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of South East Queensland, Australia. Estuar. Coast 37 (3), 763–771.
Lovelock, C.E., Cahoon, D.R., Friess, D.A., Guntenspergen, G.R., Krauss, K.W., Reef, R., et al., 2015. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. Nature 526 (7574), 559.
Lovelock, C.E., Feller, I.C., Reef, R., Hickey, S., Ball, M.C., 2017. Mangrove dieback during fluctuating sea levels. Sci. Rep. 7 (1), 1680.
Lucas, R., Finlayson, C.M., Bartolo, R., Mitchell, A., Woodfroffe, C.D., Asbridge, E., Ens, E., 2018. Historical perspectives on the mangroves of Kakadu National Park. Mar. Freshw. Res. 69 (7), 1047–1063.
Manson, F.J., Loneragan, N.R., Harch, B.D., Skilleter, G.A., Williams, L., 2005. A broad-scale analysis of links between coastal fisheries production and mangrove extent: a case-study for northeastern Australia. Fish. Res. 74 (1–3), 69–85.
Mazumder, D., Saintilan, N., Williams, R.J., 2006. Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. Mar. Freshw. Res. 57 (2), 193–199.
McKee, K.L., 2011. Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. Estuar. Coast Shelf Sci. 91 (4), 475–483.
McKee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on soil elevation change. Global Ecol. Biogeogr. 16, 545–556.
Mogensen, L.A, Rogers, K, 2018. Validation and comparison of a model of the effect of sea-level rise on coastal wetlands. Sci. Rep. 8 (1), 1–14.
Monacci, N.M., Meier-Grünhagen, U., Finney, B.P., Behling, H., Wooller, M.J., 2011. Paleoecology of mangroves along the Sibun river, Belize. Quat. Res. 76 (2), 220–228.
Moss, P.T., Dunbar, G.B., Thomas, Z., Turney, C., Kershaw, A.P., Jacobsen, G.E., 2017. A 60 000-year record of environmental change for the Wet Tropics of north-eastern Australia based on the ODP 820 marine core. J. Quat. Sci. 32 (6), 704–716.
Mulrennan, M.E., Woodroffe, C.D., 1998. Saltwater intrusion into the coastal plains of the lower Mary River, northern Territory, Australia. J. Environ. Manag. 54, 169–188.
Negandhi, K., Edwards, G., Kelleway, J.J., Howard, D., Safari, D., Saintilan, N., 2019. Blue carbon potential of coastal wetland restoration varies with inundation and rainfall. Sci. Rep. 9, 4368.
Nerem, R.S., Beckley, B.D., Fasullo, J.T., Hamlington, B.D., Masters, D., Mitchum, G.T., 2018. Climate-change-driven accelerated sea-level rise detected in the altimeter era. Proc. Natl. Acad. Sci. U.S.A. 115 (9), 2022–2025.
Nicholas, W.A., Nichol, S.L., Howard, F.J.F., Picard, K., Dulfer, H., Radke, L.C., et al., 2014. Pockmark development in the Petrel sub-basin, Timor Sea, northern Australia: seabed habitat mapping in support of CO_2 storage assessments. Continent. Shelf Res. 83, 129–142.
Oliver, T.S., Rogers, K, Chafer, C.J., Woodroffe, C.D., 2012. Measuring, mapping and modelling: an integrated approach to the management of mangrove and saltmarsh in the Minnamurra RIver estuary, southeast Australia. Wetl. Ecol .Manag. 20 (4), 353–371.
Punwong, P., Selby, K., Marchant, R., 2018. Holocene mangrove dynamics and relative sea-level changes along the Tanzanian coast, East Africa. Estuar. Coast Shelf Sci. 212, 105–117.
Rogers, K., Saintilan, N., Heijnis, H., 2005. Mangrove encroachment of salt marsh in Western Port Bay, Victoria: the role of sedimentation, subsidence, and sea level rise. Estuaries 28 (4), 551–559.
Rogers, K., Wilton, K.M., Saintilan, N., 2006. Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. Estuar. Coast Shelf Sci. 66 (3–4), 559–569.

Rogers, K., Saintilan, N., Copeland, C., 2012. Modelling wetland surface elevation dynamics and its application to forecasting the effects of sea-level rise on estuarine wetlands. Ecol. Model. 244, 148–157.
Rogers, K., Saintilan, N., Howe, A.J., Rodríguez, J.F., 2013. Sedimentation, elevation and marsh evolution in a south-eastern Australian estuary during changing climatic conditions. Estuar. Coast Shelf Sci. 133, 172–181.
Rogers, K., Saintilan, N., Woodroffe, C.D., 2014a. Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: implications for coastal wetland response to climate change. Estuar. Coast Shelf Sci. 149, 46–56.
Rogers, K., Saintilan, N., Copeland, C., 2014b. Managed retreat of saline coastal wetlands: challenges and opportunities identified from the Hunter River Estuary, Australia. Estuar. Coast 37 (1), 67–78.
Rogers, K., Boon, P.I., Branigan, S., Duke, N.C., Field, C.D., Fitzsimons, J.A., et al., 2016. The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. Mar. Pol. 72, 139–155.
Rogers, K., Krauss, K.W., 2018. Moving form generalisations to specificity about mangrove-saltmarsh dynamics. Wetlands. https://doi.org/10.1007/s13157-018-1067-9.
Rogers, K., Kelleway, J., Saintilan, N., Megonigal, P., Adams, J., Holmquist, J.R., Meng, L., Schille-Beers, L., Zawadski, A., Mazumder, D., Woodroffe, C., 2019a. Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. Nature 567 (7746), 91.
Rogers, K., Saintilan, N., Mazumder, D., Kelleway, J.J., 2019b. Mangrove dynamics and blue carbon sequestration. Biol. Lett. 15 (3), 20180471.
Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., et al., 2001. Structure and function of south-east Australian estuaries. Estuar. Coast Shelf Sci. 53 (3), 351–384.
Saintilan, N., 1997. Mangroves as successional stages on the Hawkesbury River estuary, New South Wales. Wetlands 16, 99–107.
Saintilan, N., 2003. The influence of nutrient enrichment upon mangrove seedling establishment and growth in the Hawkesbury River estuary, New South Wales, Australia. Wetlands 21, 29–35.
Saintilan, N., 2004. Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. Estuar. Coast Shelf Sci. 61 (4), 591–601.
Saintilan, N., Hashimoto, R., 1999. Mangrove-saltmarsh dynamics on a prograding bayhead delta in the Hawkesbury River estuary, New South Wales, Australia. Hydrobiologia 413, 95–102.
Saintilan, N., Williams, R.J., 1999. Mangrove transgression into saltmarsh environments in south-east Australia. Global Ecol. Biogeogr. Lett. 8, 117–124.
Saintilan, N., Wilton, K., 2001. Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetl. Ecol. Manag. 9, 409–420.
Saintilan, N., Wilson, N.C., Rogers, K., Rajkaran, A., Krauss, K.W., 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Global Change Biol. 20 (1), 147–157.
Saintilan, N., Rogers, K., Toms, C., Stein, E.D., Jacobs, D., 2016. Intermittent estuaries: linking hydro-geomorphic context to climate change resilience. J. Coast Res. 75 (sp1), 133–137.
Saintilan, N., Mazumder, D., 2017. Mass spawning of crabs: ecological implications in subtropical Australia. Hydrobiologia 803 (1), 239–250.
Saintilan, N., Rogers, K., McKee, K.L., 2019. The shifting saltmarsh-mangrove ecotone in Australasia and the Americas. In: Coastal Wetlands. Elsevier, pp. 915–945.
Saintilan, N., Khan, N.S., Ashe, E., Kelleway, J.J., Rogers, K., Woodroffe, C.D., Horton, B.P., 2020. Thresholds of mangrove survival under rapid sea level rise. Science 368 (6495), 1118–1121.
Skilleter, G.A., Olds, A., Loneragan, N.R., Zharikov, Y., 2005. The value of patches of intertidal seagrass to prawns depends on their proximity to mangroves. Mar. Biol. 147 (2), 353–365.
Spalding, M.D., Blasco, F., Field, C.D., 2010. World Atlas of Mangroves. Routledge.
Staples, D.J., Vance, D.J., 1986. Emigration of juvenile banana prawns Penaeus merguiensis from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. Mar. Ecol. Prog. Ser. 27 (239), 52.
Sukardjo, S., Alongi, D.M., Kusmana, C., 2013. Rapid litter production and accumulation in Bornean mangrove forests. Ecosphere 4 (7), 1–7.
Tamura, T., Saito, Y., Sieng, S., Ben, B., Kong, M., Sim, I., et al., 2009. Initiation of the Mekong River delta at 8 ka: evidence from the sedimentary succession in the Cambodian lowland. Quat. Sci. Rev. 28 (3–4), 327–344.

Thom, B.G., Wright, L.D., Coleman, J.M., 1975. Mangrove ecology and deltaic-estuarine geomorphology, Cambridge Gulf-Ord River, western Australia. J. Ecol. 63, 203–222.

Tossou, M.G., Akoègninou, A., Ballouche, A., Sowunmi, M.A., Akpagana, K., 2008. The history of the mangrove vegetation in Bénin during the Holocene: a palynological study. J. Afr. Earth Sci. 52 (4–5), 167–174.

Traill, L.W., Perhans, K., Lovelock, C.E., Prohaska, A., McFallan, S., Rhodes, J.R., Wilson, K.A., 2011. Managing for change: wetland transitions under sea-level rise and outcomes for threatened species. Divers. Distrib. 17 (6), 1225–1233.

Umitsu, M., Buman, M., Kawase, K., Woodroffe, C.D., 2001. Holocene palaeoecology and formation of the Shoalhaven River deltaic-estuarine plains, southeast Australia. Holocene 11 (4), 407–418.

Woodroffe, C.D., Thom, B.G., Chappell, J., 1985. Development of widespread mangrove swamps in mid-Holocene times in northern Australia. Nature 317, 711–713.

Woodroffe, C.D., 2018. Mangrovbe response to sea level rise: palaeoecological insights from macrotidal systems in northern Australia. Mar. Freshw. Res. 69 (6), 917–932.

Woodroffe, C.D., Chappell, J., Thom, B.G., Wallensky, E., 1989. Depositional model of a macrotidal estuary and floodplain, South Alligator River, Northern Australia. Sedimentology 36, 737–756.

White, N.J., Haigh, I.D., Church, J.A., Koen, T., Watson, C.S., Pritchard, T.R., et al., 2014. Australian sea levels—trends, regional variability and influencing factors. Earth Sci. Rev. 136, 155–174.

Wilson, N.C., 2009. The Distribution, Growth, Reproduction and Population Genetics of a Mangrove Species, Rhizophora Stylosa Griff. Near its Southern Limits in New South Wales, Australia. Sch. Arts Sci. Australian Catholic University, Sydney.

Wilson, N.C., Saintilan, N., 2012. Growth of the mangrove species Rhizophora stylosa Griff. at its southern latitudinal limit in eawstern Australia. Aquat. Bot. 101, 8–17.

Winn, K.O., Saynor, M.J., Eliot, M.J., Eliot, I., 2006. Saltwater intrusion and morphologicvla change at the mouth of the east Alligator river, Northern Territory. J. Coast Res. 22, 137–149.

Woodroffe, C.D., Thom, B.G., Chappell, J., Wallensky, E., Grindrod, J., 1987. Relative sea level in the South Alligator River region, north Australia, during the Holocene. Search 4, 198–200.

Woods, J.L.D., 2012. The evolution of a Holocene estuarine barrier on the Coromandel Coast, New Zealand. Geogr. Res. 50 (1), 89–101.

Yando, E.S., Osland, M.J., Willis, J.M., Day, R.H., Krauss, K.W., Hester, M.W., 2016. Salt marsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. J. Ecol. 104 (4), 1020–1031.

Yulianto, E., Sukapti, W.S., Rahardjo, A.T., Noeradi, D., Siregar, D.A., Suparan, P., Hirakawa, K., 2004. Mangrove shoreline responses to Holocene environmental change, Makassar Strait, Indonesia. Rev. Palaeobot. Palynol. 131 (3–4), 251–268.

SCIENTIFIC REPORTS

OPEN

Blue carbon potential of coastal wetland restoration varies with inundation and rainfall

Received: 6 June 2018
Accepted: 19 February 2019
Published online: 13 March 2019

Karita Negandhi[1], Grant Edwards[2], Jeffrey J. Kelleway[2], Dean Howard[2,3], David Safari[2] & Neil Saintilan[2]

There is a growing interest in how the management of 'blue carbon' sequestered by coastal wetlands can influence global greenhouse gas (GHG) budgets. A promising intervention is through restoring tidal exchange to impounded coastal wetlands for reduced methane (CH_4) emissions. We monitored an impounded wetland's GHG flux (CO_2 and CH_4) prior to and following tidal reinstatement. We found that biogeochemical responses varied across an elevation gradient. The low elevation zone experienced a greater increase in water level and an associated greater marine transition in the sediment microbial community (16 S rRNA) than the high elevation zone. The low elevation zone's GHG emissions had a reduced sustained global warming potential of 264 g m^{-2} yr^{-1} CO_2-e over 100 years, and it increased to 351 g m^{-2} yr^{-1} with the removal of extreme rain events. However, emission benefits were achieved through a reduction in CO_2 emissions, not CH_4 emissions. Overall, the wetland shifted from a prior CH_4 sink (−0.07 to −1.74 g C m^{-2} yr^{-1}) to a variable sink or source depending on the elevation site and rainfall. This highlights the need to consider a wetland's initial GHG emissions, elevation and future rainfall trends when assessing the efficacy of tidal reinstatement for GHG emission control.

For centuries humans have modifi d the hydrological characteristics of low-lying coastal environments to promote agricultural and aquaculture development, to mitigate fl od risk, to control insect infestation or as an artefact of transport corridors[1,2]. Th s has largely been achieved through the imposition of levee banks restricting tidal exchange, leaving wetlands to be either drained or freshened. Tidal wetland loss has accelerated through the second half of the 20th century[3], with largescale coastal reclamation occurring in mangrove forests of SE Asia[4], coastal wetlands of China[5], coastal fl odplains in eastern Australia[6], and North American saltmarshes[7,8]. Such modifi ations have resulted in up to a 50% reduction of tidal wetlands worldwide since 1900[9].

The isolation of tidal wetlands alters the biogeochemical characteristics of soils, with profound implications for greenhouse gas emissions (GHG; CO_2 and CH_4). Wetland drainage promotes the remineralization of organic carbon, leading to substantial CO_2 emissions[10] and provides opportunity for aerobic oxidation of CH_4[11]. Reduction of tidal saltwater connections can also enhance methane (CH_4) production[12–14], as sea-water associated microbes can reduce CH_4 emissions through two processes: (1) hindering production by outcompeting methanogenic archaea for electrons[15] and (2) promoting the anaerobic oxidation of CH_4[16]. The obstruction of tidal flow to coastal wetlands over several continents has likely created additional freshwater wetland CH_4 sources, contributing to global warming[17], though few tests of this assumption are documented.

The potential GHG mitigation benefits of tidal reinstatement are additive: CH_4 emission reduction is accompanied by the restoration of "blue carbon" ecosystems, with mangrove and saltmarsh being noted for relatively high rates of carbon sequestration[18–20]. In the context of emerging carbon trading markets[21] and national greenhouse gas inventories[14], the prospect of tidal reinstatement appeals to managers and investors as an offset mechanism for several reasons. First, the opportunities are likely to be numerous and at a large spatial scale (thousands of hectares). Second, measurable benefits are potentially gained over short time periods (weeks to months), being mediated by rapidly responding hydrological and microbial conditions. Thi d, avoided emissions are permanent, in the sense that the benefit is not negated by subsequent management interventions or pertubations[8,22].

[1]Office of Environment and Heritage, New South Wales, Australia. [2]Department of Environmental Sciences, Macquarie University, New South Wales, Australia. [3]Department of Environmental, Earth and Atmospheric Sciences, University of Massachusetts Lowell, Massachusetts, United States. Grant Edwards is deceased. Correspondence and requests for materials should be addressed to K.N. (email: karitaln@gmail.com)

There is currently little guidance on how to account for the emission benefits of tidal reinstatement of impounded marshes. The 2013 Supplement to the 2006 IPCC Guidelines for National GHG Inventories: Wetlands[14] makes no reference to tidal (saline) reinstatement of impounded wetlands as a blue carbon mechanism, nor does it allow for the comparison of emission factors for impounded and natural tidal wetlands. Kroeger *et al.*[8] provide suggested emissions factors, though these are based largely on Poffenbarger *et al.*[13] who compared emissions across a gradient of salinities, and the emissions factors reported in Hiraishi *et al.*[14]. There is clearly insuffici t experimental data on whether tidal reinstatement has the promised benefit for signifi ant emissions reduction.

The Hunter estuary of New South Wales (NSW), Australia underwent tidal restriction in 1956, and over ensuing decades impounded formerly tidal fl odplains have transitioned to brackish and freshwater wetlands[23]. More recently, several large-scale tidal reinstatements[24] have restored over 1000 ha of coastal tidal wetland prior to the third phase of tidal reinstatement at Tomago in 2015. We took the opportunity to monitor the Phase 3 tidal reinstatement to test the following three hypotheses: (i) tidal restoration would alter microbial assemblages increasing the representation of sulfate-reducers; (ii) tidal reinstatement would transition the restored wetland from a contributor to a mitigator of radiative forcing through reduced CH_4 emissions; and (iii) these changes would be similar across low and high intertidal elevations within the restored wetland.

Study Approach

Monitoring equipment was installed 3.5 months before fl odgates at Tomago, NSW wetland were lowered to re-introduce tidal waters (12 Nov 2015), to measure water level, salinity, conductivity, and CO_2 and CH_4 fl x (using an Eddy co-variance tower). Equipment remained for 8.5 months after tidal reinstatement. Periods of exceptionally high rainfall occurred following tidal reinstatement, which allowed us to explore the influence of rainfall on gas flux. The Eddy covariance tower was positioned in the wetland such that its flux footprint would cover high and low elevation zones according to the wind direction. Two sampling locations below mean sea level (−12 cm Australian Height Datum (AHD) and −8 cm AHD) and two sampling locations above mean sea level (12 cm AHD and 8 cm AHD) were identified for sampling of microbial communities. All four locations were within 40 m of the Eddy co-variance tower. Rainfall data were acquired from the nearby (~12.5 km) weather station of Williamtown RAAF, NSW.

Results and Discussion

Hydrological changes. Before reinstatement, water levels ranged from 0 to 0.69 m and 0 to 0.55 m for the low (−0.04 m AHD) and high (0.10 m AHD) elevations sampling locations respectively, with high rainfall events the primary drivers for large inundation events (Fig. 1c). Surface runoff from the hinterland likely contributed to higher water levels at low elevation. Overall, tidal reinstatement increased inundation of the wetland, with the proportion of time inundated increasing from 66% pre-reinstatement to 91% post-reinstatement for the lower elevation sampling locations and from 21% to 50% for the higher elevation sampling locations.

Within four days after tidal reinstatement a rain event of 35 mm occurred and was followed by two extreme rain periods of 123 mm and 422 mm over several days (22 to 27 Dec and 5 to 18 Jan, respectively) five weeks later. Both of these events were above the regional average rainfall for December and January of 80 and 100 mm, respectively. Two more above-average rain events also occurred in April (147 mm) and June (151 mm). These large rain events still induced spikes in water level (Fig. 1c) and were followed by a decrease in salinity (Supplementary Fig. S1).

Microbial communities as an indicator of tidal impact. Microbial communities collected before and after tidal reinstatement at high and low elevation sites were used to identify temporal trends in response to tidal inundation. The more diverse surface sediment microbial communities at the low elevation (Supplementary Tables S1 and S2) site sustained a signifi ant change after tidal reinstatement between December and March (ANOSIM $p < 0.01$, global $R > 0.69$; Supplementary Fig. S3). December samples, 25 days post-reinstatement, clustered with 'before' communities and also with the high elevation sites communities, which did not show a signifi ant community change (Fig. 2). By March 2016, the 'after' reinstatement community was dissimilar to communities 'before' reinstatement. The top 3 Orders that decreased after tidal reinstatement at the low elevation sites were ones commonly associated with freshwater sediment (*Rhodospirillales* and *Rhizobiales*)[25] and soil (*OPB35 soil grp. uncls.*)[26]. Together they contributed 7.4% (SIMPER) of the community dissimilarity after tidal impact. After March, the water level and salinity at the low elevation site was consistently >0.1 m and >12.7 ppt respectively, indicating a more sustained saltwater inundation. The bacterial community also shifted to one more representative of a marine environment. The top two Orders that increased were *Desulfobacterales* and *Clostridales*, contributing to 7% of the community shift after fl oding (Supplementary Fig. S2). *Desulfobacterales* are anaerobic and often found in saline environments[27]. Moreover, together with the presence of *Clostridales*, they have the functional capability to take up carbonate and fix CO_2[28]. The archaeal community was dominated by *Woesearchaeota DHVEG-6* and *Archaea unclassified* (Supplementary Fig. S5) at both elevations, yet the low elevation area experienced a 15% community change after tidal reinstatement, which is attributed to three Genera commonly associated with higher salinities (*Halarchaeum*, *Halobacteriales unclass. and Marine Benthic Group-B unclass.*; Supplementary Fig. S2).

GHG patterns before and after tidal reinstatement. Natural and managed wetlands are known to have different GHG emissions[29,30]. The observation of an impounded wetland as a CH_4 sink (−0.07 to −1.74 g C m^{-2} y^{-1}) is unusual (before tidal reinstatement, Table 1), but can be explained in terms of salinity. Before tidal reinstatement, the salinity average was slightly <18 ppt (17.4 avg) and ranged from 16.7 to 18.3, with the presence of a sulfuric soil layer at ~0.3 m deep[31] likely contributing to inhibiting of CH_4 production. Water level increases from rain events did increase the CH_4 flux, but not enough to impede the presence of a CH_4 sink (Fig. 1b, Aug

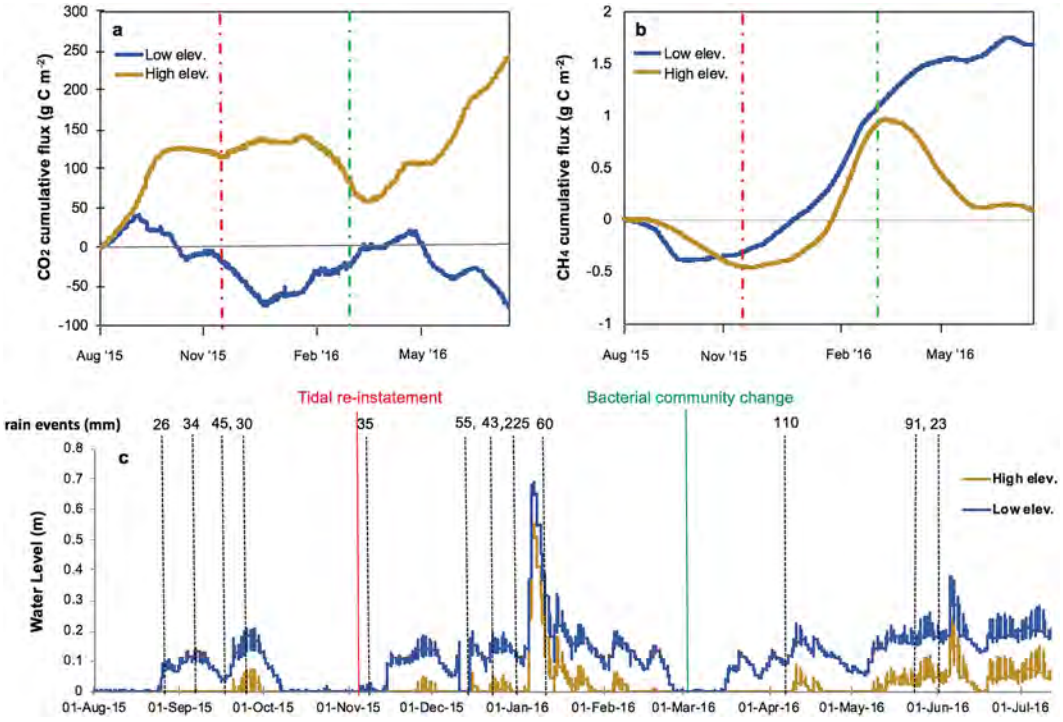


Figure 1. Flux lines at high and low elevation sites for (**a**) CO_2 and (**b**) CH_4. Flux is cumulative for each 30 minute measurement period. Vertical lines indicate when fl odgates where open (red, 12 Nov 2015) and when a change in the microbial community was detected at the low elevation (green, Mar 2016). Area between these vertical lines are when extreme rainfalls occurred, which are indicated with (**c**) timeline of water level, rain events >25 mm, and tidal reinstatement for low elevation and high elevation sites.

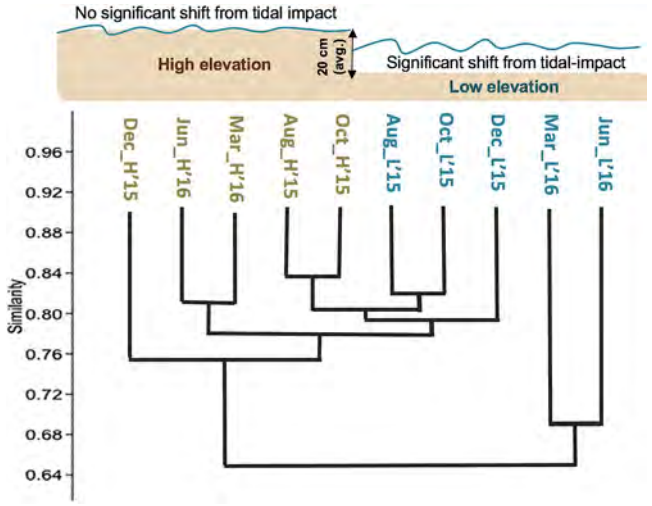


Figure 2. Surface sediment bacterial community dissimilarity tree (Bray-Curtis; shared OTUs at 97%). Branch lengths indicate the amount of differentiation among communities. March and June low elevation communities after tidal reinstatement have the longest branches and form their own cluster (31% dissimilar from other communities), indicating a signifi ant change in the community occurring at the taxonomic level of Order (ANOSIM $p < 0.01$, $R > 0.69$; Supplementary Fig. S3). Each community time point represents two bacterial samples of 11,062 sequences (reads).

– 12 Nov). Another eastern Australian coastal wetland (~800 km North), subject to substantial freshwater input was also a reported CH_4 sink (-3.4 mg C m^{-2} y^{-1}) when the groundwater table was high (-252 mm)[32]. These hitherto overlooked ecosystem sinks are not insignifi ant compared to the global average soil sink strength for CH_4 (0.003–20.7 g C m^{-2} yr^{-1}; ref.[33]).

	CO_2 g C m^{-2} yr^{-1}	CH_4 g C m^{-2} yr^{-1}	CO_2 g C m^{-2} yr^{-1}	CH_4 g C m^{-2} yr^{-1}
	High Elevation		Low Elevation	
All Events				
Before (Aug–Nov)	420 ± 22	−1.74 ± 0.04	−57 ± 31	−0.07 ± 0.08
After (Nov–Jul)	191 ± 23	0.82 ± 0.07	−94 ± 32	2.40 ± 0.08
After (Mar–Jul)	430 ± 28	−1.92 ± 0.08	−152 ± 29	1.03 ± 0.12
No Rain				
Before (Aug–Nov)	420 ± 23	−1.67 ± 0.05	−63 ± 32	−0.12 ± 0.08
After (Nov–Jul)	350 ± 24	−0.65 ± 0.07	−180 ± 29	1.54 ± 0.09
After (Mar–Jul)	522 ± 28	−2.59 ± 0.09	−217 ± 27	0.67 ± 0.01

Table 1. Carbon dioxide and CH_4 emissions for both high and low elevation sites before and after tidal reinstatement with associated standard errors. Emissions were calculated for immediately after tidal inundation (Nov–Jul), when a change in the surface bacterial community was detected (Mar–Jul), and with the removal of rain event impacts (Supplementary Fig. S1) to see the true influence of tidal reinstatement on GHG emissions.

The increase in salinity in late February and shift in bacterial community detected at the low elevation site in March indicates that the above average rainfalls during Dec – Jan may have impeded the initial saltwater introduction from tidal reinstatement in November. Using March as the starting point for when GHG emissions refl ct tidal influence, the low elevation zones CO_2 flux decreased by 95 g C m^{-2} yr^{-1}, which is similar to the CO_2 tier 1 emission factor benefits for restored saltmarsh that has been drained for >30 years (91 g C m^{-2} yr^{-1};[8]). The low elevation zones increased CH_4 flux of 0.96 g C m^{-2} yr^{-1} (Table 1). While the average CH_4 emission was positive from March – July, a net GHG reduction was still achieved ranging from −296 to −264 g m^{-2} yr^{-1} of CO_2-e (CO_2 equivalents) over 100 yrs (Fig. 3a). Th s net reduction range was seen through the use of a single pulse metric, global warming potential (GWP)[34], and also with using a sustained warming/cooling (SGWP/SGCP)[35]. Within the same time period, the high elevation area ranged from a net increase in CO_2 equivalents using GWP (27 g m^{-2} yr^{-1}) to a slight reduction using SGWP/SGCP (−9 g m^{-2} yr^{-1}). Even with the higher radiative forcing of CH_4, the carbon emissions are dominated by CO_2 emissions for both elevation categories (Fig. 3b,c). These results underscore the need to measure both CO_2 and CH_4 in characterising the effects of tidal reinstatement on GHG flux.

Importantly, the outcomes were quite different between the adjacent higher and low elevation wetland zones. After tidal reinstatement, the low elevation zone had a reduced atmospheric GWP compared to the high elevation increasing its GWP (Fig. 3a). These emission reductions were achieved unexpectedly through a reduction in CO_2 and in spite of an increase in CH_4. Th s ran counter to the expected blue carbon emission reduction mechanism of neutral benefit in CO_2 and reduction in CH_4[8]. We attribute this to (i) a low to negative CH_4 emission prior to reinstatement associated with higher than expected salinity and (ii) the signifi ance of rainfall influencing GHG flux post-reinstatement, particularly at the higher elevation site.

Rain Influence. Spikes in CH_4 emission from both the low elevation and high elevation zones were observed in relation to a succession of high rainfall events. The late December to January events, shortly following tidal reinstatement, provide an example (Fig. 1b,c). Together these events decreased the salinity to ~7 ppt (Supplementary Fig. S1), well below the 18 ppt threshold for decreased CH_4 production proposed by Poffenbarger *et al.*[13]. Th s increased CH_4 production is sustained across both elevation zones until March when the salinity started increasing (Supplementary Fig. S1). A decrease or plateau in CH_4 cumulative flux also occurred in March and was sustained through July for both zones. Th s coincided with an increase in inundation time at the high elevation sampling site from 0% in March to 94% in June and 100% in July. The low elevation site was inundated 58% in March to 100% of the time from April to July.

There is evidence that the presence of a more sustained tidal inundation time in the low elevation zone acted to buffer the impact of rainwater decreasing soil salinity. During a 3-day rain event (DOY 156–158; 114 mm; Supplementary Fig. S1), the salinity increased to 18 ppt refl cting a controlling influence of tidal ponding on salinity and CH_4 flux. Indeed, when salinity levels were <17.45 ppt, CH_4 flux was signifi antly higher ($p = 0.047$; Fig. 4). Removing time periods where rainfall decreased salinity and increased fluxes (Supplementary Fig. S1), the net CH_4 flux decreased for both elevation zones after fl oding (Table 1). Tidal reinstatement does not therefore prevent the freshening of upper intertidal habitat during high rainfall periods, and attendant CH_4 production. However, the presence of surface fl oding by tidal inundation decreased the duration of exposure to rainwater induced CH_4 emission.

Freshwater inputs from the large rain events corresponded to opposing CO_2 trends for the two elevation zones. They occurred in relation to reduced CO_2 emissions at the high elevation zone and increased CO_2 emissions at the low elevation zone. At the low elevation zone, the decrease in CO_2 flux (Fig. 1a), was possibly an artefact of inundation (Table 1; after all events) and the increased presence of *Desulfobacterales* and *Clostridales* following reinstatement. For both CO_2 and CH_4, the influence of rain events was more pronounced for the high elevation zone, as less tidal influence left fresh rainwater to dominate inundation periods (Fig. 1c). As previously seen[36], CO_2 flux responses to rain were more rapid than CH_4, which exhibited a time lag (Supplementary Fig. S1) during soil rewetting. Rain events would no longer be 'rewetting' the soil, in the low elevation zone, once it transitioned to sustained inundation (58 to 100% inundation time from Mar – Jul), and hence no CO_2 flux reaction was seen to rain events after March.

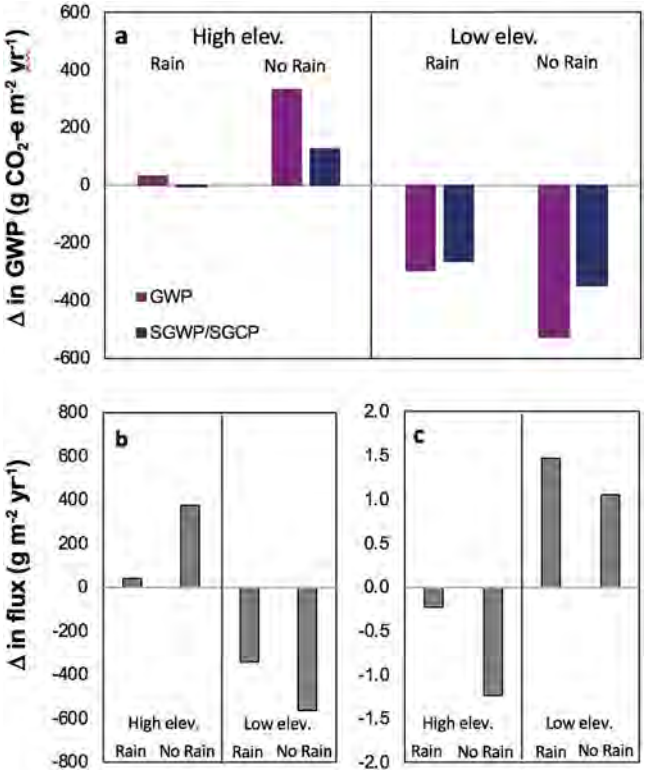


Figure 3. The low elevation zone had a reduced carbon flux in CO_2-equivalents after tidal reinstatement, especially with a subset of rain events removed (Supplementary Fig. S1). Despite CH_4's higher radiative forcing than CO_2, the small change in its flux after inundation compared to CO_2 means GWP follows the CO_2 trend. (**a**) Change in CO_2-equivalents between before (Aug–Nov) and after (Mar–Jul) tidal reinstatement for high and low elevation sites using global warming potential (GWP*; violet) and a sustained global warming/cooling potential (SGWP/SGCP**; black). Both are for over 100 yrs and including rain events. Change in (**b**) CO_2 and (**c**) CH_4 flux for before (Aug–12 Nov) and after (Mar–Jul) tidal impact. *CH_4 expressed in CO_2 equivalent as IPCC's GWP for 100 yrs (x34; this factor includes climate carbon feedback, such as CH_4 oxidation to CO_2[34]). **CH_4 expressed in CO_2 equivalents as sustained global warming/cooling potential for 100 yrs (x45 for warming and x203 for cooling). Here the sustained gas warming (positive CH_4 flux) and the sustained gas cooling (negative CH_4 flux for uptake/sink) are representative of a flux that persists over time rather than a one-time pulse[35].

Excluding these rain events, the low elevation zone transformed to a CO_2 sink (-217 g C m^{-2} yr^{-1}) and lower CH_4 source (0.67 g C m^{-2} yr^{-1}), while the high elevation zone was a CO_2 source (522 g C m^{-2} yr^{-1}) and CH_4 sink (-2.59 g C m^{-2} yr^{-1}) over the same period (Table 1). Less inundation time and greater exposure of surface sediments to the atmosphere in the high elevation zones likely supports the stronger CH_4 uptake rates. With the removal of rain events, the low elevations CO_2 sink strength is >2x as strong as that reported for restored salt-marshes (-91 g C m^{-2} yr^{-1};[14]). The ability of the low elevation zone, under anoxic conditions, to mediate CH_4 emissions and decrease emissions resulted in reduced carbon emissions including rain events or excluding rain events (Fig. 3).

Conclusions

Our results show that a rapid shift to a reduced GHG ecosystem can occur within three months after tidal reinstatement, mediated by a relatively rapid transition of the microbial community to become more representative of marine conditions. We observed fundamental differences in the greenhouse gas dynamics between elevation zones within a single wetland, with the low elevation zone experiencing prolonged tidal inundation (Fig. 1c), greater microbial community change (Fig. 2), and a lower carbon GWP/SGWP (Fig. 3). The results provide a unique insight into the impact tidal reinstatement can have in promoting a transition to a blue carbon ecosystem, though we acknowledge the lack of true experimentation control.

The GHG benefits of tidal reinstatement are mediated by rainfall inundation. Here large rain events over the summer impeded the influence of tidal reinstatement on microbial assemblages until our autumn sampling. Furthermore, these soils have been classifi d as potential acid sulfate soils[31] and did harbour sulfate reducing bacteria before inundation. The combined presence of sulfate reducers (which outcompete methanogens for electrons required for CH_4 production[15]) and drier soils facilitating aerobic oxidation of CH_4[11] can help explain the CH_4 uptake prior to tidal reinstatement. The presence of sulfate-reducing bacteria could have also aided in a more rapid community transition once reinstatement occurred. The Family that increased the most after tidal reinstatement was *Desulfobacteraceae*, which includes taxa that are sulfate-reducing bacterial partners of anaerobic

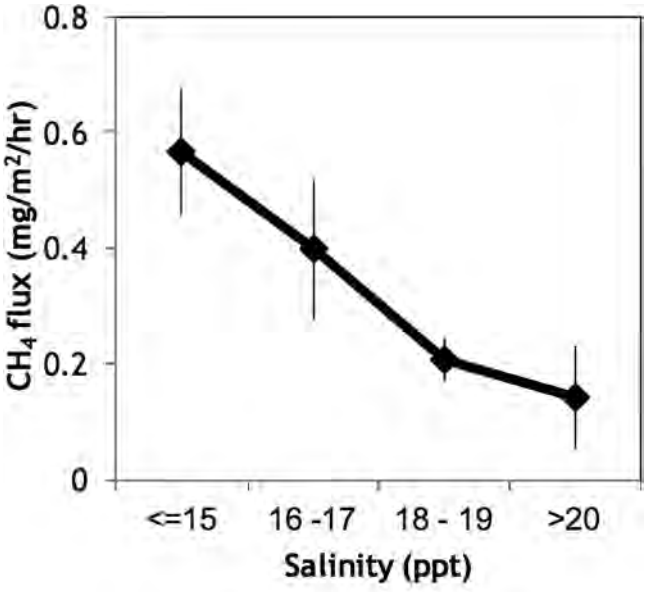


Figure 4. Decrease in CH_4 flux with increase in salinity from the low elevation site. Error bars show variability in flux within salinity ranges. When salinity is ≤17.43 ppt, the CH_4 flux is signifi antly higher ($p = 0.047$, $d = 0.1579$; kolomogorov-Smirnov).

methanotrophic archaea carrying out anaerobic oxidation of CH_4[37]. Therefore, these minerogenic soils provide an ideal coastal environment where blue carbon storage can occur with tidal reinstatement. The caveat is that in lowland floodplain environments with a prior Holocene history of seawater inundation, post-impoundment conditions may still be conducive to anaerobic CH_4 oxidation, rendering the net GHG benefits primarily through CO_2 reduction. With CO_2 and CH_4 having substantially different radiative forcings[38], the GHG benefits of blue carbon coastal ecosystems will likely vary spatially.

Net GHG emissions were reduced in the tidally restored low elevation wetland zone but not in an adjacent higher elevation zone, which experienced lower levels of tidal inundation and greater exposure to rainfall ponding. Th s highlights a critical need for further experimental data on the relationships between elevation, hydrology, climate and GHG dynamics. It is possible, for example, that the observed die-off of grasses (*P. vaginatum*) and sedges (*B. caldwellii*) following the conversion of the low elevation site to more permanent fl oding decreased autotrophic respiration. The capacity of high to extreme rainfall events and ensuing brackish groundwater fluxes to interrupt the methane sink potential of low elevation zones highlights the need to consider rainfall trends, including shifts in rainfall intensity under climate change[39], when assessing the efficacy of tidal reinstatement as an emission control mechanism.

Methods

Site. The fi ld experiment was carried out at Tomago wetland (−32.9487°; 151.8347°) within the Hunter estuary of NSW, Australia. Prior to tidal reinstatement, the brackish grassland was dominated by *Paspalum vaginatum*. The high elevation site also included the remnant saltmarsh species *Sporobolus virginicus*, *Triglochin striatum* and *Juncus kraussii*. Comparatively, the low elevation site was intermixed with *Bolboschoenus caldwellii*. Following tidal reinstatement, lower elevation area transitioned to open water and/or mudflat, and the presence of *P. vaginatum* decreased across the wetland. Mature Swamp Oak Floodplain Forest bordered north, east and south of the wetland and a narrow strip of tall (~2 m) *Phragmites australis* reedswamp bordered the west of the wetland for the duration of the monitoring period.

Sampling design. Before fl odgates were lowered to reinstate tidal fl w on 12 November 2015, monitoring equipment was installed. Th s included water level (April 2015, HOBO® U20L), salinity (15 Oct 2015, 36 cm depth, HOBO® U24 conductivity and temperature logger), and an Eddy co-variance tower (4 Aug 2015, LI-COR®). The Eddy covariance tower was positioned in the middle of the wetland allowing its flux footprint would pass over both zones according to the wind direction. Two sampling locations below mean sea level (−12 cm AHD) and −8 cm AHD, and two sampling locations above mean sea level (8 cm AHD and 12 cm AHD) were identifi d for sampling of microbial communities. All four locations were within 40 m of the Eddy co-variance tower.

Rainfall data were acquired from the nearby (~12.5 km) weather station of Williamtown RAAF (Australian Bureau of Meteorology, www.bom.gov.au). All monitoring equipment was left for 7.5 months following tidal reinstatement. Rainfall events >25 mm (Fig. 1) and decrease in salinity were used to identify times freshwater input from rainfall impacted carbon flux (Supplementary Fig. S1). Removal of these times (shaded grey in Supplementary Fig. S1) represent 'No Rain' data. Microbial samples were collected five times throughout the

study. At each sampling time point, four samples were collected with two replicates taken at separate locations within each elevation site (details below).

Water level. A HOBO U20L water level loggers (Onset Computer Corporation, Massachusetts, USA) were deployed on April, 2015 – adjacent to a low elevation sampling site (elevation of logger = −0.04 m AHD). Pressure measurements were recorded at 15 minute intervals, and water depth estimated by correcting for barometric pressure data from a nearby weather gauge (Williamtown RAAF). Water levels for the high elevation sampling site (mean elevation of 0.10 m AHD) were modelled based on the vertical difference between this mean high elevation and that of the low elevation water logger (i.e. +16 cm elevation).

Eddy co-covariance flux. A complete *Li-Cor* (Li-Cor Biosciences), Eddy Covariance system consisting of the Li-7500 and Li-7700 open path fast response sensors for CO_2, H_2O, and CH_4, coupled with a Gill Windmaster 3D sonic anemometer and the Li-7550 with SmartFlux for real-time data processing was deployed at the Tomago site. Samples were collected at 20 Hz at a tower height of 3.45 meters above the surface. Quality control flags were calculated for each averaging period using the scheme of Foken *et al.*[40] and fluxes given a 2 flag were discarded from further analyses. Calculation of eddy covariance fluxes and quality control was undertaken using EddyPro 5.2.1 (Li-Cor Biosciences) and further calculations/statistical analyses were performed using Matlab 2012b (The Mathworks Inc., Natick, MA, USA) and R version 3.3.3.

Gap filling for cumulative flux. Determination of flux footprint regions was achieved using the two-dimensional footprint method of Klujn *et al.*[41]. The total spatial extent of the footprint was set as the region accounting for 80% of the flux intensity calculated by this method. Two impact regions were defi ed for sectors between 135° and 280° (low elevation, south and south-west in relation to the Tower) and for >280° or <135° (high elevation, north and north-east in relation to the Tower). Flux footprints were then assigned to a region only if >80% of the total flux intensity within the defi ed total spatial extent was found to originate within the appropriate sector. For each flux species within each impact region, gaps in the data were filled according to time of day by averaging temporally local observed values. An initial two-week period was centred about each unknown flux value and the estimated flux was calculated as the mean of all observed flux values, for the same 1.5 hour of day, within this two-week period. A minimum of 5 observed values was required for each gap fill calculation. If less observed flux values were found within the initial two-week period then this period was incrementally extended by two days (one before and one after) until the minimum number of observed flux values was acquired. Cumulative and average fluxes for both impact sites across the study period were then calculated from all observed and calculated flux values.

Microbial samples. Surface soil and sediment samples were collected in Aug 2015, Oct 2015, Dec 2015, Mar 2016 and Jun 2016 between 12:00 and 2:00 pm. At each sampling time point, four samples were collected with two replicates taken at separate locations within each of the ~1.0 ha elevation sites. Care was taken to avoid sampling in soils disturbed by foot traffi or prior sampling. A sterile 15 ml falcon tube was used as mini corer to a depth of 2.3 cm. Th s 3 ml of soil or sediment was placed on ice and transferred to an −80 °C freezer within 2 hrs of collection. Samples were homogenized (mixed within tube after thawed) before transferring 0.25 g to use for DNA extraction following instructions of the MO BIO Kit (PowerSoil DNA Isolation Kit #12888). Extracted DNA was diluted to concentrations of 5.3 to 16.9 ng/μL (nan-drop spectrophotometer) and amplification was performed following the Earth Microbiome Project[42]. Briefly, a PCR reaction mixture of PCR grade H_2O (13 μL), MasterMix (10 μL, 5 Prime HotMaster Mix), template DNA (1 μL), and 10 μM of each MiSeq primer (515 F and 806 R, both 16 S rRNA primers; 0.5 μL). These primers have recently been shown to have a bias against *Crenarchaeota*/*Th umarchaeota*[43]. Amplifi ation cycles included denaturing at 94 °C for 3 minutes, 35 cycles of denaturing at 94 °C for 45 s, annealing at 50 °C for 1 min, extensions at 72 °C for 1 min 30 s, and a fi al extension at 72 °C for 10 min. Most samples amplifi d using 1 μL of template DNA, except one sample in the high and low impact site from October were only capable of amplifi ation at 1/10 μL. PCR products were purifi d, pooled in equal volumes (SequalPrep Normalization plates, ThermoFisher), and sequenced (MiSeq) at UNSW's Ramaciotti Centre for Genomics. Raw reads were submitted to NCBI Sequence Read Archive reference number SRP131614.

Resulting paired-end reads were subjected to a MiSeq pre-processing, quality control, and taxonomic analyses[44]. Paired reads were aligned, with base pair quality scores >25 given preference. Matched paired reads were then removed if they were longer >275 bp, and any ambiguous base pairs (N's). Reads were aligned using Mothur (v.1.38.0) against SILVA database (V123). Misaligned reads outside the targeted area, chimeras, and non-targeted assignments (chloroplast, mitochondria, and eukaryotes) were removed. Mothur OTUs were assigned (97% similarity) and samples were randomly resampled to 11,062 reads per sample for downstream analysis. Diversity measures were performed in Mothur. Bray Curtis similarity tree, NMDS plot, ANOSIM and SIMPER were performed in PAST (3.16).

References

1. Montague, C. L., Zale, A. V. & Percival, H. F. Ecological effects of coastal marsh impoundments: a review. *Environ. Manage.* **11**, 743–756 (1987).
2. Portnoy, J. W. & Giblin, A. E. Effects of historic tidal restrictions on salt marsh sediment chemistry. *Biogeochemistry* **36**, 275–303 (1997).
3. Hu, S., Niu, Z., Chen, Y., Li, L. & Zhang, H. Global wetlands: Potential distribution, wetland loss, and status. *Sci. Total Environ.* **586**, 319–327 (2017).
4. Richards, D. R. & Friess, D. A. Rates and drivers of mangrove deforestation in Southeast Asia, 2000–2012. *P. Natl. Acad. Sci. USA* **113**, 344–349 (2016).
5. An, S. *et al*. China's natural wetlands: past problems, current status, and future challenges. *AMBIO: A Journal of the Human Environment* **36**, 335–342 (2007).

6. Williams, R. J. & Watford, F. A. Identifi ation of structures restricting tidal fl w in New South Wales, Australia. *Wetl. Ecol. Manag.* **5**, 87–97 (1997).
7. Bridgham, S. D., Megonigal, J. P., Keller, J. K., Bliss, N. B. & Trettin, C. The carbon balance of North American wetlands. *Wetlands* **26**, 889–916 (2006).
8. Kroeger, K. D., Crooks, S., Moseman-Valtierra, S. & Tang, J. Restoring tides to reduce methane emissions in impounded wetlands: A new and potent Blue Carbon climate change intervention. *Sci. Rep.* **7**, 11914 (2017).
9. Davidson, N. C. How much wetland has the world lost? Long-term and recent trends in global wetland area. *Mar. Freshwater Res.* **65**, 934–941 (2014).
10. Pendleton, L. *et al*. Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *PLOS ONE* **7**, e43542 (2012).
11. Whalen, S. C. Biogeochemistry of methane exchange between natural wetlands and the atmosphere. *Environ. Eng. Sci.* **22**, 73–94 (2005).
12. Neubauer, S. C. On the challenges of modeling the net radiative forcing of wetlands: reconsidering Mitsch *et al*. 2013. *Landsc. Ecol.* **29**, 571–577 (2014).
13. Poffenbarger, H. J., Needelman, B. A. & Megonigal, J. P. Salinity influence on methane emissions from tidal marshes. *Wetlands* **31**, 831–842 (2011).
14. Hiraishi, T. *et al*. Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands (IPCC, Switzerland 2013, 2014).
15. Lovley, D. R., Dwyer., D. F. & Klug, M. J. Kinetic Analysis of Competition Between Sulfate Reducers and Methanogens for Hydrogen in Sediments. *Appl. Environ. Microbiol.* **43**, 1373–1379 (1982).
16. Hoehler, T. M., Alperin, M. J., Albert, D. B. & Marten, C. S. Field and laboratory studies of methane oxidation in an anoxic marine sediment: Evidence for a methanogen-sulfate reducer consortium. *Global Biogeochem. Cy.* **8**, 451–463 (1994).
17. Bridgham, S. D., Cadillo-Quiroz, H., Keller, J. K. & Zhuang, Q. Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. *Glob. Change Biol.* **19**, 1325–1346 (2013).
18. Chmura, G. L., Anisfeld, S. C., Cahoon, D. R. & Lynch, J. C. Global carbon sequestration in tidal, saline wetland soils. *Glob. Biogeochem. Cycles* **17**, 1111 (2003).
19. Mcleod, E. *et al*. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Front. Ecol. Environ* **9**, 552–560 (2011).
20. Hamilton, S. E. & Friess, D. A. Global carbon stocks and potential emissions due to mangrove deforestation from 2000 to 2012. *Nat. Clim. Change* **8**, 240–244 (2018).
21. Plan Vivo. 2013. The Plan Vivo standard for community payments for ecosystem services programmes. In.Restore America's Estuaries, and Silvestrum. VM0033 Methodology for Tidal Wetland and Seagrass Restoration. In.*: Verified Carbon Standard* (2015).
22. Macreadie, P. I. *et al*. Can we manage coastal ecosystems to sequester more blue carbon?' Frontiers in Ecology and the Environment. *Front. Ecol. Environ.* **15**, 206–213 (2017).
23. Winning, G. & Saintilan, N. Vegetation changes in Hexham Swamp, Hunter River, New South Wales, since the construction of fl odgates in 1971. *Cunninghamia* **11**, 185–194 (2009).
24. Rogers, K. *et al*. The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. *Mar. Policy* **72**, 139–155 (2016).
25. Wang, Y. *et al*. Comparison of the levels of bacterial diversity in freshwater, intertidal wetland, and marine sediments by using millions of Illumina tags. *Appl. Environ. Microbiol.* **78**, 8264–8271 (2012).
26. Deng, Y., Cui, X., Hernández, M. & Dumont, M. G. Microbial Diversity in Hummock and Hollow Soils of Th ee Wetlands on the Qinghai-Tibetan Plateau Revealed by 16S rRNA Pyrosequencing. *PLOS ONE* **9**, e103115 (2014).
27. Ruff, S. E. *et al*. Global dispersion and local diversifi ation of the methane seep microbiome. *Proc. Natl. Acad. Sci. USA* **112**, 4015–4020 (2015).
28. Taubert, M. *et al*. Protein-SIP enables time-resolved analysis of the carbon flux in a sulfate-reducing, benzene-degrading microbial consortium. *ISME J.* **6**, 2291–2301 (2012).
29. Knox, S. H. *et al*. Agricultural peatland restoration: effects of land-use change on greenhouse gas (CO_2 and CH_4) fluxes in the Sacramento-San Joaquin Delta. *Glob. Change Biol.* **21**, 750–765 (2015).
30. Emery, H. E. & Fulweiler, R. W. Incomplete tidal restoration may lead to persistent high CH_4 emission. *Ecosphere* **8**, e01968 (2018).
31. NSW Department of Primary Industries. Acid Sulfate Soils Priority Investigations for the Lower Hunter River Estuary. Report to the Department of Environment, Water, Heritage and the Arts. Department of Primary Industries (Aquatic Habitat Rehabilitation), Port Stephens (2008).
32. Welti, N., Hayes, M. & Lockington, D. Seasonal nitrous oxide and methane emissions across a subtropical estuarine salinity gradient. *Biogeochemistry.* **132**, 55–69 (2017).
33. Dutaur, L. & Verchot, L. V. A global inventory of the soil CH_4 sink, Global Biogeochem. *Cy.* **21**, GB4013 (2007).
34. Myhre, G. *et al*. Anthropogenic and Natural Radiative Forcing. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change 659–740 (Cambridge University Press, Cambridge, United Kingdom and New York, 2013).
35. Neubauer, S. C. & Megonigal, J. P. Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosystems* **18**, 1000–1013 (2015).
36. Kim, D., Vargas, R., Bond-Lamberty, B. & Turetsky, M. R. Effects of soil rewetting and thawing on soil gas fluxes: a review of current literature and suggestions for future research. *Biogeosciences* **9**, 2459 (2012).
37. Schreiber, L., Holler, T., Knittel, K., Meyerdierks, A. & Amann, R. Identifi ation of the dominant sulfate-reducing bacterial partner of anaerobic methanotrophs of the ANME-2 clade. *Environ. Microbiol.* **12**, 2327–2340 (2010).
38. Lacono, M. J. *et al*. Radiative forcing by long-lived greenhouse gases: Calculations with the AER radiative transfer models. *J. Geophys. Res.* **113**, D13103 (2008).
39. Trenberth, K. E. Changes in precipitation with climate change. *Clim. Res.* **47**, 123–138 (2011).
40. Foken, T. *et al*. Post-fi ld data quality control. In: Lee, X., Massman, W. J., Law, B. E. (Eds), *Handbook of Micrometeorology: A Guide for Surface Flux Measurements*. 181–208 (Kluwer, Dordrecht,The Netherlands, 2004).
41. Kljun, N., Calanca, P., Rotach, M. W. & Schmid, H. P. A simple two-dimensional paramertisation for flux footprint predictions (FFP). *Geosci. Model Dev.* **8**, 3695–3713 (2015).
42. Caporaso, J. G. *et al*. Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. *P. Natl. Acad. Sci. USA* **108**, 4516–4522 (2011).
43. Hugerth, L. W. *et al*. DegePrime, a Program for Degenerate Primer Design for Broad-Taxonomic-Range PCR in Microbial Ecology Studies. *Appl. Environ. Microbiol.* **80**, 5116–5123 (2014).
44. Kozich, J. J., Westcott, S. L., Baxter, N. T., Highlander, S. K. & Schloss, P. D. Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina sequencing platform. *Appl. Environ. Microbiol.* **79**, 5112–20 (2013).

Acknowledgements

M. Ostrowski for access and use of microbiology lab, M. Kennedy for access to the eddy flux tower, and K. Tewari for fi ld support, ARC linkage grant LP140100460. We dedicate this paper to the memory of our colleague Grant Edwards, who passed away following the submission of this manuscript. Th s contribution would not have been possible without his scientific vision and technical proficie cy.

Author Contributions

K.N., J.K., D.H. and D.S. performed data analysis, with guidance under G.E. and N.S. K.N., N.S., J.K., G.E. and D.H. contributed to writing. K.N., N.S., G.E., J.K. and D.S. performed fi ld work.

Additional Information

Supplementary information accompanies this paper at https://doi.org/10.1038/s41598-019-40763-8.

Competing Interests: The authors declare no competing interests.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2019

Chapter 5: Modelling, Monitoring and Management

5.1 **Saintilan N.** and Rogers K. (2013). The significance and vulnerability of Australian saltmarshes: implications for management in a changing climate. *Marine and Freshwater Research* 64 66-79

5.2 **Saintilan N.,** Horton B., Tornqvist T., Perry C., Schuerch M., Kopp P., Garner G., Ashe A. Rogers K., Albert S., Kelleway J., Shaw T., Khan N, Woodroffe C. (2023). Widespread retreat of coastal habitat likely at warming levels above 1.5˚C**.** *Nature* 621 (7977) 112-119.

5.3 Sandi, S. G., Rodriguez, J. F., Saco, P. M., **N. Saintilan** & G. Riccardi 2021, 'Accelerated sea-level rise limits vegetation capacity to sequester soil carbon in coastal wetlands: a study case in southeastern Australia', Earth's Future, vol. 9, no. 9, pp. 1–24, doi:10.1029/2020EF001901

5.4 Rogers, K., Kelleway, J. J., & **Saintilan, N.** (2023). The present, past and future of blue carbon. *Cambridge Prisms: Coastal Futures*, *1*, e30.

5.5 **Saintilan, N**., Asbridge, E., Lucas, R., Rogers, K., Wen, L., Powell, M., & Lymburner, L. (2021). Australian forested wetlands under climate change: collapse or proliferation? *Marine and Freshwater Research*. 73 (10), 1255-1262

5.6 **Saintilan N**, Lymburner L., Wen L., Haigh I., Ai E., Kelleway J.J, Rogers K., Pham D., Lucas R. The lunar nodal cycle controls mangrove canopy cover on the Australian continent. *Science Advances 8*(37), eabo6602.

5.7 Rogers, K., **Saintilan, N.,** & Copeland, C. (2014). Managed retreat of saline coastal wetlands: challenges and opportunities identified from the Hunter River Estuary, Australia. *Estuaries and coasts*, *37*, 67-78.

5.8 Rijal, S. S., Pham, T. D., Noer'Aulia, S., Putera, M. I., & **Saintilan, N.** (2023). Mapping Mangrove Above-Ground Carbon Using Multi-Source Remote Sensing Data and Machine Learning Approach in Loh Buaya, Komodo National Park, Indonesia. *Forests*, *14*(1), 94.

5.9 Kelleway, J.J., Mazumder, D., Baldock, J.A. & **Saintilan, N.** 2018, 'Carbon isotope fractionation in the mangrove Avicennia marina has implications for food web and blue carbon research', Estuarine, Coastal and Shelf Science, vol. 205, pp. 68-74

5.10 **Saintilan, N**., Rogers, K., Kelleway, J.J., Ens, E., & Sloane, D. R. (2019). Climate change impacts on the coastal wetlands of Australia. *Wetlands*, *39*(6), 1145-1154

5.11 Rogers, K., Boon, P.I., Branigan, S., Duke, N.C., Field, C.D., Fitzsimons, J.A., Kirkman, H., Mackenzie, J.R. & **Saintilan, N.** 2016, 'The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services', Marine Policy, vol. 72, pp. 139-155

5.12 K. Rogers, Macreadie, P. I., Kelleway, J. J. & **N. Saintilan** 2019, 'Blue carbon in coastal landscapes: a spatial framework for assessment of stocks and additionality', Sustainability Science, vol. 14, no. 2, pp. 453–467, doi:10.1007/s11625-018-0575-0

CSIRO PUBLISHING

Marine and Freshwater Research, 2013, **64**, 66–79
http://dx.doi.org/10.1071/MF12212

Review

The significance and vulnerability of Australian saltmarshes: implications for management in a changing climate

Neil Saintilan[A,C] *and Kerrylee Rogers*[B]

[A]Office of Environment and Heritage, Department of Premier and Cabinet. PO Box A290, Sydney South, NSW 1232, Australia.
[B]School of Earth and Environmental Science,University of Wollongong, Northfields Ave, Wollongong, NSW 2522, Australia.
[C]Corresponding author. Email: neil.saintilan@environment.nsw.gov.au

Abstract. We review the distribution, status and ecology of Australian saltmarshes and the mechanisms whereby enhanced atmospheric carbon dioxide and associated climate change have influenced and will influence the provision of ecosystem goods and services. Research in temperate and subtropical saltmarsh has demonstrated important trophic contributions to estuarine fisheries, mediated by the synchronised mass-spawning of crabs, which feed predominantly on the C_4 saltmarsh grass *Sporobolus virginicus* and microphytobenthos. Saltmarshes also provide unique feeding and habitat opportunities for several species of threatened microbats and birds, including migratory shorebirds. Saltmarshes increased in extent relative to mangrove in Australia in both tide- and wave-dominated geomorphic settings through the latter Holocene, although historic trends have seen a reversal of this trend. Australian saltmarshes have some capacity to maintain elevation with respect to rising sea level, although in south-eastern Australia, the encroachment of mangrove and, in Tasmania, conversion of shrubland to herbfield in the past half-century are consistent with changes in relative sea level. Modelling of the impacts of projected sea-level rise, incorporating sedimentation and other surface-elevation drivers, suggests that the survival of saltmarsh in developed estuaries will depend on the flexible management of hard structures and other impediments to wetland retreat.

Additional keywords: accretion, sea-level rise, temperature, wetland.

Received 8 August 2012, accepted 1 November 2012, published online 6 February 2013

Introduction

The term saltmarsh refers to an ecosystem characterised by a taxonomically broad group of vascular plants occupying the intertidal shores of estuaries, characteristically including herbs, grasses and shrubs, but excluding mangroves and other tree-form vegetation. For the purpose of the present review, saltmarsh also includes bare or sparsely vegetated hypersaline flats (including sabhka) where productivity is dominated by cyanobacteria. Saltmarsh distribution globally favours regions where mangroves are excluded by frost (Long and Mason 1983; Mendelssohn and McKee 2000), and the Australian mainland littoral zone is one of a few regions globally where mangrove and saltmarsh show sympatric development. Mangroves have received the greater research and policy attention until recently; Fairweather (1990) described coastal saltmarsh as the least studied of coastal and marine ecosystems in Australia. Ignorance of the extent and ecological significance of coastal saltmarsh may have contributed to the widespread degradation and reclamation of this habitat over the past two centuries, and in recent years, the need for urgent conservation action has been reflected in the 2004 listing of coastal saltmarsh as a threatened ecological community in New South Wales (Hughes 2004), and the inclusion in 2010 of temperate and subtropical saltmarsh on the Finalised Priority Assessment List for national listing under the *Environmental Protection and Biodiversity Conservation* (*EPBC*) *Act*.

To an appreciable extent, our ignorance of the extent and ecology of coastal saltmarsh in Australia has been overcome in the past two decades, and the present paper provides a review of recent work. The research has highlighted the vulnerability of Australian coastal saltmarsh to climate-change impacts, in common with saltmarsh globally. Given their geomorphic situation within narrow elevation ranges in the intertidal zone, saltmarshes are sentinel ecosystems in the coastal zone and already the impacts of relative sea-level rise are being manifest (Lovelock *et al.* 2009; Saintilan *et al.* 2009*b*). Elevated atmospheric carbon dioxide, temperature rise, altered fire regimes, and a range of hydrological changes may also have an impact on saltmarshes, compounding the pressure of coastal development, vehicular impacts, pollution and invasive species (Adam 2009; McKee *et al.* 2012). The purpose of the present review is to provide an overview of our understanding of Australian

Journal compilation © CSIRO 2013

saltmarshes and their ecology, to identify the key climate-change impacts and appropriate management strategies, and to highlight knowledge gaps that continue to hinder the sustainable management of this significant resource.

Distribution of saltmarsh plants

Saltmarsh vegetation globally can be classed into the following six biogeographical types: Arctic, Boreal, West Atlantic, Temperate, Dry Coast, and Tropical (Adam 1990), with consistent regional differences in dominant saltmarsh families. For example, Arctic saltmarshes are dominated by species of the genera *Puccinellia* and *Carex*, Boreal saltmarsh along the North American Atlantic coast is characterised by *Spartina patens*, *S. alterniflora* in the low marsh, and *Triglochin maritima*, *Salicornia virginica*, and *Distichlis spicata* on the Pacific coast (McKee *et al.* 2012). Temperate saltmarsh on the Atlantic coast is dominated by *S. alterniflora*, grading into *Juncus*, *Salicornia* and *Distichlis* in the higher marsh (Isacch *et al.* 2006). Tropical saltmarshes are less well surveyed, and species composition varies between wetter communities (*Spartina patens*, *S. spartinae*, *D. spicata* in tropical America) and drier hypersaline environments where succulents dominate (*Batis maritima*, *Borrichia frutescens*, *Suaeda maritima* and *Sesuvium portulacastrum*) (McKee *et al.* 2012; C. Lovelock, pers. comm. 2012).

Saintilan (2009) lists 103 species of vascular plants occurring in Australian saltmarshes, and presents their distribution by bioregion (using the Interim Bioregionalisation of Australia: IBRA). A more comprehensive list of 140 species for Victoria is presented by Boon *et al.* (2011) who noted, at a family level, strong affinities with saltmarshes on other continents. Adam (1990) explained some of these as a strong Gondwanan affiliation, with similarities in the saltmarsh flora of temperate Australia, New Zealand and South Africa and temperate South America. For example, as much as 15% of the halophytic saltmarsh flora of Victoria is shared with New Zealand (Boon *et al.* 2011). A small number of less common species show remarkable trans-hemispheric disjunctions, such as the occurrence of *Limosella australis* on the southern coast of New South Wales (NSW), but also in Wales, and *Eleocharis parvula*, rare in Australian saltmarshes but common in the northern hemisphere (Adam 2009). Both instances are thought to be the result of migratory birds transporting seeds between continents, most probably some time ago (Adam 2009).

Species distribution and temperature

There have been few systematic surveys of saltmarsh species distribution in Australia, and records of saltmarsh assemblages in individual estuaries remain scant. However, records of species occurrence have been compiled by herbaria since European colonisation and these are now linked in the Australian Virtual Herbarium to provide a national extent sufficient to describe broad geographic trends. Saintilan (2009) used records from the Australian Virtual Herbarium to compare the distribution of 93 saltmarsh plant species across 36 coastal bioregions. The result was a clear distinction between a northern saltmarsh flora and a southern saltmarsh flora, with only one-quarter of species in common.

The northern and southern saltmarsh provinces are separated on the eastern coast immediately north of the South-east Queensland bioregion, where the Brigalow Belt bioregion reaches the coast. Whereas *Sporobolus virginicus* continues to be the dominant saltmarsh species north of this point, several species characteristic of the northern saltmarsh become important, including *Tecticornia australasica*, *Fimbristylis polytrichoides*, *Fimbristylis ferruginea*, *Portulaca bicolor*, *Batis agrillicola*, *Xerochloa imberbis* and *Sesuvium portulacastrum*. On the western coast of Australia, the same distinction is made within the Carnarvon bioregion to the north of Shark Bay. On both coasts, the Tropic of Capricorn (23°30′S) provides a useful approximation of the point at which the northern and southern biogeographic provinces meet, and they may, on this basis, be more accurately described as a tropical and subtropical or temperate saltmarsh flora.

In contrast to mangroves (Saenger *et al.* 1977), and indeed most biota (Qian *et al.* 2007), saltmarsh species diversity increases with increasing latitude in Australia (Adam 1996; Saenger *et al.* 1977; Specht 1981). The increase in diversity appears strongly linked to mean minimum daily temperature, explaining nearly 80% of variation in diversity among bioregions (Saintilan 2009). Diversity increases linearly with declining mean minimum daily temperature until a threshold of 8°C is reached, after which point diversity declines. Few experimental studies have explored the relationship between temperature and germination in saltmarshes, and there are no comparable analyses for other continents. Some studies have suggested an inverse relationship between temperature and germination success (Khan and Ungar 1984; Greenwood and MacFarlane 2006).

Species distribution and hydrology

Saltmarshes occur predominantly in low wave-energy coastal environments, although the species occupying saltmarshes in Australia may be located across a broader range of landscape settings. For example, all of the species of saltmarsh shrubs (genera *Tecticornia* and *Maireana*) found in saltmarshes can be found in inland saline wetlands, and have no obvious preference for coastal environments (Saintilan 2009). The diversity of saltmarsh shrubs and their frequent occurrence in southern Australian saltmarshes may reflect recruitment from interior arid and semiarid wetlands. Most of the common saltmarsh grass and herb species are found predominantly, but not exclusively, in coastal saltmarsh environments (e.g. *Sarcocornia quinqueflora*, *Juncus kraussii*, *Ficinia nodosa*, *Selliera radicans*, *Gahnia filum*). Only a small proportion of species found in saltmarshes are found exclusively on the coast (these include *Austrostipa stipoides*, *Batis argillicola*, *Baumea juncea*, *Limonium australe*, *Limonium solanderi*, *Suaeda arbusculoides* and *Sesuvium portulacastrum*; Saintilan 2009).

Kirkpatrick and Glasby (1981), in their study of Tasmanian saltmarshes, classified the structural forms into the following four distinct groupings: communities dominated by succulent shrubs (e.g. *Tecticornia* spp.); communities dominated by low grasses (e.g. *Sporobolus virginicus*, *Zoysia macrantha*); communities dominated by sedges and tall grasses (e.g. *Juncus kraussii*; *Gahnia filum*); and communities dominated by herbs (e.g. *Sarcocornia quinqueflora*, *Wilsonia backhousei*, *Samolus*

repens). The structural classification is useful in that these forms often present zonations across the intertidal zone, although the nature of these zonations varies among climatic regions.

Mangroves are absent from Tasmania, sections of the temperate western Australian coastline, and several intermittently closed and open lakes and lagoons on the temperate eastern coast. However, for most of the Australian mainland coastline, mangroves dominate the lower- to mid-intertidal zones, restricting saltmarsh development to elevations between mean high tide and the highest astronomical tides. In the temperate and subtropical eastern coast, a herbfield and grassland dominated by *Sarcocornia quinqueflora*, *Sporobolus virginicus*, *Samolus repens* and *Triglochin striata* gives way in the upper intertidal to tall sedges and grasses. In the cooler temperate saltmarshes of Victoria, Tasmania and South Australia, shrubs of the genus *Tecticornia* dominate the lower- and mid-intertidal zone, with diverse herbfields and grasses more common in the upper intertidal (Boon *et al.* 2011).

The distribution of structural components of intertidal vegetation in Australian coastal wetlands appears related to the frequency of tidal inundation and aridity (Clarke and Hannon 1969; Clarke and Hannon 1970; Boon *et al.* 2011). Mangroves characteristically occupy flats inundated on most days, and this inundation reduces desiccation of propagules (Clarke and Myerscough 1993), and variability in soil salinity. At higher elevations in the intertidal zone, inundation becomes increasingly infrequent and varies with phases of the monthly spring tide cycle. The lower inundation frequency of the upper intertidal corresponds to a change from nitrogen to phosphorus limitation in mangroves and their stunted growth (Feller *et al.* 2003). Salinity is more variable than in the lower intertidal, being more susceptible to evaporative concentration of salts, and rapid dilution following rainfall. The upper-intertidal zone is therefore more likely to reflect regional differences in aridity. The upslope zonation of 'wet' shrub-dominated marshes to herbfields in Victorian saltmarshes (Barson and Calder 1981) is also reflected in east–west transition to increasing herb-dominated arid saltmarshes (Boon *et al.* 2011).

Although most saltmarsh plants are tolerant of saltwater, and some species (including *Sarcocornia*) can germinate in seawater salinities or greater, many saltmarsh species require periodically fresher conditions to recruit sexually (Adam 1990; Boon *et al.* 2011). For example, *Juncus kraussii* shows optimal germination in brackish to fresh water (Greenwood and MacFarlane 2006; Naidoo and Kift 2006), and fails to germinate in seawater. Saltmarsh diversity may therefore be more vulnerable to the consequences of ground- and surface-water diversions than the prevailing salinity conditions may indicate.

Saltmarsh distribution and geomorphology

With the exception of Tasmania where mangroves are absent, saltmarsh typically occupies the upper-intertidal zone, predominantly between mean high tide and mean spring tide, whereas mangrove occupies the lower-intertidal zone. The interaction of hydrology and geomorphology controls the degree of marine and fluvial sedimentation, the development of intertidal flats and ultimately the conditions suitable for saltmarsh establishment. Harris and Heap (2003) conceptualised river, wave and tide power along the length of estuaries, with optimal conditions for sediment deposition and saltmarsh development invariably occurring within the central mud basin of wave-dominated estuaries and the meandering channels of tide-dominated estuaries. The spatial distribution of depositional environments exhibits strong regional zonation and provides insight into the geomorphic settings of saltmarsh around Australia. Specifically, Harris *et al.* (2002) found that the south-eastern and south-western coasts of Australia are predominantly wave-dominated environments, whereas northern coastal areas are tide dominated.

Estuaries of tropical northern Australia are primarily tide dominated, with macrotidal regimes and seasonal flooding (Harris *et al.* 2002). Woodroffe *et al.* (1993) demonstrated a consistent 'big swamp' phase where mangrove dominated estuarine plains during the mid-Holocene for many tide-dominated settings. This phase was succeeded by further infilling and the development of hypersaline flats in dryer areas and plains vegetated with salt-tolerant plants in the upper-intertidal and supra-tidal environments. In contrast, the position of large sand islands (e.g. Moreton Island, North and South Stradbroke Island and Fraser Island) along the coastline of south-eastern Queensland shelters the coastal mainland and the leeward side of the islands from wave action (Saintilan *et al.* 2009*a*). This has created conditions suitable for the establishment of saltmarsh. Saltmarsh has developed on the leeward side of sand islands, on the back barrier deltaic deposits, and in the channels and channel-fringing flats of large mesotidal rivers.

The south-eastern Australian coastline largely comprises wave-dominated barrier estuaries in various evolutionary stages (Roy *et al.* 2001). Saltmarsh establishment is generally restricted to the central mud basin where low-energy conditions prevail (Harris and Heap 2003). Where the entrance is open or more intermittently open, both mangrove and saltmarsh colonise the intertidal zone. Saltmarsh may dominate when tidal exchange is restricted by a closed or more intermittently closed entrance; under these conditions, water levels may exceed the height of mangrove pneumatophores, thereby excluding their growth or causing widespread dieback. In Tasmania, the absence of mangroves allows saltmarsh to occupy a greater portion of the intertidal zone within wave-dominated estuaries; here, saltmarsh is common on the highly indented wave-dominated south-eastern coast (Kirkpatrick and Glasby 1981).

Tide-dominated estuaries in NSW, classified as 'drowned river valleys' (Roy 1984), occur along the central coast of NSW and at Batemans Bay in association with the Lachlan Orogen. These estuaries provide a range of settings suitable for saltmarsh establishment, although large intertidal flats rarely develop because of the deeply incised bedrock valleys that these estuaries occupy. Saltmarsh in these tide-dominated settings occurs on the meandering fluvial channel in the upper reaches of the estuary where tidal power diminishes, on fluvial deltas that develop where tributaries enter deeper waters within the drowned river valley, in the upper-intertidal zone of cut-off embayments, and on back-barrier sands near the estuary mouth (Saintilan *et al.* 2009*a*). Tide-dominated estuaries also occur in north-western Tasmania where entrances are protected from waves by large sand bars and islands, enabling saltmarsh to develop in the relatively protected environments on the open coast, although they are increasingly exposed to erosion.

The large marine embayments in Victoria and South Australia support wide-fringing saltmarsh plains. These include wave-dominated estuaries, such as the Gippsland Lakes and Barwon River in Victoria, the Coorong in South Australia, and Davenport River near Ceduna in South Australia, and tide-dominated estuaries, such as Corner Inlet, Westernport Bay and Port Phillip Bay in Victoria, and the Spencer Gulf and Gulf St Vincent in South Australia (Saintilan *et al.* 2009*a*). Limited wave power in tide-dominated estuaries allows extensive flats to develop in southern Australia; this is particularly prominent in Westernport Bay where saltmarsh occurs almost continuously around the shore in the upper-intertidal zone and on the northern shores of French Island and Philip Island (Boon *et al.* 2011). Limited wave and river power on the tide-dominated estuaries of Gulf St Vincent and Spencer Gulf create conditions of increasing salinity with increasing distance from the ocean; these 'inverse estuaries' have vast low-lying areas and hyper saline soils able to support extensive saltmarsh vegetation (Saintilan *et al.* 2009*a*).

Extensive saltmarsh occurs throughout Western Australia, although its distribution is documented primarily in grey literature. Here, saltmarsh geomorphological settings largely mirror the eastern coast of Australia; extensive saltmarsh occurs within the tide-dominated estuaries of the northern coastline such as the Ord and Fitzroy rivers, whereas smaller areas are located within wave-dominated estuaries and marine embayments of south-western Australia, such as Peel–Harvey estuary and Leschenault Inlet (Pen *et al.* 2000; Bridgewater and Cresswell 2003).

Recent changes in the extent of Australian saltmarsh

The Holocene evolution of tide- and wave-dominated environments provides valuable information regarding the response of saltmarsh to sea level and a context for the interpretation of recent changes. Estuaries dominated by tidal processes, typical of the tropical north-west, are characterised by wide upper-intertidal and supra-tidal blacksoil plains, devoid of vegetation in drier climates, or supporting saltmarsh in wetter areas (Woodroffe *et al.* 1989). Mangroves are restricted to channel-fringing environments (Woodroffe *et al.* 1985); however, in the mid-Holocene, they were far more extensive, occupying the greater part of the floodplains of the Fitzroy, Ord, Daly and Alligator Rivers (Thom *et al.* 1975; Woodroffe *et al.* 1985). The replacement of mangrove by saltmarsh and salt flats occurred as a result of estuarine infilling (Woodroffe *et al.* 1985).

Wave-dominated estuaries are largely comprised of a river-dominated bay-head delta and alluvial plain at the head, a low-energy central mud basin, and a coastal barrier with flood- and ebb-tide deltas at the entrance. Evolution of wave-dominated estuaries is well documented (Roy *et al.* 1980, 2001; Roy 1984), particularly for south-eastern Australia. Following barrier development under stable sea level conditions, the central mud basin infills with sediment and diminishes in size as a result of the seaward expansion of the bay-head delta and landward extension of the flood-tide delta. Saltmarsh and mangrove largely develop around the margins of the central mud basin; over time, the extent of these intertidal communities gradually increases as the basin infills until the point when the intertidal zones succeed to supra-tidal alluvial floodplain (Roy *et al.* 2001; Hashimoto *et al.* 2006). The replacement of mangrove by saltmarsh has been demonstrated in stratigraphic studies in barrier estuaries (Saintilan and Wilton 2001) and drowned river valleys (Saintilan and Hashimoto 1999) in south-eastern Australia.

In contrast to the longer-term Holocene trend of saltmarsh expansion within tide- and wave-dominated estuaries, historical trends have seen mangrove replace saltmarsh. Saintilan and Williams (1999) reviewed 28 surveys of mangrove and saltmarsh extent in estuaries and embayments in temperate and subtropical Australia, demonstrating a consistent pattern of mangrove expansion at the expense of saltmarsh. To these can be added surveys in Victoria for Westernport Bay (Rogers *et al.* 2005*b*); in NSW for Minnamurra River (Oliver *et al.* 2012), Homebush Bay (Rogers *et al.* 2005*a*), Jervis Bay (Saintilan and Wilton 2001) and multiple sites in NSW (Wilton 2002); and in Queensland for Moreton Bay (Manson *et al.* 2003; Eslami-Andargoli *et al.* 2009) and Pioneer River (Jupiter *et al.* 2007). A gradual extension of tidal marine influence has also been observed in the tide-dominated estuaries and coastal plains of northern Australia, with saltwater intrusion causing widespread changes in coastal vegetation in the Alligator River region (Winn *et al.* 2006), and the Mary River (Knighton *et al.* 1991; Mulrennan and Woodroffe 1998). Mangroves in the Kakadu region have expanded their range into the upper-intertidal environments by 16% over a 30-year period from 1974 (Williamson *et al.* 2011).

The causes of mangrove encroachment into saltmarsh remains a topic of active investigation. Research from south-eastern Queensland indicates that factors driving mangrove encroachment of saltmarsh may vary depending on prevailing climatic conditions and catchment land-use patterns (Eslami-Andargoli *et al.* 2009; Eslami-Andargoli *et al.* 2010). In the Kakadu region, above-average ocean water levels may be assisted by drier than average monsoonal conditions and the local influence of feral buffalo (Knighton *et al.* 1991; Winn *et al.* 2006). Mangrove expansion has been coincident with the expansion of woody terrestrial vegetation in the region, prompting Williamson *et al.* (2011) to propose that a common driver, such as elevated atmospheric carbon dioxide concentrations, might be at least partly responsible. Rogers *et al.* (2006) also demonstrated that observed rates of encroachment of mangrove into saltmarsh in south-eastern Australia exhibited a strong relationship with relative sea-level rise, which accounted for both the eustatic component of sea-level rise and compaction of the saltmarsh surface; more so, the trend of mangrove encroachment of saltmarsh may be related to adjustment of mangrove within the tidal prism, in association with recent rates of sea-level rise. Loss in saltmarsh extent and changes in saltmarsh community composition are also occurring in the absence of mangrove in south-eastern Tasmania and is attributed to sea-level rise, higher wave energy and direct human modification (Prahalad *et al.* 2011).

Processes influencing marsh surface elevation

Saltmarshes will be affected by sea-level rise if they are unable to sustain elevation with respect to water levels (termed relative elevation (Reed 1990)). Surface elevation tables (SETs) have

been employed in Australia (Rogers *et al.* 2006; Lovelock *et al.* 2011) and internationally (Cahoon *et al.* 2006), to investigate processes that may influence saltmarsh surface elevations. SETs are a precise and non-destructive method for measuring fine-scale changes in wetland surface elevations (Cahoon *et al.* 2002*a*, 2002*b*; Cahoon 2006*b*). The application of SETs in Australia has demonstrated a common discrepancy between the degree of elevation change and accretion, driven largely by processes that act to compact saltmarsh soils (Rogers *et al.* 2006; Lovelock *et al.* 2011). The degree of wetland compaction in mangrove and saltmarsh in south-eastern Australia has been correlated with fluctuations in groundwater depth, rainfall and the Southern Oscillation Index (Rogers and Saintilan 2008; Rogers *et al.* 2005*a*), which all varied in association with a severe El Niño–Southern Oscillation (ENSO)-related drought between 2001 and 2004. Lovelock *et al.* (2011) attributed compaction of wetland soils to soil characteristics, with muddy highly organic soils undergoing a greater compaction than sandy soils. Instances where elevation gain exceeded the degree of accretion have been attributed to biological processes of below-ground root development (Rogers *et al.* 2005*a*) and abandoned salt evaporation ponds that altered the hydrological regime of saltmarsh (Rogers *et al.* 2005*b*).

Although wetland hydrology and soil characteristics influence saltmarsh elevations, accretion of mineralogic and organic material is the dominant process of saltmarsh building in Australia (Rogers *et al.* 2006; Lovelock *et al.* 2011), which contrasts with peat-dominated settings in the northern hemisphere (Redfield 1972; Nyman *et al.* 2006; McKee *et al.* 2007; McKee 2011). Analysis of the SET record from south-eastern Australia between 2000 and 2010 (Rogers and Saintilan 2011) indicated that saltmarshes (and mangroves) exhibiting a greater relative elevation gain also exhibited a greater contribution of accretion to elevation gain (Fig. 1); hence, sediment supply and accretion may be essential for the long-term maintenance of saltmarsh in south-eastern Australia.

The maintenance of relative elevation in reasonably undisturbed saltmarshes in the northern hemisphere led to the concept of a marsh equilibrium elevation, whereby marsh surfaces fluctuate with sea-level change (Pethick 1981). The concept relies on low-elevation marshes building elevation (primarily through accretion) to be situated at an optimal height within the tidal prism, whereas high-elevation marshes build elevation at a slower rate (or may be reworked) to water-level changes. This inundation-dependent accretion scheme (see Fagherazzi *et al.* 2012 for review of numerical marsh evolution models) appears to be holding true in Australia under current rates of sea-level rise; strong relationships have been established between accretion and tidal range or hydroperiod (Rogers *et al.* 2005*a*, 2006), and there is little evidence of saltmarsh loss as a result of submergence. Preliminary assessments suggest that the few instances of saltmarsh loss related to water-level changes may be driven by fetch-related alterations to wind waves. Models of saltmarsh evolution are required to establish whether this equilibrium response fails when rates of saltmarsh elevation gain are too low (facilitated by insufficient sediment supply and/or plant productivity, or high soil compaction) or the rate of sea-level rise is too high for feedbacks between processes to respond accordingly.

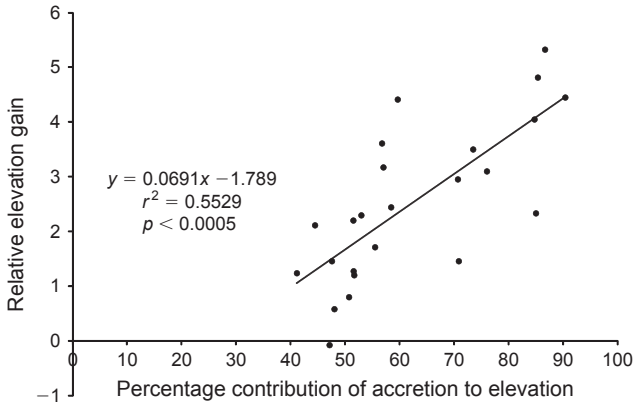


Fig. 1. Relationship between the contribution of accretion to elevation gain and elevation deficit within mangrove and saltmarsh at study sites in south-eastern Australia.

Modelling marsh responses to sea-level rise

Models of saltmarsh response to sea-level rise incorporate relationships between saltmarsh elevation, processes that influence saltmarsh elevation (such as e.g. accretion, plant productivity and sediment supply), and changes to the tidal prism. These models are becoming increasingly complex (Rybczyk and Callaway 2009; Fagherazzi *et al.* 2012), attempt to integrate both morphologic and ecological components of marsh evolution (D'Alpaos *et al.* 2007; Kirwan and Murray 2007) and have been coupled with models of adjoining systems, such as tidal flats (Mariotti and Fagherazzi 2010). This is an emerging area of saltmarsh research in Australia. SETs have been used to demonstrate that saltmarshes within south-eastern Australia exhibit low vulnerability to submergence (Rogers 2004; Rogers and Saintilan 2011), although with the caveat that rates of accretion and elevation adjustment continue and that sea level continues to rise at relatively low rates that are consistent with recent trends.

Projections of the likely response of saltmarsh to moderate rates of sea-level rise indicate that saltmarsh may be in serious decline by the end of the century. Several techniques have been employed to project changes in saltmarsh extent, including simple "bath-tub" models (Traill *et al.* 2010; Boon *et al.* 2011) that assume static wetland surfaces and do not account for morphological change occurring in conjunction with sea-level rise, the sea-level affecting marshes model (SLAMM; Clough *et al.* 2010; Akumu *et al.* 2011; Traill *et al.* 2011) and statistical techniques relying on empirical data (Oliver *et al.* 2012; Rogers *et al.* 2012). Oliver *et al.* (2012) demonstrated that model responses are highly dependent on the parameters employed within the model. However, with the exception of bath-tub techniques, all models indicate that coastal wetlands may have some capacity to adapt to low rates of sea-level rise. Under high rates of sea-level rise, the capacity to adapt is constrained by the morphology of coastal floodplains, development within coastal floodplains and management to facilitate

wetland conversion. K. Rogers (unpubl. data) explored the inherent adaptive capacity of estuarine wetlands on the Hunter River, to demonstrate that under high and accelerating rates of sea-level rise, thresholds of resilience may become exhausted after 2060. By 2100, these wetlands were projected to be located behind existing levee banks; adaptation will be dependent on the reinstatement of tidal exchange to these new communities.

Ecological significance of saltmarsh

Carbon and aquatic foodwebs

Mangroves have long been recognised as playing a significant role in estuarine and near-shore fisheries, and more recently the unique contribution of saltmarsh as a habitat for fish in Australian estuaries has been assessed. The density of fish recorded in Australian saltmarshes varies greatly among settings, with generally fewer individuals found in South Australian marshes than in the temperate and tropical marshes of the Australian eastern coast (Connolly *et al.* 1997; Bloomfield and Gillanders 2005; Connolly 2005).While the density of fish recorded in Australian saltmarshes appears to be lower than that encountered in mangroves on a unit-area basis, and in comparison to northern hemisphere saltmarshes (Shenker and Dean 1979), this may largely be explained by the occurrence of saltmarsh in the upper-intertidal zone in Australia, and the shallower depth and duration of inundation (Connolly 2009). When converted to density of fish per unit volume of water, fish density in saltmarsh in the Sydney region is comparable to adjacent mangroves (Mazumder *et al.* 2005). A study of fish assemblages in adjacent seagrass, mangrove and saltmarsh indicated that species appearing in the flooded mangrove and saltmarsh had left the seagrass habitat, which declined in fish abundance during spring tides (Saintilan *et al.* 2007).

Although systematic surveys of saltmarsh nekton diversity are scant, early evidence suggests a latitudinal cline, with higher diversity of species in lower latitudes than in higher latitudes (Mazumder *et al.* 2006). The fact that latitudinal cline in fish diversity is inversely related to floristic diversity in Australian saltmarshes would indicate that diversity is driven by a more diverse assemblage of species occupying tropical estuaries, rather than structural and niche diversity within the saltmarsh environment. Saltmarsh fish assemblages are dominated by small fish of the families Ambassidae, Atherinidae and Gobiidae (Connolly 2009). However, many species of commercial importance also visit the saltmarsh. Very high densities of banana prawns (*Fenneropenaeus merguiensis*) have been observed (Connolly 2005), and the mullet *Liza argentea* is commonly found as juveniles in saltmarshes in temperate south-eastern Australia. Surveys have recorded bream (*Acanthropagrus australis*), flathead (*Platycephalus fuscus*), whiting (*Sillago ciliata*), school prawns (*Metapenaeus macleayi*) (Mazumder *et al.* 2006; Connolly 2009) and squid (D. Mazumder, unpubl. data).

The inundated saltmarsh plain provides a unique feeding opportunity for fish. Crabs occupying the saltmarsh synchronise their larval production and release with the monthly spring tides (Mazumder *et al.* 2009), and the density of crab larvae within the saltmarsh during spring tide inundation is such that overall zooplankton density is higher at these times than in any other estuarine environment (Mazumder *et al.* 2009). Visiting zooplanktivorous fish are able to feed efficiently and voraciously during their brief residence on the saltmarsh plain (Hollingsworth and Connolly 2006; Platell and Freewater 2009), as do some species of commercial importance (Mazumder *et al.* 2006); gut fullness of ambassids leaving the saltmarsh is consistently and substantially greater than that of fish sampled from other shallow estuarine environments (Hollingsworth and Connolly 2006). Snail larvae may similarly make a contribution to the diet of some species (Mazumder *et al.* 2009). Larger predatory fish are often observed at the mouths of tidal channels draining the saltmarsh, and Mazumder *et al.* (2011) were able to demonstrate a trophic relay from the saltmarsh to the broader estuary, with zooplanktivores and omnivores feeding periodically within the inundated saltmarsh.

Grazing crabs therefore occupy a keystone position in the saltmarsh ecosystem, transforming carbon into forms utilised by a range of fish species. The most commonly encountered and wide-ranging saltmarsh crab is *Helograpsus haswellianus* (Grapsidae), being common in Tasmania (Richardson *et al.* 1998), South Australia (Imgraben and Dittman 2008), NSW (Mazumder and Saintilan 2003; Morrisey 1995), and south-eastern Queensland (Skilleter and Warren 2000). *H. haswellianus* was primarily responsible for larval export from the saltmarsh at Towra Point, NSW (Mazumder *et al.* 2006). Three other species of burrowing crab are common in temperate Australia, including two Grapsidae (*Paragrapsus laevis* and *Parasesarma erythrodactyla*) and one Ocypodidae (*Heloecius cordiformis*). In south-eastern Queensland, *Australoplax tridentata* replaces *H. cordiformis* as the common ocypodid in the saltmarsh (Skilleter and Warren 2000).

A range of food items is available to crabs in the saltmarsh; these include living saltmarsh plant material, plant detritus, including mangrove and seagrass detritus transported by the flood tide, microphytobenthos, and organisms deposited by the high tide, including copepods and amphipods, one third of which are retained in the saltmarsh following spring tide inundation (Mazumder *et al.* 2009). Shore crabs are opportunistic scavengers, with wide dietary tolerances, and determining the relative contributions of these sources of nutrition can be challenging, given the highly masticated nature of crab gut contents. However, crab foraging in saltmarsh is highly localised (Guest and Connolly 2004; Guest *et al.* 2004), and recent studies have utilised the contrasting stable isotope signatures of the common C_4 grass *Sporobolus virginicus* and C_3 plants, including mangroves and chenopod saltmarsh plants, which are relatively depleted in ^{13}C (Guest and Connolly 2006; Guest *et al.* 2006; Mazumder and Saintilan 2010), to distinguish contributing food sources. Microphytobenthos is intermediate between these two signatures, although may be locally influenced by dissolved inorganic carbon from the C_4 grass (B. Alderson and D. Mazumder unpubl. data). These studies have suggested that *S. virginicus* is an important source of nutrition for crabs in saltmarsh (Guest and Connolly 2004), although probably more so in the subtropics where the grass is the dominant autotroph. In temperate latitudes, microphytobenthos appears more important, as does a broader range of saltmarsh plant and detrital sources (Saintilan and Mazumder 2010; B. Alderson and D. Mazumder unpubl. data).

Saltmarsh molluscs, including snails, slugs, bivalves and limpets, predominantly live on saltmarsh surfaces and vegetation. These are generally regarded to be epifaunal, although some infaunal species may bury within saltmarsh soils (Ross *et al.* 2009). Saltmarsh vegetation creates a complex arrangement of microhabitats for molluscs, although a broad distribution pattern is apparent within wetlands of NSW, with *Ophicardelus* species and *Littoraria luteola* being restricted to saltmarsh habitats, and *Phallosmedusa solida*, *Cassidula zonata* and assimineids largely occurring in the upper mangrove forest and saltmarsh (Kaly 1988; Ross *et al.* 2009). Studies have suggested that the diversity and abundance of molluscs in saltmarsh correlates with vegetation (Ross *et al.* 2009). In contrast, research from Tasmania proposed that the composition of molluscs in saltmarshes was not related to plant assemblages (Richardson *et al.* 1998), although Ross *et al.* (2009) suggested that this may relate to the absence of mangrove from Tasmania and the occurrence of saltmarsh at higher elevations in NSW.

Molluscs in saltmarsh play an important trophic role as consumers and prey, yet relatively little research in Australia has focussed on their contribution to estuarine foodwebs. Observations have revealed that snails and slugs consume plant detritus, microalgae and other organic matter from the saltmarsh surface or saltmarsh vegetation (Hutchings and Recher 1981; Ross *et al.* 2009). Direct herbivory of saltmarsh vegetation was confirmed by isotope analysis by Saintilan and Mazumder (2010), and there is evidence of correlations between food available for direct herbivory and mollusc density (Ross *et al.* 2009), although this may also relate to provision of shelter by specific saltmarsh plants (Richardson *et al.* 1998). Recent research from the USA has highlighted the role of molluscs in saltmarsh die-off, by selectively consuming saltmarsh vegetation (Gedan *et al.* 2009); however, the role of herbivorous molluscs as habitat modifiers and top-down consumers has not been observed in Australia, and requires further attention. Mollusc adults and larvae are also prey for a range of estuarine predators, including eels, crabs, fish, waterbirds and mammals (Roach 1998; Hollingsworth and Connolly 2006; Mazumder *et al.* 2006); these molluscs and other invertebrates appear to make an important contribution to the diet of fish feeding in saltmarsh (Mazumder *et al.* 2006).

Although saltmarshes provide habitat for a range of invertebrates, they are well known for the provision of habitat for pestiferous and vector mosquitoes, including *Aedes vigilax*, which largely occurs in tropical and subtropical climates, *Aedes camptorhynchus*, which occurs in cooler climes, and *Aedes alternans*, which is less common but has a wider distribution (Dale and Breitfuss 2009). These invertebrates transmit a variety of arbovirus diseases, including Ross River and Barmah Forest viruses, which are debilitating and have an economic impact on healthcare resources and productivity. As a consequence, saltmarsh mosquito research has largely focussed on strategies to limit mosquito abundance and the transmission of viruses (see, for example, Williams *et al.* 2009; Hu *et al.* 2010; Knight *et al.* 2012).

Strategies to control mosquito populations include habitat modification to maintain or restore tidal flooding, chemical control using non-specific chemicals to limit the abundance of adult mosquitoes, and biological control facilitated by the consumption of larvae by fish and shrimp (Morton *et al.* 1987, 1988; Morris *et al.* 2002). *Pseudomugil signifer*, a small fish commonly found in saltmarsh, was found in laboratory studies to prey on mosquito larvae but was satiated at moderate densities (Willems *et al.* 2005). Mosquito control in Australia has largely focussed on runnelling to promote tidal exchange; chemical control is generally only implemented under emergency situations where there is a risk of disease transmission to humans, whereas biological control is currently ineffective at controlling vector mosquitoes (Dale and Breitfuss 2009). It is apparent that integrated approaches have the greatest success, as in the Northern Territory where drainage channels are maintained annually and supplemented with aerial spraying. This research in Northern Territory also indicates that when undertaken effectively, the cost of large-scale habitat modification to control mosquitoes may be offset by the added benefit of saltmarsh restoration facilitated by the reinstatement of tidal exchange (Jacups *et al.* 2012). However, these management approaches should also consider the impact on non-target species, such as fish, which have been found to exhibit lower abundance in the vicinity of saltmarsh runnels, perhaps in response to limited prey availability (Connolly 2005).

Physical habitat structure and itinerant vertebrates

Large vertebrate animals also use Australian saltmarshes. In this regard, saltmarsh is perhaps best known for providing roosting and foraging habitat for waterbirds; however, they also provide feeding habitat for terrestrial birds, insectivorous bats, the water mouse (*Xeromys myoides*) and a range of incidental visitors, including macropods (e.g. swamp wallaby (*Wallabia bicolor*), eastern grey kangaroo (*Macropus giganteus*)), reptiles and amphibians (goannas and monitors (*Varanus* species), red-bellied black snakes (*Pseudechis porphyriacus*), estuarine crocodiles (*Crocodylus porosus*) eastern long-necked turtles (*Chelodina longicollis*)) and numerous introduced animals (rabbits, foxes, rats and hares) (Laegdsgaard *et al.* 2009). The habitat role that saltmarsh plays for these vertebrate species is significant; for example, the water mouse, which nests within saltmarsh, mangrove and coastal freshwater wetlands, is vulnerable at international, national and state levels (IUCN; Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999*; Queensland *Nature Conservation* (*Wildlife*) *Regulation 1994*). Availability of suitable habitat may be a strong limiting factor on the distribution and abundance of the water rat (Russell and Hale 2009). Few studies have documented the importance of saltmarsh to insectivorous bats; however, Laegdsgaard *et al.* (2004) detected eight insectivorous bat species over saltmarsh, with saltmarsh noted to provide significant foraging benefit to *Chalinolobus gouldii*, *Mormopterus ridei* and *Vespadelus* species, because they commonly avoid foraging in open habitats. Recorded feeding buzzes from insectivorous bats over saltmarsh reportedly coincide with the emergence of mosquitoes following spring high tides (Belbasé 2005; Gonsalves *et al.* in press).

The habitat role that saltmarsh plays for waterbirds is well documented (Laegdsgaard *et al.* 2009); they provide feeding habitat for terrestrial birds, including birds of prey (e.g. swamp harrier (*Circus approximans*), whistling kite (*Haliastur*

spehnurus)), small passerines (e.g. endemic species white-fronted chat (*Epthianura albifrons*), and little grassbird (*Megalurus gramineus*)); they act as a refuge for common colonial waterbird species when inland wetlands may be dry (e.g. Australian white ibis (*Threskiornis molucca*), cattle egret (*Ardea ibis*)) (Kingsford and Norman 2002); they act as a drought refuge for Australian breeding shorebird species, and some species are reported to breed in saltmarsh when conditions are not favourable elsewhere (e.g. black winged stilt (*Himantopus himantopus*), and masked lapwing (*Vanellus miles*)) (Marchant and Higgins 1993). Migratory shorebird species roost and feed in intertidal environments, with many species avoiding mangrove in preference to the open expanse of saltmarsh (Zharikov and Milton 2009). Shallow saltmarsh pools are particularly important as a night roost in the Hunter estuary (Spencer *et al.* 2009). As signatory to agreements with China (China–Australia Migratory Bird Agreement, CAMBA), Japan (JAMBA) and the Republic of Korea (ROKAMBA) aimed at maintaining migratory shorebird habitat, Australian authorities must consider the preservation of habitat values of saltmarsh. In addition, the habitat role that wetlands play for waterbirds has also ensured that several saltmarsh wetlands in Australia are included on the 'list of wetlands of international importance' identified under the Ramsar Convention, including Moreton Bay, Hunter Estuary Wetlands, Towra Point Nature Reserve, Corner Inlet, Western Port, The Coorong and Peel–Yalgorup System.

Despite these efforts to conserve saltmarsh as waterbird habitat, recent analyses have highlighted trends of declining abundance of many shorebird species that use the eastern Asian–Australasian flyway in Moreton Bay (Wilson *et al.* 2011) and other sites (Wetlands International 2006). Several causes have been identified for this decline, including climate-change influences on breeding habitat in the Arctic, loss of stopover sites throughout Asia, and reduction in area and quality of non-breeding grounds primarily in Australia (Wilson *et al.* 2011). An analysis of shorebird abundance data from Moreton Bay established that selection of safe and open supra-tidal roosting sites, including supra-tidal spits and sandbars and saltmarsh in the upper intertidal, was strongly affected by proximity to a large foraging area, field of view and the composition of the surrounding landscape (Zharikov and Milton 2009); decline in the availability of roosting sites with these characteristics may influence the abundance of shorebirds. Similarly, a recent study highlighted the decline in the Sydney region of the small passerine white fronted chat (*Epthianura albifrons*), which is predominantly found in saltmarsh, and found the species was particularly sensitive to human-induced disturbance and habitat loss. Population declines for birds relying on saltmarsh highlight the need for a review of existing management plans and the preparation of recovery plans for species in serious decline (Jenner *et al.* 2011).

Biomass, nutrient cycling and carbon sequestration

Mangrove and saltmarsh are among the most efficient ecosystems globally at sequestering carbon (Pidgeon 2009), a capacity that currently places these wetlands at the forefront of scientific and policy interest. 'Blue Carbon', as it is commonly known, is the potential of marine ecosystems to trap and bury atmospheric carbon dioxide (Nellemann *et al.* 2009). This efficiency occurs because methane emissions are dramatically reduced in environments where methanogenic bacteria are inhibited by salt (Poffenbarger *et al.* 2011), and because the biogeochemical conditions in tidal wetlands are conducive to long-term carbon retention (DeLaune *et al.* 1990; Choi and Wang 2004). A review by Duarte *et al.* (2005) reported a mean organic carbon burial rate of 1.51 Mg ha year^{-1} for saltmarsh (maximum 17.2 Mg ha year^{-1}), exceeding the maximum burial rate of undisturbed Amazonian forest (1.02 Mg ha year^{-1}) (Grace *et al.* 1995; Nellemann *et al.* 2009).

However, Australian saltmarsh communities are likely to vary greatly in their capacity to fix and bury carbon. Livesley and Andrusiak (2012) sampled in the *Sclerostegia* saltbush in Westernport Bay, Victoria, which they estimated to be relatively high in carbon store (105.7 Mg C ha^{-1}). Saltbushes of the genus *Sclerostegia* and *Halosarcia* (or *Tecticornia* following Shepherd and Wilson 2007) dominate saltmarsh communities in southern Australia, and Livesley and Andrusiak (2012) have provided the only quantified record for this community type. The saltmarsh rush *Juncus kraussii* maintains a high above-ground productivity in NSW (0.81 kg m^{-2} year^{-1}) (Clarke and Jacoby 1994) and south-western Australia (0.3–1.3 kg m^{-2} year^{-1}) (Congdon and McComb 1980), a value higher than the above-ground productivity estimates for the two sympatric species of mangrove, *Avicennia marina* (0.31 kg m^{-2} year^{-1}) and *Aegiceras corniculatum* (0.21 kg m^{-2} year^{-1}) (Clarke 1994). The high rate of productivity translates into a relatively high carbon concentration in sediment accumulated in *Juncus* wetlands on the Hawkesbury River (N. Saintilan and K. Rogers, unpubl. data). However, because the occurrence of *J. kraussii* may be indicative of the presence of low soil salinities (Zedler *et al.* 1995; Naidoo and Kift 2006), perhaps associated with fresh groundwater intrusions or contribution of fresh surface-water runoff, these wetlands may yield greater methane emissions than do the saltmarsh grasses and herbs found elsewhere. A comparison of soil carbon budgets across saltmarsh communities in the region would be an important avenue for further investigation. The *Sporobolus virginicus–Sarcocornia quinqueflora* association is the most widespread saltmarsh vegetation community on the Australian eastern coast (Adam *et al.* 1988), and contributes carbon to estuarine food-webs across the region (Guest and Connolly 2004; Mazumder *et al.* 2011). The standing biomass of this community is relatively low (Clarke and Jacoby 1994) and roots are shallow, suggesting that the rate of accumulation of recalcitrant carbon in the soil may be low for these communities, although no measures have been published.

Much of this carbon is stable if soil conditions are preserved, although several factors may threaten the longevity of carbon preserved in estuarine soils. The dynamic geomorphology to which mangroves and saltmarshes are adapted is one such factor; eroding shorelines act to reset carbon stores (Alongi 2011). However, the temperate setting, limited catchment area and protected entrance of many of the east-flowing rivers of eastern Australia have given rise to relatively quiescent conditions for carbon accumulation in estuaries. For example, at several locations on the Hawkesbury River, Saintilan and

Hashimoto (1999) found well preserved mangrove soils 70 cm below the contemporary saltmarsh surface dating from 1700 ± 90 years to 490 ± 70 years before present. The size of the carbon store at one site is $\sim 260\ Mg\ C\ ha^{-1}$. Similarly, Saintilan and Wilton (2001) found well preserved peats at Cararma Inlet and Curremembene Creek, Jervis Bay, preserved beneath the saltmarsh.

Summary of climate-change vulnerability

The ecosystem goods and services provided by saltmarsh in Australia are likely to be affected by environmental changes related to enhanced levels of atmospheric carbon. Elevated carbon dioxide potentially has direct effects on the competitive advantage of plant species in the intertidal zone. The growth of mangroves is enhanced by elevated carbon dioxide, particularly in low-salinity conditions (Farnsworth *et al.* 1996; Ball *et al.* 1997), and may partly explain the proliferation of woody vegetation over non-woody vegetation in the Kakadu region (Williamson *et al.* 2011), as has been postulated for the expansion of woody vegetation into terrestrial grasslands (Bond and Midgley 2000; Eamus and Palmer 2007). The efficacy of this mechanism may be reduced in competition with some saltmarsh species (McKee and Rooth 2008) and more experimental data are required for Australian species interactions. Equally, elevated carbon dioxide may promote the growth of C_3 photosynthesising plants over C_4 saltmarsh plants, which may have flow-on effects to estuarine foodwebs, given the proven trophic significance of the dominant C_4 grass *Sporobolus virginicus* in Australian estuaries (Guest and Connolly 2006; Saintilan and Mazumder 2010).

Increased temperature associated with elevated greenhouse-gas concentrations has the potential to influence saltmarsh extent and diversity. The strong inverse relationship between minimum monthly temperature and saltmarsh species diversity in Australia would suggest that significant warming might threaten the survival of some cold-dependant species, while further promoting the proliferation of the essentially tropical mangrove genera. The invasive saltmarsh plant *Spartina* spp. is currently restricted to small but dense patches in several Tasmanian and Victorian estuaries (Williamson 1996; Adam 2009), and higher temperatures may promote its further proliferation (Boon *et al.* 2011), as has been observed in the Netherlands (Loebl *et al.* 2006).

Sea-level rise presents an opportunity and threat to coastal saltmarsh, depending on rates of sediment supply, local topographic conditions and barriers to transgression. Several studies have strongly implicated relative sea-level rise as a driver of changes already observed, including, tidal-creek reactivation and saline intrusion in brackish wetlands in tropical Australia (Winn *et al.* 2006), mangrove encroachment in south-eastern Australia (Rogers *et al.* 2006), and conversion of *Tecticornia* shrubland to *Sarcocornia* herbfield and open water in Tasmania (Prahalad *et al.* 2011). In many developed coastal lowlands, the fate of coastal saltmarsh as an ecological community rests with local planning instruments. Because climate change-related sea-level rise is projected to accelerate in the 21st century (Meehl *et al.* 2007), there is an urgent need to explore adaptation options for these communities, particularly through management actions that promote the accommodation and retreat of saltmarsh to higher elevations (Rogers *et al.* 2012). In addition, climate change may increase the frequency and intensity of storm events (CSIRO and BOM 2007), which may contribute to saltmarsh maintenance by enhancing sedimentation, or saltmarsh loss by compressing saltmarsh surfaces or causing erosion (Cahoon 2006*a*). Other factors, such as altered rainfall patterns and catchment land-use change, may also alter sediment supply to estuaries and the capacity of saltmarsh to remain *in situ* as sea levels rise.

Management implications, recommendations and knowledge gaps

Climate change is occurring against the backdrop of multiple threats to saltmarsh, resulting from the situation of saltmarsh occurring in the heavily populated coastal zone. Several reviews have documented the impacts of reclamation, pollution, recreation use and grazing on coastal saltmarsh in Australia (Adam 2009; Laegdsgaard *et al.* 2009; Boon *et al.* 2011), and recovery times from small disturbances in the upper-intertidal zone can extend to years (Laegdsgaard 2002). Improved legislative protection and inclusion in regional planning policies have done much to arrest the incremental loss of saltmarsh in Australia (Laegdsgaard *et al.* 2009). However, sea-level rise poses a new set of planning challenges, changing the focus from the protection of existing saltmarsh to the protection of opportunities for adaptation. Models of the impact of sea-level rise on wetlands in the region have indicated that further losses of saltmarsh are inevitable. Rogers *et al.* (2012) demonstrated that a continuation of current sea-level trends for the Hunter estuary will lead to an increase in land available for mangrove and saltmarsh if passive retreat is allowed. The continuing survival of mangrove and saltmarsh will depend on the managed retreat of these ecosystems, currently inhibited in NSW by in excess of 4000 impediments to tidal flow (Williams and Watford 1997). One-third of these impediments, if removed or regulated, would provide opportunities for wetland restoration (Williams and Watford 1997), although opportunities for retreat are incrementally removed as 'sea-change' population growth continues along the coast. Appropriate zoning by local planning agencies is hampered by restricted coverage of detailed (LiDAR-derived) elevation modelling, and limited application of dynamic wetland-response modelling.

The removal of impediments to tidal inundation of coastal lowland has the dual benefit of climate change adaptation and mitigation. Rates of accumulation of carbon and loss will vary within estuaries (Alongi 2012), as will rates of gaseous flux (Poffenbarger *et al.* 2011), with some mangroves and saltmarshes being net exporters or emitters of carbon. The success of mangrove and saltmarsh restoration programs under REDD+ and PES frameworks will be linked to long-term stability of the site and the soil carbon stores being accumulated (Alongi 2011). Careful site selection is important in this context. Upstream sites within estuaries represent a higher risk, with more dynamic fluvial drivers of geomorphic change and a greater likelihood of methanogenesis. Restoring mangrove and saltmarsh wetland within reclaimed lowland floodplains protected by floodgates presents a high likelihood of success in controlled environments

amenable to experimental manipulation. Careful monitoring of carbon benefits derived from such projects leading to improved predictive modelling of carbon flux will increase confidence in the market over time.

Because of competing pressure on coastal land, saltmarsh management responses to climate change must be innovative, with consideration given to win–win options, as described above, or 'no regrets' options where a net social or economic benefit is gained, irrespective of the influence of climate change (Parry *et al.* 2007). 'Living shorelines', a term used to describe the protective effect that vegetation can have on shorelines by binding soils, trapping sediments and baffling tidal flow and wave action, are gaining in popularity internationally (Currin *et al.* 2010; Gedan *et al.* 2011). This 'no regrets' option is yet to be fully explored in Australia because of community misconceptions on the value of shoreline vegetation and loss of visual amenity; however, management actions that create or maintain vegetated shorelines not only act as a defence to sea-level rise, erosion and storm surge, but they also provide multiple ecosystem services, including habitat creation and carbon sequestration.

References

Adam, P. (1990). 'Saltmarsh Ecology.' (Cambridge University Press: Cambridge, UK.)

Adam, P. (1996). Saltmarsh. In 'State of the Marine Environment Report for Australia. Technical Annexe 1'. (Eds L. P. Zann and P. Kailola.) pp 97–105 (Department of Environment, Sport and Territories: Canberra.)

Adam, P. (2009). Australian saltmarshes in global context. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp. 1–22. (CSIRO Publishing: Melbourne.)

Adam, P., Wilson, N. C., and Huntley, B. (1988). The phytosociology of coastal saltmarsh vegetation in New South Wales. *Wetlands(Australia)* **7**, 35–57.

Akumu, C., Pathirana, S., Baban, S., and Bucher, D. (2011). Examining the potential impacts of sea level rise on coastal wetlands in north-eastern NSW, Australia. *Journal of Coastal Conservation* **15**, 15–22. doi:10.1007/S11852-010-0114-3

Alongi, D. M. (2011). Carbon payments for mangrove conservation: ecosystem constraints and uncertainties of sequestration potential. *Environmental Science & Policy* **14**, 462–470. doi:10.1016/J.ENVSCI.2011.02.004

Alongi, D. M. (2012). Carbon sequestration in mangrove forests. *Carbon Management* **3**, 313–322. doi:10.4155/CMT.12.20

Ball, M. C., Cochrane, M. J., and Rawson, H. M. (1997). Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO_2. *Plant, Cell & Environment* **20**, 1158–1166. doi:10.1046/J.1365-3040.1997.D01-144.X

Barson, M. M., and Calder, D. M. (1981). The vegetation of the Victorian coast. *Proceedings of the Royal Society of Victoria* **92**, 55–65.

Belbasé, S. (2005). Presence and activity of inestivorous bats in saltmarsh habitat at Kooragang Nature Reserve, Newcastle. B.Sc.(Hons) Thesis, Australian Catholic University, North Sydney.

Bloomfield, A., and Gillanders, B. (2005). Fish and invertebrate assemblages in seagrass, mangrove, saltmarsh, and nonvegetated habitats. *Estuaries and Coasts* **28**, 63–77. doi:10.1007/BF02732754

Bond, W. J., and Midgley, G. F. (2000). A proposed CO_2 controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**, 865–869. doi:10.1046/J.1365-2486.2000.00365.X

Boon, P. I., Allen, T., Brook, J., Carr, G., Frood, D., Harty, C., Hoye, J., McMahon, A., Mathews, S., Rosengren, N., Sinclair, S., White, M., and Yugovic, J. (2011). 'Mangroves and Coastal Saltmarsh of Victoria: Distribution, Condition, Threats and Management.' (Institute for Sustainability and Innovation, Victoria University: Melbourne.)

Bridgewater, P., and Cresswell, I. D. (2003). Identifying biogeographic patterns in Australian saltmarsh and mangal systems: a phytogeographic analysis. *Phytocoenologia* **33**, 231–250. doi:10.1127/0340-269X/2003/0033-0231

Cahoon, D. (2006*a*). A review of major storm impacts on coastal wetland elevations. *Estuaries and Coasts* **29**, 889–898.

Cahoon, D. (2006*b*). 'Surface Elevation Table (SET).' Available at http://www.pwrc.usgs.gov/set/ (accessed 25 October 2012).

Cahoon, D. R., Lynch, J. C., Hensel, P., Boumans, R., Perez, B. C., Segura, B., and Day, J. W., Jr (2002*a*). High-precision measurements of wetland sediment elevation: I. Recent improvements to the sedimentation–erosion table. *Journal of Sedimentary Research* **72**, 730–733. doi:10.1306/020702720730

Cahoon, D. R., Lynch, J. C., Perez, B. C., Segura, B., Holland, R. D., Stelly, C., Stephenson, G., and Hensel, P. (2002*b*). High-precision measurements of wetland sediment elevation: II. The rod surface elevation table. *Journal of Sedimentary Research* **72**, 734–739. doi:10.1306/020702720734

Cahoon, D. R., Hensel, P. F., Spencer, T., Reed, D. J., McKee, K. L., and Saintilan, N. (2006). Coastal wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In 'Wetlands and Natural Resource Management'. (Eds J. T. A. Verhoeven, B. Beltman, R. Bobbink and D. F. Whigham.) pp. 271–292. (Springer: Berlin.)

Choi, Y., and Wang, Y. (2004). Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. *Global Biogeochemical Cycles* **18**, GB4016. doi:10.1029/2004GB002261

Clarke, L. D., and Hannon, N. J. (1969). The mangrove swamp and salt marsh communities of the Sydney district: II. The Holocoenotic complex with particular reference to physiography. *Journal of Ecology* **57**, 213–234. doi:10.2307/2258216

Clarke, L. D., and Hannon, N. J. (1970). The mangrove swamp and saltmarsh communities of the Sydney district: III. Plant growth in relation to salinity and waterlogging. *Journal of Ecology* **58**, 351–369. doi:10.2307/2258276

Clarke, P. J. (1994). Baseline studies of temperate mangrove growth and reproduction: demographic and litterfall measures of leafing and flowing. *Australian Journal of Botany* **42**, 37–48. doi:10.1071/BT9940037

Clarke, P. J., and Jacoby, C. A. (1994). Biomass and above-ground productivity of salt-marsh plants in south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **45**, 1521–1528. doi:10.1071/MF9941521

Clarke, P. J., and Myerscough, P. J. (1993). The intertidal distribution of the grey mangrove (*Avicennia marina*) in southeastern Australia: the effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. *Australian Journal of Ecology* **18**, 307–315. doi:10.1111/J.1442-9993.1993.TB00458.X

Clough, J. S., Park, R. A., and Fuller, R. (2010). 'SLAMM 6 Beta Technical Documentation, Release 6.0 Beta.' (Warren Pinnacle Consulting: Warren, VT.)

Congdon, R. A., and McComb, A. J. (1980). Productivity and nutrient content of *Juncus kraussii* in an estuarine marsh in south-western Australia. *Australian Journal of Ecology* **5**, 221–234. doi:10.1111/J.1442-9993.1980.TB01246.X

Connolly, R. M. (2005). Modification of saltmarsh for mosquito control in Australia alters habitat use by nekton. *Wetlands Ecology and Management* **13**, 149–161. doi:10.1007/S11273-004-9569-Z

Connolly, R. (2009). Fish on Australian saltmarshes. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp 131–148. (CSIRO Publishing: Melbourne.)

Connolly, R. M., Dalton, A., and Bass, D. A. (1997). Fish use of an inundated saltmarsh flat in a temperate Australian estuary. *Australian Journal of Ecology* **22**, 222–226. doi:10.1111/J.1442-9993.1997.TB00662.X

CSIRO and BOM (2007). 'Climate Change in Australia.' (CSIRO and the Australian Bureau of Meteorology: Canberra.)

Currin, C. A., Chappell, W. S., and Deaton, A. (2010). Developing alternative shoreline armoring strategies: the living shoreline approach in North Carolina. In 'Puget Sound Shorelines and the Impacts of Armoring'. (Eds H. Shipman, M. N. Dethier, G. Gelfenbaum, K. L. Fresh and R. S. Dinicola.) pp. 91–102. US Geological Survey Scientific Investigations Report 2010–5254, US Geological Survey, Reston, VA.

D'Alpaos, A., Lanzoni, S., Marani, M., and Rinaldo, A. (2007). Landscape evolution in tidal embayments: modeling the interplay of erosion, sedimentation, and vegetation dynamics. *Journal of Geophysical Research* **112**, F01008. doi:10.1029/2006JF000537

Dale, P., and Breitfuss, M. (2009). Ecology and management of mosquitoes. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp. 167–178. (CSIRO Publishing: Melbourne.)

DeLaune, R. D., Patrick, W. H., and Van Breemen, N. (1990). Processes governing marsh formation in a rapidly subsiding coastal environment. *Catena* **17**, 277–288. doi:10.1016/0341-8162(90)90021-5

Duarte, C., Middelburg, J. J., and Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* **2**, 1–8. doi:10.5194/BG-2-1-2005

Eamus, D., and Palmer, A. R. (2007). Is climate change a possible explanation for woody thickening in arid and semi-arid regions? *Research Letters in Ecology* **2007**, 1. doi:10.1155/2007/37364

Eslami-Andargoli, L., Dale, P., Sipe, N., and Chaseling, J. (2009). Mangrove expansion and rainfall patterns in Moreton Bay, southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science* **85**, 292–298. doi:10.1016/J.ECSS.2009.08.011

Eslami-Andargoli, L., Dale, P. E. R., Sipe, N., and Chaseling, J. (2010). Local and landscape effects on spatial patterns of mangrove forest during wetter and drier periods: Moreton Bay, southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science* **89**, 53–61. doi:10.1016/J.ECSS.2010.05.011

Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenspergen, G. R., Temmerman, S., D'Alpoas, A., van de Koppel, J., Rybczyk, J. M., Reyes, E., Graft, C., and Clough, J. (2012). Numerical models of saltmarsh evolution: ecological, geomorphic, and climatic factors. *Reviews of Geophysics* **50**, RG1002. doi:10.1029/2011RG000359

Fairweather, P. G. (1990). Ecological changes due to our use of the coast: research needs *versus* effort. *Proceedings of the Ecological Society of Australia* **16**, 71–77.

Farnsworth, E. J., Ellison, A. M., and Gong, W. K. (1996). Elevated CO_2 alters anatomy, physiology, growth and reproduction of red mangroves (*Rhizophora mangle* L.). *Oecologia* **108**, 599–609. doi:10.1007/BF00329032

Feller, I. C., McKee, K. L., Whigham, D. F., and O'Neill, J. P. (2003). Nitrogen *versus* phosphorus limitation across and ecotonal gradient in a mangrove forest. *Biogeochemistry* **62**, 145–175. doi:10.1023/A:1021166010892

Gedan, K. B., Silliman, B. R., and Bertness, M. D. (2009). Centuries of human-driven change in saltmarsh ecosystems. *Annual Review of Marine Science* **1**, 117–141. doi:10.1146/ANNUREV.MARINE.010908.163930

Gedan, K., Kirwan, M., Wolanski, E., Barbier, E., and Silliman, B. (2011). The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. *Climatic Change* **106**, 7–29. doi:10.1007/S10584-010-0003-7

Gonsalves, L., Lamb, S., Law, B., Monamy, V. (in press). Do mosquitos influence bat activity in coastal saltmarsh. *Wildlife Research*. doi:10.1071/WR12148

Grace, J., Lloyd, J., McIntyre, J., Miranda, A. C., Meir, P., Miranda, H. S., Nobre, C., Moncrieff, J., Massheder, J., Malhi, Y., Wright, I., and Gash, J. (1995). Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992 to 1993. *Science* **270**, 778–780. doi:10.1126/SCIENCE.270.5237.778

Greenwood, M. E., and MacFarlane, G. R. (2006). Effects of salinity and temperature on the germination of *Phragmites australis*, *Juncus kraussii*, and *Juncus acutus*: implications for estuarine restoration initiatives. *Wetlands* **26**, 854–861. doi:10.1672/0277-5212(2006)26[854:EOSATO]2.0.CO;2

Guest, M. A., and Connolly, R. M. (2004). Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. *Aquatic Ecology* **38**, 599–609. doi:10.1007/S10452-004-0442-1

Guest, M. A., and Connolly, R. M. (2006). Movement of carbon among estuarine habitats: the influence of saltmarsh patch size. *Marine Ecology Progress Series* **310**, 15–24. doi:10.3354/MEPS310015

Guest, M. A., Connolly, R. M., and Loneragan, N. R. (2004). Carbon movement and assimilation by invertebrates in estuarine habitat at a scale of metres. *Marine Ecology Progress Series* **278**, 27–34. doi:10.3354/MEPS278027

Guest, M. A., Connolly, R. M., Lee, S. Y., Loneragan, N. R., and Breitfuss, M. J. (2006). Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement. *Oecologia* **148**, 88–96. doi:10.1007/S00442-005-0352-5

Harris, P. T., and Heap, A. D. (2003). Environmental management of clastic coastal depositional environments: inferences from an Australian geomorphic database. *Ocean and Coastal Management* **46**, 457–478. doi:10.1016/S0964-5691(03)00018-8

Harris, P. T., Heap, A. D., Bryce, S. M., Porter-Smith, R., Ryan, D. A., and Heggie, D. T. (2002). Classification of Australian clastic coastal depositional environments based upon a quantitative analysis of wave, tidal, and river power. *Journal of Sedimentary Research* **72**, 858–870. doi:10.1306/040902720858

Hashimoto, T. R., Saintilan, N., and Haberle, S. G. (2006). Mid-Holocene development of mangrove communities featuring rhizophoraceae and geomorphic change in the Richmond River Estuary, New South Wales, Australia. *Geographical Research* **44**, 63–76. doi:10.1111/J.1745-5871.2006.00360.X

Hollingsworth, A., and Connolly, R. M. (2006). Feeding by fish visiting inundated subtropical saltmarsh. *Journal of Experimental Marine Biology and Ecology* **336**, 88–98. doi:10.1016/J.JEMBE.2006.04.008

Hu, W., Mengersen, K., Dale, P., and Tong, S. (2010). Difference in mosquito species (Diptera: Culicidae) and the transmission of Ross River Virus between coastline and inland areas in Brisbane, Australia. *Environmental Entomology* **39**, 88–97. doi:10.1603/EN07037

Hughes, L. (2004). Coastal saltmarsh in the NSW North Coast, Sydney Basin and SE Corner Bioregions – endangered ecological community listing. NSW Scientific Committee – final determination. NSW Office of Environment and Heritage., Sydney.

Hutchings, P. A., and Recher, H. F. (1981). The fauna of Australian mangroves. *Proceedings of the Linnean Society of New South Wales* **106**, 83–121.

Imgraben, S., and Dittman, S. (2008). Leaf litter dynamics and litter composition in two temperate South Australian mangrove forests. *Journal of Sea Research* **59**, 83–93. doi:10.1016/J.SEARES.2007.06.004

Isacch, J. P., Costa, C. S., Rodríguez-Gallego, L., Conde, D., Escapa, M., Gagliardini, D. A., and Iribarne, O. O. (2006). Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. *Journal of Biogeography* **33**, 888–900. doi:10.1111/J.1365-2699.2006.01461.X

Jacups, S., Warchot, A., and Whelan, P. (2012). Anthropogenic ecological change and impacts on mosquito breeding and control strategies in saltmarshes, Northern Territory, Australia. *EcoHealth* **9**, 183–194.

Jenner, B., French, K., Oxenham, K., and Major, R. E. (2011). Population decline of the white-fronted chat (*Epthianura albifrons*) in New South Wales, Australia. *Emu* **111**, 84–91. doi:10.1071/MU10038

Jupiter, S., Potts, D., Phinn, S., and Duke, N. (2007). Natural and anthropogenic changes to mangrove distributions in the Pioneer River Estuary (Qld, Australia). *Wetlands Ecology and Management* **15**, 51–62. doi:10.1007/S11273-006-9011-9

Kaly, U. L. (1988). Distribution, abundance and size in mangrove and saltmarsh gastropods. Ph.D. Thesis, University of Sydney.

Khan, M. A., and Ungar, I. A. (1984). The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. *American Journal of Botany* **71**, 481–489. doi:10.2307/2443323

Kingsford, R. T., and Norman, F. I. (2002). Australian waterbirds – products of the continent's ecology. *Emu* **102**, 47–69. doi:10.1071/MU01030

Kirkpatrick, J. B., and Glasby, J. (1981). 'Saltmarsh in Tasmania: Distribution, Community, Composition and Conservation.' Occassional Paper No. 8. (Department of Geography, University of Tasmania: Hobart.)

Kirwan, M. L., and Murray, A. B. (2007). A coupled geomorphic and ecological model of tidal marsh evolution. *Proceedings of the National Academy of Sciences, USAa* **104**, 6118–6122. doi:10.1073/PNAS.0700958104

Knight, J., Griffin, L., Dale, P., and Phinn, S. (2012). Oviposition and larval habitat preferences of the saltwater mosquito, *Aedes vigilax*, in a subtropical mangrove forest in Queensland, Australia. *Journal of Insect Science* **12**. doi:10.1673/031.012.0601

Knighton, A. D., Mills, K., and Woodroffe, C. D. (1991). Tidal-creek extension and saltwater intrusion in northern Australia. *Geology* **19**, 831–834. doi:10.1130/0091-7613(1991)019<0831:TCEASI>2.3.CO;2

Laegdsgaard, P. (2002). Recovery of small denuded patches of the dominant NSW coastal saltmarsh specie (*Sporobolus virginicus* and *Sarcocornia quinqueflora*) and implications for restoration using donor sites. *Ecological Management & Restoration* **3**, 200–204. doi:10.1046/J.1442-8903.2002.00113.X

Laegdsgaard, P., Monamy, V., and Saintilan, N. (2004). Investigating the presence of threatened insectivorous bats on coastal NSW saltmarsh habitat. *Wetlands (Australia)* **22**, 29–41.

Laegdsgaard, P., Kelleway, J., Williams, R. J., and Harty, C. (2009). Protection and management of coastal saltmarsh. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp. 149–166. (CSIRO Publishing: Melbourne.)

Livesley, S. J., and Andrusiak, S. M. (2012). Temperate mangrove and saltmarsh sediments are a small methane and nitrous oxide source but important carbon store. *Estuarine, Coastal and Shelf Science* **97**, 19–27. doi:10.1016/J.ECSS.2011.11.002

Loebl, M., van Beuskon, J. E. E., and Reise, K. (2006). Is spread of the neophyte *Spartina anglica* recently enhanced by increasing temperatures? *Aquatic Ecology* **40**, 315–324. doi:10.1007/S10452-006-9029-3

Long, S. P., and Mason, C. F. (1983). 'Saltmarsh Ecology.' (Blackie and Son Ltd: Glasgow.)

Lovelock, C. E., Skilleter, G., and Saintilan, N. (2009). Tidal wetlands and climate change. In 'Marine Climate Change Impacts and Adaptation Report Card for Australia 2009'. (Eds E. S. Poloczanska, A. J. Hobday and A. J. Richardson.) NCCARF Publication 05/09. (National Climate Change Adaptation Research Facility, Brisbane)

Lovelock, C., Bennion, V., Grinham, A., and Cahoon, D. (2011). The role of surface and subsurface processes in keeping pace with sea level rise in intertidal wetlands of Moreton Bay, Queensland, Australia. *Ecosystems* **14**, 745–757. doi:10.1007/S10021-011-9443-9

Manson, F. J., Loneragan, N. R., and Phinn, S. R. (2003). Spatial and temporal variation in distribution of mangroves in Moreton Bay, subtropical Australia: a comparison of pattern metrics and change detection analyses based on aerial photographs. *Estuarine, Coastal and Shelf Science* **57**, 653–666. doi:10.1016/S0272-7714(02)00405-5

Marchant, S., and Higgins, P. J. (1993). 'Handbook of Australian, New Zealand and Antarctic Birds. Vol. 2: Raptors to Lapwings.' (Oxford University Press: Melbourne.)

Mariotti, G., and Fagherazzi, S. (2010). A numerical model for the coupled long-term evolution of saltmarshes and tidal flats. *Journal of Geophysical Research* **115**, F01004. doi:10.1029/2009JF001326

Mazumder, D., and Saintilan, N. (2003). A comparison of sampling techniques in the assessment of burrowing crab abundance in saltmarsh and mangrove environments. *Wetlands (Australia)* **21**, 1–15.

Mazumder, D., and Saintilan, N. (2010). Mangrove leaves are not a significant source of carbon and nitrogen for temperate mangrove crabs in Australia. *Wetlands* **30**, 375–380. doi:10.1007/S13157-010-0021-2

Mazumder, D., Saintilan, N., and Williams, R. (2005). Temporal variation in fish catch using pop nets in mangrove and saltmarsh flats at Towra Point, NSW, Australia. *Wetlands Ecology and Management* **13**, 457–467. doi:10.1007/S11273-004-0814-2

Mazumder, D., Saintilan, N., and Williams, R. J. (2006). Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. *Marine and Freshwater Research* **57**, 193–199. doi:10.1071/MF05040

Mazumder, D., Saintilan, N., and Williams, R. J. (2009). Zooplankton inputs and outputs in the saltmarsh at Towra Point, Australia. *Wetlands Ecology and Management* **17**, 225–230. doi:10.1007/S11273-008-9102-X

Mazumder, D., Saintilan, N., Williams, J. R., and Szymczak, R. (2011). Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. *Marine and Freshwater Research* **62**, 11–19. doi:10.1071/MF10076

McKee, K. L. (2011). Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuarine, Coastal and Shelf Science* **91**, 475–483. doi:10.1016/J.ECSS.2010.05.001

McKee, K. L., and Rooth, J. E. (2008). Where temperate meets tropical: multi-factorial effects of elevated CO2, nitrogen enrichment, and competition on a mangrove–saltmarsh community. *Global Change Biology* **14**, 971–984. doi:10.1111/J.1365-2486.2008.01547.X

McKee, K. L., Cahoon, D. R., and Feller, I. C. (2007). Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* **16**, 545–556. doi:10.1111/J.1466-8238.2007.00317.X

McKee, K., Rogers, K., and Saintilan, N. (2012). Response of saltmarsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In 'Global Change and the Function and Distribution of Wetlands'. (Ed. B. A. Middleton.) pp. 63–96. (Springer: The Netherlands.)

Meehl, G. A., Stocker, T. F., Collins, W. D., Griedlingstein, P., Gaye, A. T., Gregory, J. M., Kitoh, A., Knutti, R., Murphy, J. M., Noda, A., Raper, S. C. B., Watterson, I. G., Weaver, A. J., and Zhao, Z.-C. (2007). Global climate projections. In 'Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change'. (Eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller.) pp. 740–845. (Cambridge University Press: Cambridge, UK.),

Mendelssohn, I. A., and McKee, K. L. (2000). Saltmarshes and mangroves. In 'North American Terrestrial Vegetation'. (Ed. M. G. Barbour and W. D. Billings.) pp. 501–563. (Cambridge University Press: Cambridge, UK.)

Morris, C. D., Dale, P. E. R., and Stanfast, H. (Eds) (2002). 'Australian Mosquito Control Manual.' (Mosquito Control Association of Australia: Brisbane.)

Morrisey, D. (1995). Saltmarshes. In 'Coastal Marine Ecology of Temperate Australia'. (Eds A. J. Underwood and M. G. Chapman.) pp. 205–220. (University of New South Wales Press: Sydney.)

Morton, R. M., Pollock, B. R., and Beumer, J. P. (1987). The occurrence and diet of fishes in a tidal inlet to a saltmarsh in southern Moreton Bay,

Queensland. *Australian Journal of Ecology* **12**, 217–237. doi:10.1111/J.1442-9993.1987.TB00945.X

Morton, R., Beumer, J., and Pollock, B. (1988). Fishes of a subtropical Australian saltmarsh and their predation upon mosquitoes. *Environmental Biology of Fishes* **21**, 185–194. doi:10.1007/BF00004862

Mulrennan, M. E., and Woodroffe, C. D. (1998). Saltwater intrusion into the coastal plains of the Lower Mary River, Northern Territory, Australia. *Journal of Environmental Management* **54**, 169–188. doi:10.1006/JEMA.1998.0229

Naidoo, G., and Kift, J. (2006). Responses of the saltmarsh rush *Juncus kraussii* to salinity and waterlogging. *Aquatic Botany* **84**, 217–225. doi:10.1016/J.AQUABOT.2005.10.002

Nellemann, C., Corcoran, E., Duarte, C. M., Valdés, L., DeYoung, C., Fonseca, L., and Grimsditch, G. E. (2009). 'Blue Carbon. A Rapid Response Assessment.' (United Nations Environment Programme: GRID-Arendal, Norway.)

Nyman, J. A., Walters, R. J., Delaune, R. D., and Patrick, W. H., Jr (2006). Marsh vertical accretion via vegetative growth. *Estuarine, Coastal and Shelf Science* **69**, 370–380. doi:10.1016/J.ECSS.2006.05.041

Oliver, T., Rogers, K., Chafer, C., and Woodroffe, C. (2012). Measuring, mapping and modelling: an integrated approach to the management of mangrove and saltmarsh in the Minnamurra River estuary, southeast Australia. *Wetlands Ecology and Management* **20**, 353–371.

Parry, M. K., Canziani, O. F., Palutikof, J. P., van der Linden, P. J., and Hanson, C. E. (2007). 'Appendix 1: Glossary. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.' (Cambridge University Press: Cambridge, UK.)

Pen, L., Semeniuk, V., and Semeniuk, C. A. (2000). Peripheral wetland habitats and vegetation of the Leschenault Inlet estuary. *Journal of the Royal Society of Western Australia* **83**, 293–316.

Pethick, J. S. (1981). Long-term accretion rates on tidal saltmarshes. *Journal of Sedimentary Research* **51**, 571–577.

Pidgeon, E. (2009). Carbon sequestration by coastal marine habitats: important missing sinks. In 'The Management of National Coastal Carbon Sinks'. (Eds D. Laffoley and G. Grimsditch.) pp. 47–51. (IUCN: Gland, Switzerland.)

Platell, M. E., and Freewater, P. (2009). Importance of saltmarsh to fish species of a large south-eastern Australian estuary during a spring tide cycle. *Marine and Freshwater Research* **60**, 936–941. doi:10.1071/MF08164

Poffenbarger, H., Needelman, B., and Megonigal, J. (2011). Salinity influence on methane emissions from tidal marshes. *Wetlands* **31**, 831–842. doi:10.1007/S13157-011-0197-0

Prahalad, V. N., Kirkpatrick, J. B., and Mount, R. E. (2011). Tasmanian coastal saltmarsh community transitions associated with climate change and relative sea level rise 1975–2009. *Australian Journal of Botany* **59**, 741–748.

Qian, H., Fridley, J. D., and Palmer, M. W. (2007). The latitudinal gradient of species-area relationships for vascular plants of North America. *American Naturalist* **170**, 690–701. doi:10.1086/521960

Redfield, A. C. (1972). Development of a New England saltmarsh. *Ecological Monographs* **42**, 201–237. doi:10.2307/1942263

Reed, D. J. (1990). The impact of sea-level rise on coastal saltmarshes. *Progress in Physical Geography* **14**, 465–481. doi:10.1177/030913339001400403

Richardson, A. M. M., Swain, R., and Wong, V. (1998). Relationship between the crustacean and molluscan assemblages of Tasmanian saltmarshes and the vegetation and soil conditions. *Marine and Freshwater Research* **49**, 785–799. doi:10.1071/MF97097

Roach, A. C. (1998). Effects of predation on the size structure of the gastropod *Salinator solida* (Martens) populations at Towra Point, NSW, Australia. *Marine and Freshwater Research* **49**, 779–784. doi:10.1071/MF97098

Rogers, K. (2004). Mangrove and saltmarsh surface elevation dynamics in relation to environmental variables in southeastern Australia. Ph.D. Thesis, University of Wollongong, NSW.

Rogers, K., and Saintilan, N. (2008). Relationships between surface elevation and groundwater in mangrove forests of southeast Australia. *Journal of Coastal Research* **24**, 63–69. doi:10.2112/05-0519.1

Rogers, K., and Saintilan, N. (2011). Coastal wetland vulnerability to sea-level rise in southeastern Australia. Final report prepared for the Environmental Trust. NSW Department of Environment, Climate Change and Water, Sydney.

Rogers, K., Saintilan, N., and Cahoon, D. (2005*a*). Surface elevation dynamics in a regenerating mangrove forest at Homebush Bay, Australia. *Wetlands Ecology and Management* **13**, 587–598. doi:10.1007/S11273-004-0003-3

Rogers, K., Saintilan, N., and Heijnis, H. (2005*b*). Mangrove encroachment of saltmarsh in Western Port Bay, Victoria: the role of sedimentation, subsidence and sea level rise. *Estuaries* **28**, 551–559. doi:10.1007/BF02696066

Rogers, K., Wilton, K. M., and Saintilan, N. (2006). Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science* **66**, 559–569. doi:10.1016/J.ECSS.2005.11.004

Rogers, K., Saintilan, N., and Copeland, C. (2012). Modelling wetland surface elevation and its application to forecasting the effects of sea-level rise on estuarine wetlands. *Ecological Modelling* **244**, 148–157. doi:10.1016/J.ECOLMODEL.2012.06.014

Ross, P., Minchinton, T., and Ponder, W. (2009). The ecology of molluscs in Australian saltmarshes. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp. 75–114. (CSIRO Publishing: Melbourne.)

Roy, P. S. (1984). New South Wales Estuaries: their origin and evolution. In 'Coastal Geomorphology in Australia'. (Ed. B. G. Thom.) pp. 99–121. (Academic Press: Sydney.)

Roy, P. S., Thom, B. G., and Wright, L. D. (1980). Holocene sequences on an embayed high-energy coast: an evolutionary model. *Sedimentary Geology* **26**, 1–19. doi:10.1016/0037-0738(80)90003-2

Roy, P. S., Williams, R. J., Jones, A. R., Yassini, I., Gibbs, P. J., Coates, B., West, R. J., Scanes, P. R., Hudson, J. P., and Nichol, S. (2001). Structure and function of south-east Australian estuaries. *Estuarine, Coastal and Shelf Science* **53**, 351–384. doi:10.1006/ECSS.2001.0796

Russell, T. L., and Hale, P. T. (2009). Conservation of the false water rat (*Xeromys myoides*) depends on landscape complementation. *Australian Mammalogy* **31**, 81–87. doi:10.1071/AM09006

Rybczyk, J. M., and Callaway, J. C. (2009). Surface elevation models. In 'Coastal Wetlands: an Integrated Ecosystem Approach'. (Eds G. M. E. Perillo, E. Wolanski, D. R. Cahoon and M. M. Brinson.) pp. 835–854. (Elsevier: Amsterdam.)

Saenger, P., Specht, M. M., Specht, R. L., and Chapman, V. J. (1977). Mangal and coastal saltmarsh communities in Australasia. In 'Ecosystems of the World I: Wet Coastal Ecosystems'. (Ed. V. J. Chapman.) pp. 293–345. (Elsevier: Amsterdam.)

Saintilan, N. (2009). Biogeography of Australian saltmarsh plants. *Austral Ecology* **34**, 929–937. doi:10.1111/J.1442-9993.2009.02001.X

Saintilan, N., and Hashimoto, T. R. (1999). Mangrove–saltmarsh dynamics on a bay-head delta in the Hawkesbury River estuary, New South Wales, Australia. *Hydrobiologia* **413**, 95–102. doi:10.1023/A:1003886725832

Saintilan, N., and Mazumder, D. (2010). Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. *Marine and Freshwater Research* **61**, 615–620. doi:10.1071/MF09187

Saintilan, N., and Williams, R. J. (1999). Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography* **8**, 117–124. doi:10.1046/J.1365-2699.1999.00133.X

Saintilan, N., and Wilton, K. (2001). Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. *Wetlands Ecology and Management* **9**, 409–420. doi:10.1023/A:1012073018996

Saintilan, N., Hossain, K., and Mazumder, D. (2007). Linkages between adjacent seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. *Wetlands Ecology and Management* **15**, 277–286. doi:10.1007/S11273-006-9028-0

Saintilan, N., Rogers, K., and Howe, A. (2009*a*). Geomorphology and habitat dynamics. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp. 53–74. (CSIRO Publishing: Melbourne.)

Saintilan, N., Rogers, K., and McKee, K. (2009*b*). Salt-marsh–mangrove interactions in Australia and the Americas. In 'Coastal Wetlands: an Integrated Ecosystem Approach'. (Eds G. M. E. Perillo, E. Wolanski, D. R. Cahoon and M. M. Brinson.) pp. 855–883. (Elsevier: Amsterdam.)

Shenker, J. M., and Dean, J. M. (1979). The utilisation of an intertidal saltmarsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. *Estuaries and Coasts* **2**, 154–163. doi:10.2307/1351729

Shepherd, K. A., and Wilson, P. G. (2007). Incorporation of the Australian genera *Halosarcia, Pachycornia, Sclerostegia* and *Tegicornia* into *Tecticornia* (Salicornioideae, Chenopodiaceae). *Australian Systematic Botany* **20**, 319–331. doi:10.1071/SB07002

Skilleter, G. A., and Warren, S. (2000). Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. *Journal of Experimental Marine Biology and Ecology* **244**, 107–129. doi:10.1016/S0022-0981(99)00133-1

Specht, R. L. (1981). Biogeography of halophytic angiosperms (salt-marsh, mangrove and sea-grass). In 'Ecological Biography of Australia'. (Ed. A. Keast.) pp. 575–589. (Dr. W. Junk Publishers: The Hague, Belgium.)

Spencer, J., Monamy, V., and Breitfuss, M. (2009). Saltmarsh as habitat for birds and other vertebrates. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp. 149–165. (CSIRO Publishing, Melbourne)

Thom, B. G., Wright, L. D., and Coleman, J. M. (1975). Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf–Ord River, Western Australia. *Journal of Ecology* **63**, 203–232. doi:10.2307/2258851

Traill, L. W., Bradshaw, C. J. A., Delean, S., and Brook, B. W. (2010). Wetland conservation and sustainable use under global change: a tropical Australian case study using magpie geese. *Ecography* **33**, 818–825. doi:10.1111/J.1600-0587.2009.06205.X

Traill, L. W., Perhans, K., Lovelock, C. E., Prohaska, A., McFallan, S., Rhodes, J. R., and Wilson, K. A. (2011). Managing for change: wetland transitions under sea-level rise and outcomes for threatened species. *Diversity & Distributions* **17**, 1225–1233. doi:10.1111/J.1472-4642.2011.00807.X

Wetlands International (2006). 'Waterbird Population Estimates.' (Wetlands International: Wageningen, The Netherlands.)

Willems, K. J., Webb, C. E., and Russell, R. C. (2005). A comparison of mosquito predation by the fish *Pseudomugil signifier* Kner and *Gambusia holbrooki* (Girard) in laboratory trials. *Journal of Vector Ecology* **30**, 87–90.

Williams, R. J., and Watford, F. A. (1997). Identification of structures restricting tidal flow in New South Wales, Australia. *Wetlands Ecology and Management* **5**, 87–97. doi:10.1023/A:1008283522167

Williams, S. R., Kokkinn, M. J., Fricker, S. R., Schneemilch, M. J., Humphrey, M. J., and Williams, C. R. (2009). Mosquitoes (Diptera: Culicidae) of the Spencer Gulf Coast of South Australia. *Transactions of the Royal Society of South Australia* **133**, 51–56.

Williamson, R. (1996). *Spartina* in Victoria – an overview. In 'Proceedings of the Australasian Conference on *Spartina* Control (10–12 May 1995)'. (Eds J. A. E. Rash, R. C. Williamson and S. J. Taylor.) pp. 26–29. (Department of Conservation and Natural Resources: Yarram, Vic.)

Williamson, G., Boggs, G., and Bowman, D. (2011). Late 20th century mangrove encroachment in the coastal Australian monsoon tropics parallels the regional increase in woody biomass. *Regional Environmental Change* **11**, 19–27. doi:10.1007/S10113-010-0109-5

Wilson, H. B., Kendall, B. E., Fuller, R. A., Milton, D. A., and Possingham, H. P. (2011). Analyzing variability and the rate of decline of migratory shorebirds in Moreton Bay, Australia. *Conservation Biology* **25**, 758–766. doi:10.1111/J.1523-1739.2011.01670.X

Wilton, K. M. (2002). Coastal wetland habitat dynamics in selected New South Wales estuaries. Ph.D. Thesis, Australian Catholic University, North Sydney.

Winn, K. O., Saynor, M. J., Eliot, M. J., and Elio, I. (2006). Saltwater intrusion and morphological change at the mouth of the East Alligator River, Northern Territory. *Journal of Coastal Research* **22**, 137–149. doi:10.2112/05A-0011.1

Woodroffe, C. D., Thom, B. G., and Chappell, J. (1985). Development of widespread mangrove swamps in mid-Holocene times in northern Australia. *Nature* **317**, 711–713. doi:10.1038/317711A0

Woodroffe, C. D., Chappell, J., Thom, B. G., and Wallensky, E. (1989). Depositional model of a macrotidal estuary and floodplain, South Alligator River, northern Australia. *Sedimentology* **36**, 737–756. doi:10.1111/J.1365-3091.1989.TB01743.X

Woodroffe, C. D., Mulrennan, M. E., and Chappell, J. (1993). Estuarine infill and coastal progradation, southern van Diemen gulf, northern Australia. *Sedimentary Geology* **83**, 257–275. doi:10.1016/0037-0738(93)90016-X

Zedler, J. B., Nelson, P., and Adam, P. (1995). Plant community organisation in New South Wales saltmarshes: species mosaics and potential causes. *Wetlands* **14**, 1–18.

Zharikov, Y., and Milton, D. A. (2009). Valuing coastal habitats: predicting high-tide roosts of non-breeding migratory shorebirds from landscape composition. *Emu* **109**, 107–120. doi:10.1071/MU08017

Article

Widespread retreat of coastal habitat is likely at warming levels above 1.5 °C

https://doi.org/10.1038/s41586-023-06448-z

Received: 15 March 2020

Accepted: 18 July 2023

Published online: 30 August 2023

Open access

Check for updates

Neil Saintilan[1,2]✉, Benjamin Horton[3,4], Torbjörn E. Törnqvist[5], Erica L. Ashe[6], Nicole S. Khan[7], Mark Schuerch[8], Chris Perry[9], Robert E. Kopp[6], Gregory G. Garner[6], Nicholas Murray[10], Kerrylee Rogers[11], Simon Albert[12], Jeffrey Kelleway[11], Timothy A. Shaw[3], Colin D. Woodroffe[11], Catherine E. Lovelock[13], Madeline M. Goddard[14], Lindsay B. Hutley[14], Katya Kovalenko[15], Laura Feher[16] & Glenn Guntenspergen[17]

Several coastal ecosystems—most notably mangroves and tidal marshes—exhibit biogenic feedbacks that are facilitating adjustment to relative sea-level rise (RSLR), including the sequestration of carbon and the trapping of mineral sediment[1]. The stability of reef-top habitats under RSLR is similarly linked to reef-derived sediment accumulation and the vertical accretion of protective coral reefs[2]. The persistence of these ecosystems under high rates of RSLR is contested[3]. Here we show that the probability of vertical adjustment to RSLR inferred from palaeo-stratigraphic observations aligns with contemporary in situ survey measurements. A deficit between tidal marsh and mangrove adjustment and RSLR is likely at 4 mm yr^{-1} and highly likely at 7 mm yr^{-1} of RSLR. As rates of RSLR exceed 7 mm yr^{-1}, the probability that reef islands destabilize through increased shoreline erosion and wave overtopping increases. Increased global warming from 1.5 °C to 2.0 °C would double the area of mapped tidal marsh exposed to 4 mm yr^{-1} of RSLR by between 2080 and 2100. With 3 °C of warming, nearly all the world's mangrove forests and coral reef islands and almost 40% of mapped tidal marshes are estimated to be exposed to RSLR of at least 7 mm yr^{-1}. Meeting the Paris agreement targets would minimize disruption to coastal ecosystems.

Coastal ecosystems have long been recognized as indispensable to the well-being and subsistence of millions of people[4]. Marine vegetation and fringing reefs attenuate wave energy, protecting coastlines while providing habitat to distinctive assemblages of species. Coral reefs are productive ecosystems of high ecological value, and reef islands—consisting of biogenic carbonate sands—are frequently inhabited by communities dependent on these resources[2]. Vegetated coastal ecosystems (mangroves, tidal marshes, seagrass meadows and kelp forests) are foundational to coastal fisheries[5] and are, in addition, well placed to contribute to CO_2 removal in efforts to maintain warming below 2 °C. Global guidelines[6] and a growing understanding of conservation and restoration opportunities are enabling an increasing number of coastal nations to account for carbon that is captured and stored in coastal and marine ecosystems ('blue carbon') while enhancing the coastal protection afforded by living shorelines[7]. Several jurisdictions have enacted or are progressing incentives for tidal wetland protection, restoration and/or creation[8] to reverse centuries of decline, slowing the rate of mangrove loss[9] and demonstrating the potential for rebuilding coastal ecosystems damaged by the human population footprint in the coastal zone[10].

These important ecosystems face an uncertain future as a result of human-induced climate change. Many of the most important coastal ecosystems show biogenic responses to RSLR that enhance their physical resilience[11]. The potential for high rates of sedimentation, productivity and organic matter preservation in mangroves and tidal marshes and the productivity of coral reefs have enabled them to grow vertically with RSLR over millennia[12]. We refer to this process as 'vertical adjustment'. Vertical adjustment can maintain a wetland above a drowning threshold, a buffer referred to as 'elevation capital'[13]. For reef island systems, vertical adjustment maintains the uppermost portions of a reef near mean sea level. Where the rate of vertical adjustment falls behind the rate of RSLR, an elevation deficit emerges, and the surface is exposed to increasing depth and duration of inundation. This change in inundation may enhance vertical adjustment[3], but if a

[1]School of Natural Sciences, Macquarie University, Sydney, New South Wales, Australia. [2]Institute of Plant Science and Microbiology, Universität Hamburg, Hamburg, Germany. [3]Earth Observatory of Singapore, Nanyang Technological University, Singapore, Singapore. [4]Asian School of the Environment, Nanyang Technological University, Singapore, Singapore. [5]Department of Earth and Environmental Sciences, Tulane University, New Orleans, LA, USA. [6]Department of Earth and Planetary Sciences and Rutgers Institute of Earth, Ocean and Atmospheric Sciences, Rutgers University, Piscataway, NJ, USA. [7]Department of Earth Sciences, Swire Institute of Marine Science and Institute of Climate and Carbon Neutrality, University of Hong Kong, Hong Kong, Hong Kong. [8]Catchments and Coasts Research Group, Department of Geography, University of Lincoln, Lincoln, UK. [9]Geography, Faculty of Environment, Science & Economy, University of Exeter, Exeter, UK. [10]College of Science and Engineering, James Cook University, Townsville, Queensland, Australia. [11]School of Earth Atmospheric and Life Sciences and GeoQuEST Research Centre, University of Wollongong, Wollongong, New South Wales, Australia. [12]School of Civil Engineering, The University of Queensland, Brisbane, Queensland, Australia. [13]School of Biological Sciences, The University of Queensland, Brisbane, Queensland, Australia. [14]Research Institute of Environment and Livelihoods, Faculty of Science and Technology, Charles Darwin University, Darwin, Northern Territory, Australia. [15]Natural Resources Research Institute, University of Minnesota–Duluth, Duluth, MN, USA. [16]US Geological Survey, Wetland and Aquatic Research Centre, Lafayette, LA, USA. [17]US Geological Survey, Eastern Ecological Research Center, Beltsfield, MD, USA. ✉e-mail: neil.saintilan@mq.edu.au

deficit is sustained for a sufficiently long period, elevation capital is exhausted. For wetlands, retreat and a transition to open water may occur, and in reef islands, submergence of reef crests will increase wave exposure and wave over-topping frequency. Whether the areal extent of the habitat expands or contracts over time depends on the rate of loss and the rate of new habitat formation, both both of which are influenced by RSLR[14].

Contemporary observations of high accretion rates in coastal ecosystems have indicated resilience under current and projected RSLR rates, prompting reassessment of their vulnerability in modelling studies[3,11,14]. Conversely, studies emerging from the palaeo record show a comparatively high vulnerability of mangroves[12] and tidal marshes[15,16] to rates of RSLR that are anticipated in coming decades under moderate and high emissions scenarios[17]. Palaeo records show that most coral reef islands formed during the later stages of the Holocene epoch under conditions of stable or falling relative sea level[2] (RSL). The upper limits of resilience to projected RSLR remains an important knowledge gap, with wide ranging implications for coastal zone protection and management.

Here we analyse three independent lines of evidence to assess the vulnerability and exposure of coastal ecosystems to the higher rates of sea-level rise (4 mm yr^{-1} to more than 10 mm yr^{-1}) projected under global warming scenarios. We focus on intertidal and supratidal ecosystems that undergo vertical adjustment from biogenic feedbacks, facilitating resilience to RSLR: mangroves, tidal marshes and coral reef island systems. We exclude beaches, rocky reefs and rock platforms, for which biogenic feedbacks with RSLR are largely absent, and subtidal vegetated ecosystems (seagrass meadows and kelp forests) for which thermal stress is likely to be the primary driver of change, rather than RSLR[18,19]. First, we review the behaviour of these ecosystems over the range of sea-level histories encountered following the Last Glacial Maximum 19 thousand years ago (ka), and particularly since 10 ka. Second, for mangroves and tidal marshes, we document elevation trends in relation to contemporary rates of RSLR using a global network of survey benchmarks, the surface elevation table-marker horizon (SET-MH) network. Third, we analyse the extent to which contemporary coastal ecosystems show conversion to open water (hereafter referred to as 'retreat') under a range of settings with varying rates of RSLR. From these three lines of evidence, we estimate the probability of coastal ecosystem retreat in relation to RSLR rates and model the response of the world's existing coastal ecosystems under the RSLR projections of the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report[17], including potential compensation through conversion of terrestrial uplands (hereafter 'landward migration'). From these analyses a picture emerges of the narrowing boundaries of the 'safe operating space'[20] for coastal ecosystems: the climate futures expected to be of low risk to existing ecosystems.

Responses to past sea-level rise

RSL varies globally in response to both water and land vertical movement[21]. Coastlines continue to adjust to the loss of ice sheets after the previous glacial period, particularly in higher latitudes, a process called glacial isostatic adjustment[21,22] (GIA). GIA modelling provides insights into sea-level trends since the last deglaciation. These observations and models have been applied to interpret rates of RSLR associated with the timing of mangrove and tidal marsh retreat and/or advance in stratigraphic successions, with results showing broad consistency among settings[12,15].

Rapid global mean sea-level (GMSL) rise (over 10 mm yr^{-1}) during several periods since the Last Glacial Maximum has drowned mangrove forests and tidal marshes (Fig. 1). Periods of rapid GMSL rise include: (1) meltwater pulse 1A (14.6–14.3 ka) which drowned mangroves, tidal marshes and coral reefs, the remains of which have been found at water depths of around 90 m; and (2) a rapid rise in GMSL 11.3–11.0 ka, leaving relict features at water depths of around 50 m. Interspersed with these phases have been periods of slower GMSL rise, allowing extended periods of coastal ecosystem expansion (Fig. 1; Methods). For example, mangrove sediments associated with preserved coastal palaeo channels on the Sahul Shelf (northwest of mainland Australia) and the Sunda Shelf (western South China Sea) dating to 16.0–14.5 ka were probably drowned during meltwater pulse 1A (Methods). Mangrove forests re-established in India from around 10 ka on the former delta of the Ganges–Brahmaputra River (Fig. 1) and the northeast Australian continental shelf (Queensland). In both locations, RSLR declined to between 6 and 7 mm yr^{-1}, and rates of sedimentation were high. These forests were subsequently drowned during a period of more rapid RSLR of 7 to 8 mm yr^{-1} between 9.0 and 8.5 ka (Methods). Widespread mangrove forest development commenced around 8.5–7.5 ka in Southeast Asia, northern and eastern Australia, South America and Africa (Fig. 1) as the rate of RSLR declined[12] below 7 mm yr^{-1} (Fig. 2c), and mangroves associated with large rivers were able to maintain their intertidal position by trapping sediment and accumulating root mass.

Tidal marshes in Great Britain were 9 times more likely to retreat than advance during the Holocene when RSLR exceeded 7.1 mm yr^{-1}, based on more than 780 reconstructions of tidal marsh evolution[15] (Fig. 2b). In the Mississippi Delta, only short-lived and rapidly retreating fringing tidal marshes existed before 8.2 ka, with retreat occurring in approximately 50 years before RSLR slowed[16] to less than 6 to 9 mm yr^{-1}. Tidal marsh retreat took longer (centuries), as RSLR dropped below 6 mm yr^{-1} after around 8.2 ka, but marshes did not stop retreating in the Mississippi Delta[16] until RSLR was less than 3 mm yr^{-1} (Fig. 2b).

Sea level stabilized in the mid-Holocene in those parts of the world that were distant from former centres of glaciation, and many coral reefs—especially in the Pacific—reached sea level with diversification of reef habitats[23]. Subsequent fall of sea level relative to these regions resulted in emergent reef platforms, some of which became suitable habitat for mangroves, and on which it became possible for reef islands to form[24]. Infilling of estuaries resulted in development of extensive coastal plains[12], reducing intertidal areas previously covered by mangroves, including in coastal Northern Australia (South Alligator River, Fitzroy River, Ord River, Cleveland Bay and Richmond River), Thailand (Great Songkhla Lakes) and Vietnam (Mekong River and Red River).

The palaeo record therefore indicates a capacity for vertical adjustment to rates of RSLR similar to those encountered in the instrumental period. If these rates of RSLR are sustained, coastal lowlands may be re-occupied by tidal wetlands where migration is permitted, and in many places this encroachment has already commenced[25]. The potential for increased extent in these regions under higher sea level is captured in global wetland adjustment models[14,26]. However, there is consistent evidence that vertical adjustment and habitat extent are greatly reduced[12,23] as RSLR approaches 7 to 8 mm yr^{-1}.

Elevation trends under current sea-level rise

Mangrove and tidal marsh accretion can increase with the rate of RSLR. Increased inundation depth and duration can facilitate both mineral deposition[27] and higher plant productivity and root mass accumulation[11]. Rates of accretion measured against artificial marker horizons and radiometric markers often correspond to high rates of RSLR encountered in settings where land is subsiding[3,28,29]. High rates of accretion (10 to 20 mm yr^{-1}) have been observed in contemporary mangroves and tidal marshes on active deltas[29,30], and accretion in the intertidal zone increases with increased depth and duration of inundation[3]. The assumption that accretion enables vertical adjustment to RSLR is the basis of projections of possible resilience under projected future rates[31], but the assumption requires testing against fixed elevation benchmarks.

To assess the relationship between accretion of surface sediment, vertical adjustment and sea-level rise in contemporary coastal wetlands, we used the SET-MH method (Fig. 2d; Methods). The SET-MH

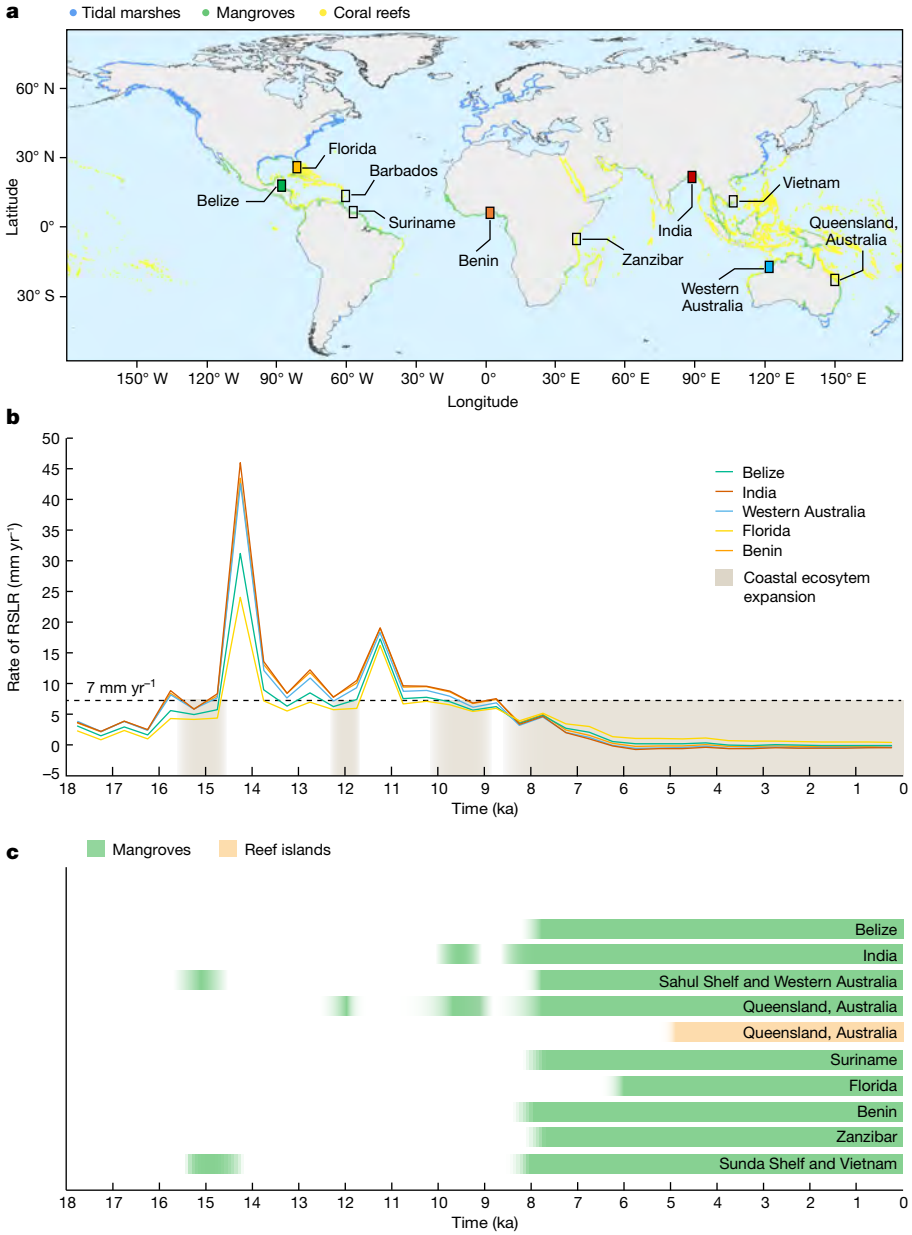


Fig. 1 | Coastal ecosystem responses to RSLR following the Last Glacial Maximum. a, Present-day distribution of mapped coastal ecosystems and the location of case studies highlighted in **b**,**c**. **b**, Median rates of RSLR over time derived from GIA modelling (Methods). **c**, Timing of habitat advance and retreat for a selection of locations (Methods). Mangrove, tidal marsh and coral reef island development is predominantly associated with periods of RSLR of less than 7 mm yr^{-1}.

uses a benchmark survey rod coupled with an introduced sediment horizon to assess the relationship between accretion and elevation gain[32]. SET-MH data in tidal marshes show that shallow subsidence (the difference between sediment accretion and elevation gain) increases with accretion rate and the rate of RSLR[28,29]. A previous analysis of a globally distributed network of 477 tidal marsh SET-MH stations showed that the increase in the subsidence rate with increasing accretion was non-linear[29]. For this reason, elevation deficits emerged under rates of RSLR similar to those inferred from the stratigraphic record[29] (Fig. 2e and Extended Data Fig. 2). We repeated this Bayesian analysis for 190 SET-MH installations in mangrove forests (Methods), estimating the cumulative probability of vertical adjustment at or exceeding the rate of RSLR at the SET-MH stations (Fig. 2f and Extended Data Fig. 2). The results were consistent with those for tidal marshes. We found that an elevation deficit at mangrove sites is very likely ($P > 0.9$) at RSLR between 7 and 8 mm yr^{-1} (Fig. 2f), consistent with tidal marshes monitored using the same method (Fig. 2e). These observations concur with the limits of tidal marsh and mangrove stability in relation to palaeo-RSLR as inferred from the stratigraphic record[29] and described previously (Fig. 2a–c).

Habitat change under current sea-level rise

As a third line of evidence, we assessed whether changes in the extent of tidal marsh and open water were consistent with RSLR and/or the deficit between RSLR and marsh vertical adjustment (Extended Data Fig. 3; Methods). Previous surveys of contemporary North American tidal marshes in low-to-moderate tidal range settings[33] found that habitat retreat commenced at a RSLR of 4 to 6 mm yr^{-1}. For example, the Maryland Eastern Shore is retreating[34] under a long-term RSLR trend of around 6 mm yr^{-1}. In a comprehensive analysis of tidal marshes in the contiguous USA, gains in tidal marsh were found to be inversely related

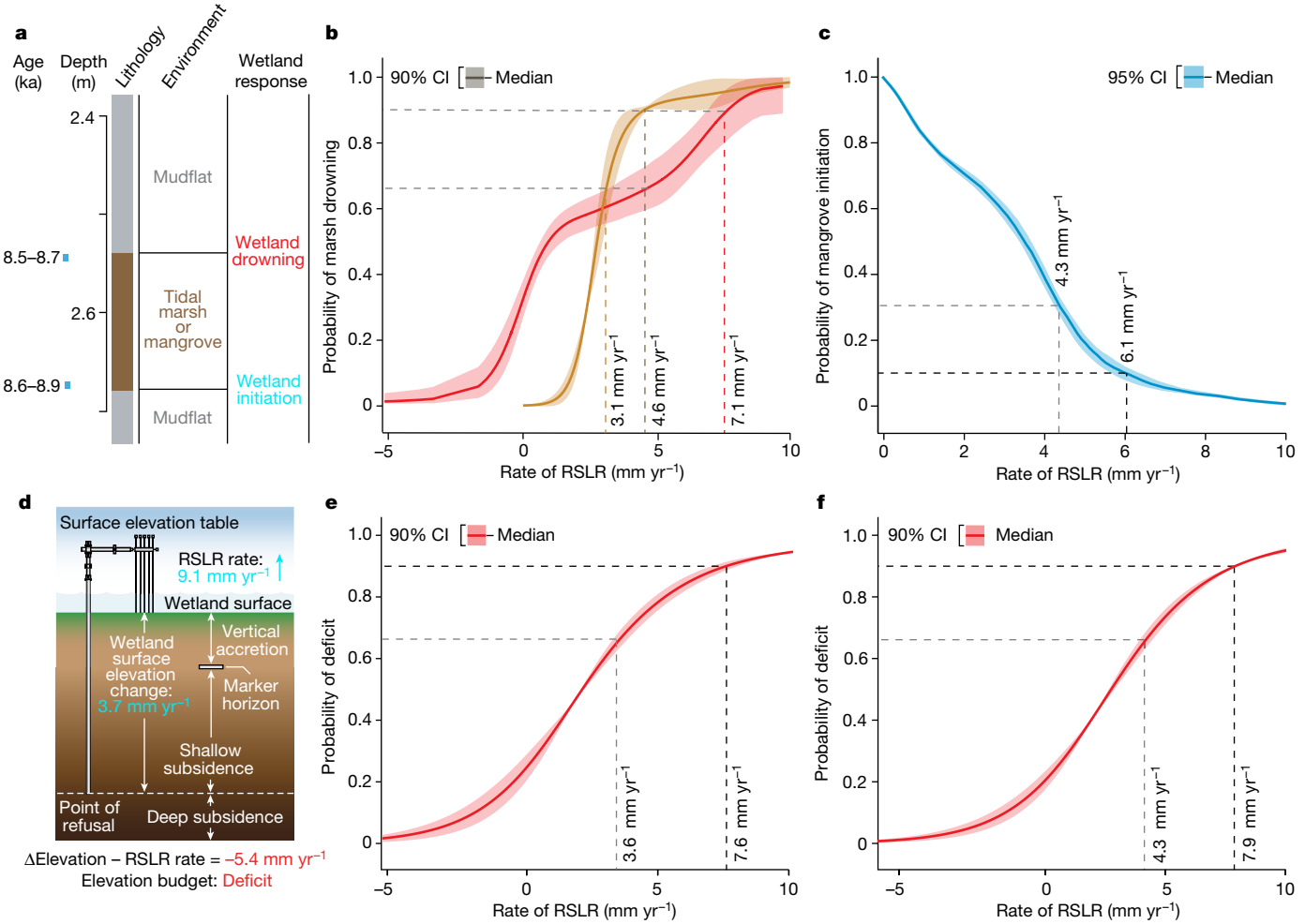


Fig. 2 | Probability of vertical adjustment of mangrove and tidal marsh to rising sea levels. a–**c**, Palaeo-stratigraphic assessments (**a**) of marsh adjustment or retreat for tidal marshes (**b**) and the probability of the initiation of sustained mangrove vertical adjustment[12] (**c**), in relation to rates of RSLR encountered over the past 10,000 years. **b**, The red line represents minerogenic UK marshes[15] and the orange line represents organic marshes of the Mississippi Delta[14]. **d**–**f**, Results in **a**–**c** are compared with vertical adjustment as assessed by the surface elevation table (**d**), analysed for the probability of a deficit between vertical adjustment and RSLR for the same period of measurement, for 477 tidal marsh SET-MH installations[29] (**e**) and 190 mangrove SET-MH installations (**f**). Adopting IPCC likelihood definitions (Methods), we indicate in each case the probability thresholds at which mangrove or marsh drowning becomes likely ($P \geq 0.66$) or very likely ($P \geq 0.90$). The corresponding histograms for each RSLR increment are shown in Extended Data Fig. 2. **b**,**c**,**e**,**f**, The line represents the median and the shaded region shows 90% confidence interval (CI).

to RSLR, with some marsh loss associated with short-term perturbations, notably hurricanes[34]. RSLR was also associated with reduced normalized difference vegetation index (NDVI) values for vegetation adjacent to the marsh[34], possibly resulting from saline water intrusion.

We used high-resolution global mapping of surface water change[35] and tidal wetland extent[36] in the immediate vicinity of tidal marsh SET-MH stations globally to determine the influence of contemporary RSLR, elevation capital and elevation deficit on marsh loss. Canopy cover obscured observations of surface water in mangroves. We found that tidal marsh sites were likely to show a trend towards increased presence of surface water ($P > 0.66$) once RSLR exceeded 2.3 mm yr^{-1} (Extended Data Fig. 3). The frequency of surface water observations at marsh sites increased with both the rate of RSLR ($r^2 = 0.16$, $P < 0.001$; Extended Data Fig. 4) and marsh elevation deficit ($r^2 = 0.14$, $P < 0.001$; Extended Data Figs. 4 and 5). The relationship between surface water change and marsh elevation deficit was evident in lower elevation marsh sites ($r^2 = 0.20$) rather than higher elevation sites ($r^2 = 0.03$; Extended Data Fig. 5), illustrating the temporary resilience conferred by elevation capital. We also found a significant relationship between the proportion of tidal marsh conversion to open water habitat and RSLR ($P = 0.018$). Tidal marshes were as likely as not ($P = 0.5$) to be retreating as RSLR increased above 5.4 mm yr^{-1} (Extended Data Fig. 3), with relatively few marshes advancing. This estimate of retreat may be conservative because patches of interior marsh break-up may not have been identified (Methods). The ameliorating influence of elevation capital was also evident in the extent of marsh retreat. Where marshes had higher than the median elevation capital, there was no relationship between marsh retreat and RSLR ($P = 0.850$). At lower than the median elevation capital, the relationship was highly significant ($P = 0.002$).

There are relatively few data on the change to reef-top habitats. Surveys of reef island planiform change in the tropical western Pacific and Indian Oceans have shown a remarkable degree of stability under rates of RSLR up to the contemporary GMSL rate[37,38]. Our collation of existing data on reef island morphometric changes ($n = 872$) from the Indian and Pacific Oceans shows a higher probability of island contraction at rates of RSLR above the rate of contemporary GMSL rise (Methods; Extended Data Fig. 3c). Island size reduction is likely ($P \geq 0.66$) at RSLR above 6.2 mm yr^{-1}. The rate of RSLR in the Solomon Islands has averaged between 7 and 10 mm yr^{-1} since 1994 (ref. 39), and in the exposed northern Isabel Province, five of the twenty vegetated reef islands have completely eroded, leaving dead mangrove trunks on hard coral[40]. A further six islands contracted by more than 20% in the

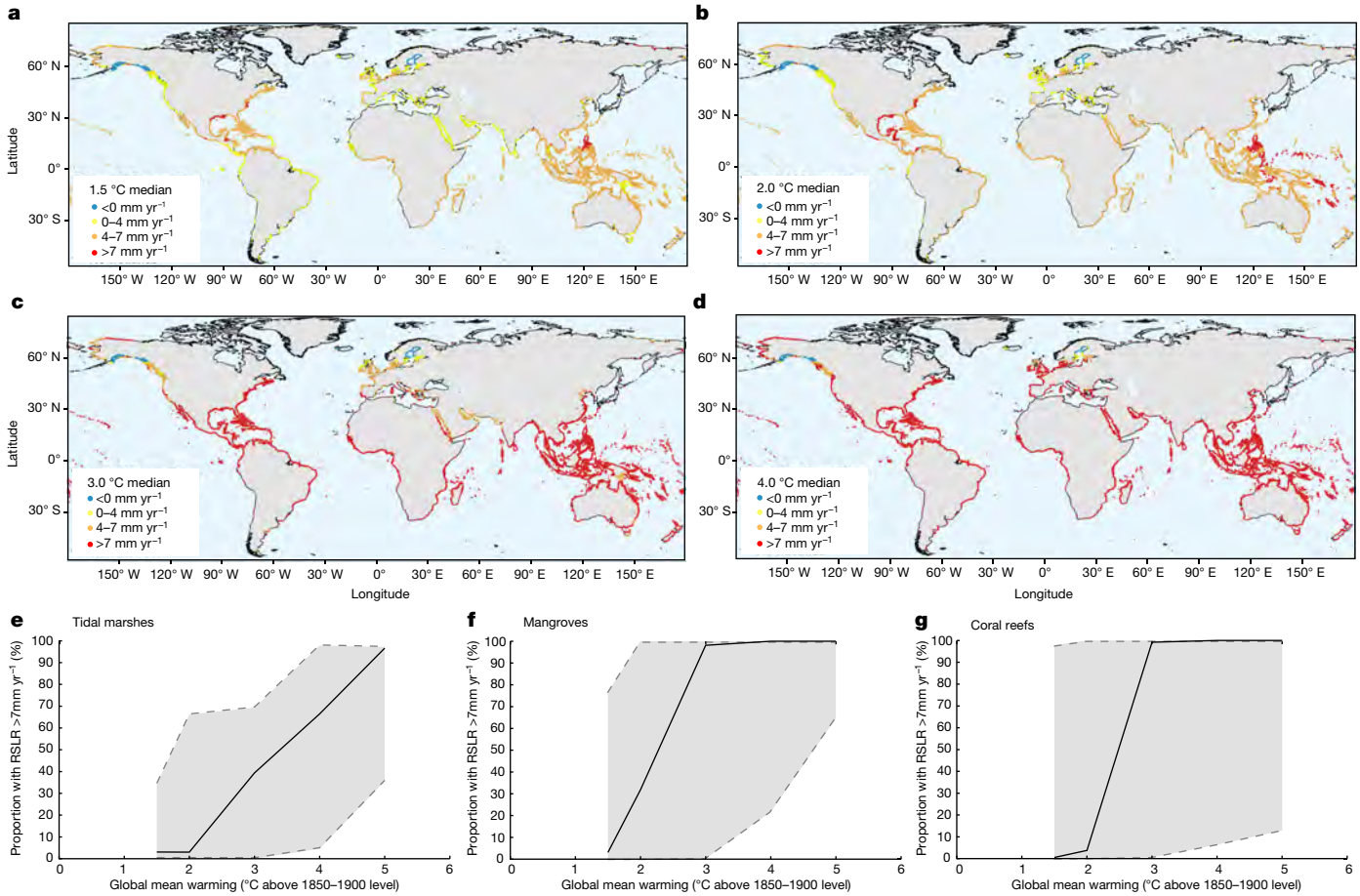


Fig. 3 | Projected exposure of coastal ecosystems to RSLR. a–d, Coastlines with mapped mangrove, tidal marsh or reef habitat subject to >4 mm yr^{-1} and >7 mm yr^{-1} RSLR over 2080–2100 under the median projections for 1.5 °C (**a**), 2.0 °C (**b**), 3.0 °C (**c**) and 4.0 °C (**d**) warming scenarios relative to 1850–1900. Note that projected rates of RLSR rely to a considerable extent on tide gauge records that may capture local anomalies (for example, due to fluid extraction) that could produce locally higher rates. **e–g**, The proportion of global tidal marsh (**e**), mangrove (**f**) and coral reef (**g**) habitat subject to 7 mm yr^{-1} of RSLR by 2100 in the scenarios shown in **a–d**, as well as the 5 °C scenario. Error bands show the 17–83% likely range. These projections do not take into account the possibility that ice sheet instabilities substantially increase RSLR in warming scenarios exceeding 2 °C.

period 1947–2014. These observations conform to RSLR thresholds modelled for the stability of reef islands in the Marshall Islands group based on palaeo sea-level reconstructions[41]. The reef islands in the western tropical Pacific provide insights into probable outcomes for intertidal wetland and supratidal islands on reef tops globally under conditions of accelerating RSLR projected to 2100.

Projected response to future sea-level rise

Modelling of spatial variability in RSLR was completed in the IPCC AR6 for each warming scenario[42]. We compared regional RSLR projections to 2080–2100 with the distribution of mangroves, tidal marshes and coral reefs across the globe (Fig. 3; Methods). For each of the modelled scenarios, we determined the proportion of mangrove, tidal marsh and coral reef island habitat occurring where RSLR is projected to rise to levels for which eventual retreat of mangroves and tidal marshes is likely (4 mm yr^{-1}) or very likely (7 mm yr^{-1}), the best estimate from our combined palaeo and instrumental observations. For reef islands (a subset of mapped reefs), contraction or increasing island instability by RSLR of 7 mm yr^{-1} is likely (Extended Data Fig. 2c), although we cannot yet specify a rate of RSLR at which contraction is highly likely, given the scarcity of contemporary observations at higher rates of RSLR, and because this threshold will vary with the rate of surrounding reef vertical growth, reef flat width, wave exposure, island size and height, and reef-derived sediment supply.

In the 1.5 °C scenario, the likely ($P \geq 0.66$) rate of GMSL rise at 2080–2100 is between 2.4 and 6.4 mm yr^{-1}. Coastlines subject to rates of RSLR of 4 to 7 mm yr^{-1} correspond to centres of contemporary mangrove development, notably Southeast Asia and the Caribbean. Under this rate of RSLR, elevation deficits are likely ($P = 0.66–0.90$; Fig. 2). The probability of reaching a rate of RSLR at which elevation deficits are very likely (7 mm yr^{-1}) remains low (<11%), although coastlines subject to high rates of land subsidence—including, for example, the US Gulf Coast and Southeast Asian deltas[28,43]—are projected to exceed this rate. Median projections for the 2 °C warming scenario suggest that one third of global mangroves are subject to ≥7 mm yr^{-1} and nearly all exposed to ≥4 mm yr^{-1} of RSLR, although there is comparatively little change in the proportion of tidal marshes and reefs exposed to ≥7 mm yr^{-1} of RSLR (Table 1). Under 3 °C of warming, nearly all tropical and subtropical latitude coastlines are exposed to ≥7 mm yr^{-1} of RSLR, and these are the locations of most of the world's mangroves and coral reefs. Median RSLR projections along the world's coastlines therefore show the probability of elevation deficits in mangroves shifting from likely to very likely between 2 °C and 3 °C of global warming (Fig. 3 and Table 1).

At high latitudes, portions of coastline have declining RSLR owing to gravitational, rotational and elastic deformational effects resulting from mass loss of glaciers and the Greenland Ice Sheet offsetting GMSL rise. For this reason, proportional loss of existing tidal marsh with RSLR is expected to be lower than for mangroves with increased

Table 1 | Median estimates (and 17–83% likely range) of the proportion of existing mangrove, tidal marsh and coral reef island vulnerable to elevation deficit and eventual loss under the five AR6 RSLR warming scenarios[17]

	Mangrove		Tidal marsh		Coral reefs
	Likely	Very likely	Likely	Very likely	Likely
1.5 °C	0.81 (0–1.0)	0.03 (0–0.77)	0.34 (0.03–0.69)	0.03 (0–0.34)	0.01 (0–0.98)
2.0 °C	0.99 (0.02–1.0)	0.32 (0–1.0)	0.65 (0.06–0.98)	0.03 (0–0.66)	0.04 (0–1.0)
3.0 °C	1.00 (0.75–1.0)	0.98 (0–1.0)	0.67 (0.31–0.98)	0.39 (0–0.69)	0.99 (0.01–1.0)
4.0 °C	1.00 (0.99–1.0)	1.00 (0.22–1.0)	0.70 (0.63–0.98)	0.66 (0.04–0.98)	1.00 (0.06–1.0)
5.0 °C	1.00 (1.0–1.0)	1.00 (0.64–1.0)	0.97 (0.93–0.97)	0.97 (0.36–0.97)	1.00 (0.13–1.0)

For mangroves and tidal marshes, loss is the proportion of existing area exposed to 4 mm yr^{-1} (likely loss; $P > 0.66$) and 7 mm yr^{-1} (very likely loss; $P > 0.9$) of RSLR based on probability distributions presented in Fig. 2, and the RSLR modelling in Fig. 3. For coral reef islands, the proportion refers to numbers of reefs, and uses the conservative estimate of likely vulnerability to RSLR at 7 mm yr^{-1} (the full dataset with uncertainties is presented as Extended Data Table 1).

warming. At 2 °C warming, the high-latitude European and North American west coasts remain below 4 mm yr^{-1} RSLR under median estimates, and at 3 °C the Baltic Sea and Gulf of Alaska remain below 4 mm yr^{-1}. Tidal marsh habitat is likely to expand in extent in northern Siberia under higher RSLR owing to limited topographic and human development impediments (Fig. 4 and Extended Data Fig. 6). Far northern coastlines therefore emerge as important future habitats for tidal marsh—as also projected for seagrass meadows and kelp forests[19,30,44]—under warmer temperatures and reduced ice cover and ice scour, increasing their relative contribution to blue carbon capture and storage at high latitudes.

The influence of global change drivers

The behaviour of future ecosystems may not always be anticipated by palaeo and contemporary analogues. Processes influencing vertical adjustment of coastal wetlands and reefs to sea-level rise may be modified by climate change, though often the influence is to supress vertical adjustment. Land-use change driven by population growth may increase sediment supply by rivers, subsidizing sediment accumulation in coastal deltas[45,46]. Counteracting this is the association between economic development and dam construction, an intervention that retains sediment within catchments. Sediment yields to coastal environments in the global north are nearly half those prior to such hydrological modifications[45]. Major hydrological developments in Southeast Asian rivers have negative implications for the resilience of mangroves to sea-level rise[47].

Elevated concentrations of atmospheric CO_2 and associated climate change may modify biotic feedbacks to sea-level rise. Long-term field mesocosm experiments in Chesapeake Bay, USA have shown that root growth and marsh vertical adjustment was enhanced by the atmospheric CO_2 fertilization effect[48] and moderate warming (approximately 1.7 °C above ambient[49]). However, as observed RSLR increased above 7 mm yr^{-1}, water stress negated the benefit of elevated CO_2 (ref. 50), and temperatures above 1.7 °C increasingly promoted organic carbon remineralization, lowering elevation gain[50].

Ocean acidification and thermal stress will supress reef vertical growth due to impacts on coral cover, unless rapid adaptation occurs. Recent estimates identify low accretion potential (averaging 1.8 ± 2.2 mm yr^{-1}) across many tropical western Atlantic reefs[51], compared with rates derived from palaeo-reef core records[51]. Currently

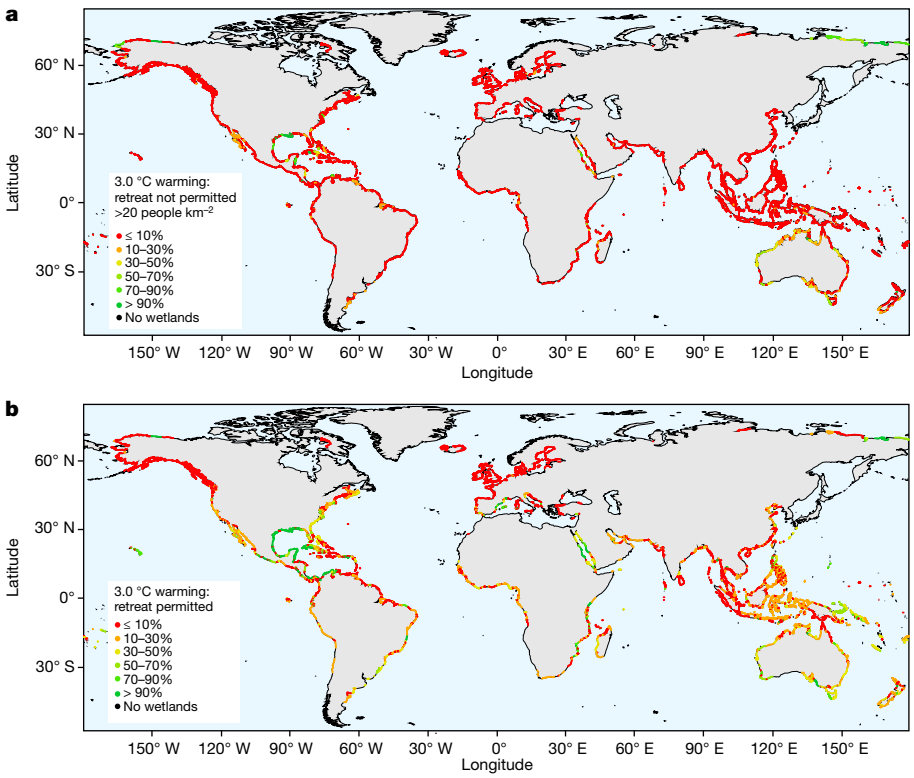


Fig. 4 | Wetland inland retreat potential. The percentage of the current wetland area that could potentially be compensated for via inland retreat until 2100, calculated for the 3.0 °C warming scenario (Methods). **a**, The scenario for wetland inland retreat capacity possible with a population density below 20 people per km^2. **b**, The scenario for wetland inland retreat unimpeded by population density (the no barriers scenario[14]; Methods). Scenarios restricting landward encroachment under lower populations density thresholds are shown in Extended Data Fig. 6.

less than half of reefs in the western Atlantic and Indian Ocean have maximum accretion potential rates matching altimetry-derived rates of sea-level rise[51]. Recent modelling of the impacts of climate change on reef accretion potential to 2100 suggest that increasingly severe and frequent bleaching events will further limit reef accretion potential[52] (even in the absence of other confounding local disturbance pressures). The potential of reef-top habitats and reef islands to accrete will therefore be influenced by increasing water depths above the surrounding fringing reefs and probable shifts in the abundance and production rates of biota from which sediment is derived. Both may negatively affect future reef-top habitats and will almost certainly impinge upon cultural use and sustainability[14].

Implications for management

The committed loss of coastal habitats under high warming scenarios should not discourage conservation and restoration efforts. Under small elevation deficits, centuries may elapse before the elevation capital of a wetland is exhausted, and this will provide sufficient time for the supply of ecosystems services, including those critical for well-being and sustenance. Over the current century, landward migration driven by sea-level rise may compensate wetland loss, or even facilitate wetland expansion and associated carbon burial potential[53]. Extensive mangrove forest development in the mid-Holocene, coupled with high rates of vertical accretion under 4 to 7 mm yr^{-1} RSLR promoted blue carbon capture and storage at a scale that may have contributed to an observed decline in global atmospheric CO_2 concentrations for this period[12]. In the near-term, increased GMSL potentially allows for the recolonization of these coastal floodplains, expanding mangrove area while promoting higher rates of organic carbon accumulation than currently encountered[53]. Although intensive coastal development in Asia has reduced coastal wetland extent in former biogeographic centres[36] and is likely to restrict landward retreat (Fig. 4), extensive coastal floodplains provide viable opportunities for mangrove landward migration and even aerial expansion in northern and northwestern Australia[54], the northern Gulf of Mexico[55], Siberia and—depending on opportunities for restoration in more populated areas—Central America, Colombia and the western Mediterranean (Fig. 4.). In the Gulf of Mexico and northern Australia, mangrove forest and tidal creek encroachment under higher rates of RSLR is already being observed[25,56].

The implication of the gap between the Paris Agreement aspiration (2 °C with an aim of 1.5 °C) and the pathways consistent with the implementation of current policies (2.4 °C to 3.5 °C by 2080–2100, medium confidence[57]) is profound for coastal ecosystems. Warming above 2 °C would restore the conditions faced by mangroves and tidal marshes under previous high RSLR periods and would likely expose most of the world's mangrove and two thirds of the world's tidal marsh to elevation deficits (Table 1). Warming of 3 °C by 2100 would accelerate GMSL rise to rates consistent with a high probability of eventual tidal marsh and mangrove retreat and increased reef island instability for much of their geographic extent. Once reached, these rates of RSLR are projected to persist for centuries to millennia[58]. The thermal inertia of ocean waters is likely to drive irreversible ice sheet grounding line retreat where bedrock slopes away from the coast[58], ensuring ongoing marine ice sheet instability[59]. Projected elevation deficits therefore define committed losses upon the exhaustion of elevation capital. Our analysis therefore suggests that the long-term contribution of blue carbon to climate mitigation is compromised under higher emissions scenarios. While preserving organic carbon in situ in many settings[12,53], narrower, younger and more transitional wetlands would predominate[23]. As a result, coastlines and reef islands that are currently protected will be increasingly exposed to erosion and retreat, consistent with palaeo observations[16,23].

Coastal ecosystems represent another of the numerous tipping elements for climate change impacts and rank among the more vital to human well-being and vulnerable to imminent warming levels[60]. The non-linear response to external forcing as seen in a wide range of ecosystems is closely associated with the concept of safe operating space, which promotes planetary boundaries being maintained a safe distance from critical thresholds of unacceptable environmental change[20]. Our findings demonstrate that the boundaries for a safe operating space for coastal ecosystems are approaching, and will be set by near-term emissions pathways. They also highlight the importance of mitigating against local environmental stressors (such as pollution in coral reefs) and restoring cleared and degraded wetlands to enhance resilience against climate change and coastal recession. In the face of irrevocable disruption under high rates of RSLR, the most effective means of promoting the continued survival of widespread mangrove forests, tidal marshes and coral reef islands is to achieve the Paris Agreement goal of net zero emissions by 2050. To this end, a contribution will be made by the preservation, restoration and landward accommodation of coastal blue carbon ecosystems.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-023-06448-z.

1. Morris, J. T. et al. Contributions of organic and inorganic matter to sediment volume and accretion in tidal wetlands at steady state. *Earths Future* **4**, 110–121 (2016).
2. Perry, C. T. et al. Implications of reef ecosystem change for the stability and maintenance of coral reef islands. *Global Change Biol.* **17**, 3679–3696 (2011).
3. Kirwan, M. L., Temmerman, S., Skeehan, E. E., Guntenspergen, G. R. & Fagherazzi, S. Overestimation of marsh vulnerability to sea level rise. *Nat. Clim. Change* **6**, 253–260 (2016).
4. Costanza, R. et al. Changes in the global value of ecosystem services. *Global Environ. Change* **26**, 152–158 (2014).
5. Jänes, H. et al. Quantifying fisheries enhancement from coastal vegetated ecosystems. *Ecosystem Services* **43**, 101105 (2020).
6. Hiraishi, T. et al. *2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands* (IPCC, 2014).
7. Herr, D., von Unger, M., Laffoley, D. & McGivern, A. Pathways for implementation of blue carbon initiatives. *Aquat. Conserv.* **27**, 116–129 (2017).
8. Kelleway, J. J. et al. A national approach to greenhouse gas abatement through blue carbon management. *Global Environ. Change* **63**, 102083 (2020).
9. Friess, D. A. et al. Mangroves give cause for conservation optimism, for now. *Curr. Biol.* **30**, R153–R154 (2020).
10. Duarte, C. M. et al. Rebuilding marine life. *Nature* **580**, 39–51 (2020).
11. Morris, J. T., Sundareshwar, P., Nietch, C. T., Kjerfve, B. & Cahoon, D. R. Responses of coastal wetlands to rising sea level. *Ecology* **83**, 2869–2877 (2002).
12. Saintilan, N. et al. Thresholds of mangrove survival under rapid sea level rise. *Science* **368**, 1118–1121 (2020).
13. Cahoon, D. R., Lynch, J. C., Roman, C. T., Schmit, J. P. & Skidds, D. E. Evaluating the relationship among wetland vertical development, elevation capital, sea-level rise, and tidal marsh sustainability. *Estuaries Coast.* https://doi.org/10.1007/s12237-018-0448-x (2019).
14. Schuerch, M. et al. Future response of global coastal wetlands to sea-level rise. *Nature* **561**, 231–234 (2018).
15. Horton, B. P. et al. Predicting marsh vulnerability to sea-level rise using Holocene relative sea-level data. *Nat. Commun.* **9**, 2687 (2018).
16. Törnqvist, T. E., Jankowski, K. L., Li, Y.-X. & González, J. L. Tipping points of Mississippi Delta marshes due to accelerated sea-level rise. *Sci. Adv.* **6**, eaaz5512 (2020).
17. IPCC. in *Climate Change 2021: The Physical Science Basis* (eds Masson-Delmotte, V. et al.) Ch. 9 (Cambridge Univ. Press, 2021).
18. Smale, D. A. Impacts of ocean warming on kelp forest ecosystems. *New Phytol.* **225**, 1447–1454 (2020).
19. Valle, M. et al. Projecting future distribution of the seagrass *Zostera noltii* under global warming and sea level rise. *Biol. Conserv.* **170**, 74–85 (2014).
20. Rockström, J. et al. A safe operating space for humanity. *Nature* **461**, 472–475 (2009).
21. Horton, B. P. et al. Mapping sea-level change in time, space, and probability. *Annu. Rev. Environ. Resour.* **43**, 481–521 (2018).
22. Khan, N. S. et al. Inception of a global atlas of sea levels since the Last Glacial Maximum. *Quat. Sci. Rev.* **220**, 359–371 (2019).
23. Törnqvist, T. E., Cahoon, D. R., Morris, J. T. & Day, J. W. Coastal wetland resilience, accelerated sea-level rise, and the importance of timescale. *AGU Adv.* **2**, e2020AV000334 (2021).
24. Kench, P., Smithers, S. & McLean, R. Rapid reef island formation and stability over an emerging reef flat: Bewick Cay, Northern Great Barrier Reef, Australia. *Geology* **40**, 347–350 (2012).

25. Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A. & Krauss, K. W. Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biol.* **20**, 147–157 (2014).
26. Ouyang, X., Connolly, R. M. & Lee, S. Y. Revised global estimates of resilience to sea level rise for tidal marshe. *Environ. Chall.* **9**, 100593 (2022).
27. French, J. Tidal marsh sedimentation and resilience to environmental change: exploratory modelling of tidal, sea-level and sediment supply forcing in predominantly allochthonous systems. *Mar. Geol.* **235**, 119–136 (2006).
28. Jankowski, K. L., Törnqvist, T. E. & Fernandes, A. M. Vulnerability of Louisiana's coastal wetlands to present-day rates of relative sea-level rise. *Nat. Commun.* **8**, 14792 (2017).
29. Saintilan, N. et al. Constraints on the adjustment of tidal marshes to accelerating sea level rise. *Science* **377**, 523–527 (2022).
30. Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K. M. & Pedersen, M. F. Arctic kelp forests: diversity, resilience and future. *Global Planet. Change* https://doi.org/10.1016/j.gloplacha.2018.09.005 (2019).
31. Kirwan, M. L. et al. Limits on the adaptability of coastal marshes to rising sea level. *Geophys. Res. Lett.* https://doi.org/10.1029/2010GL045489 (2010).
32. Cahoon, D. R. et al. High-precision measurements of wetland sediment elevation: II. The rod surface elevation table. *J. Sediment. Res.* **72**, 734–739 (2002).
33. Watson, E., Raposa, K., Carey, J., Wigand, C. & Warren, R. Anthropocene survival of southern New England's salt marshes. *Estuaries Coast.* **40**, 617–625 (2017).
34. Campbell, A. D., Fatoyinbo, L., Goldberg, L. & Lagomasino, D. Global hotspots of salt marsh change and carbon emissions. *Nature* **612**, 701–706 (2022).
35. Pekel, J.-F., Cottam, A., Gorelick, N. & Belward, A. S. High-resolution mapping of global surface water and its long-term changes. *Nature* **540**, 418–422 (2016).
36. Murray, N. J. et al. High-resolution mapping of losses and gains of Earth's tidal wetlands. *Science* **376**, 744–749 (2022).
37. Duvat, V. K. A global assessment of atoll island planform changes over the past decades. *Wiley Interdiscip. Rev. Clim. Change* **10**, e557 (2019).
38. Kench, P. S., Ford, M. R. & Owen, S. D. Patterns of island change and persistence offer alternate adaptation pathways for atoll nations. *Nat. Commun.* **9**, 605 (2018).
39. Becker, M. et al. Sea level variations at tropical Pacific islands since 1950. *Global Planet. Change* **80**, 85–98 (2012).
40. Albert, S. et al. Interactions between sea-level rise and wave exposure on reef island dynamics in the Solomon Islands. *Environ. Res. Lett.* **11**, 054011 (2016).
41. Kane, H. H. & Fletcher, C. H. Rethinking reef island stability in relation to anthropogenic sea level rise. *Earth's Future* **8**, e2020EF001525 (2020).
42. Garner, G. G. et al. IPCC AR6 sea level projections, version 20210809. *Zenodo* https://doi.org/10.5281/zenodo.5914710 (2021).
43. Nicholls, R. J. et al. A global analysis of subsidence, relative sea-level change and coastal flood exposure. *Nat. Clim. Change* **11**, 338–342 (2021).
44. Marbà, N., Krause-Jensen, D., Masqué, P. & Duarte, C. M. Expanding Greenland seagrass meadows contribute new sediment carbon sinks. *Sci. Rep.* **8**, 14024 (2018).
45. Dethier, E. N., Renshaw, C. E. & Magilligan, F. J. Rapid changes to global river suspended sediment flux by humans. *Science* **376**, 1447–1452 (2022).
46. Nienhuis, J. et al. Reply to: Concerns about data linking delta land gain to human action. *Nature* **614**, E26–E28 (2023).
47. Lovelock, C. E. et al. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* **526**, 559–563 (2015).
48. Langley, J. A., McKee, K. L., Cahoon, D. R., Cherry, J. A. & Megonigal, J. P. Elevated CO_2 stimulates marsh elevation gain, counterbalancing sea-level rise. *Proc. Natl Acad. Sci. USA* **106**, 6182–6186 (2009).
49. Smith, A. J., Noyce, G. L., Megonigal, J. P., Guntenspergen, G. R. & Kirwan, M. L. Temperature optimum for marsh resilience and carbon accumulation revealed in a whole-ecosystem warming experiment. *Global Change Biol.* **28**, 3236–3245 (2022).
50. Zhu, C., Langley, J. A., Ziska, L. H., Cahoon, D. R. & Megonigal, J. P. Accelerated sea-level rise is suppressing CO_2 stimulation of tidal marsh productivity: A 33-year study. *Sci. Adv.* **8**, eabn0054 (2022).
51. Perry, C. T. et al. Loss of coral reef growth capacity to track future increases in sea level. *Nature* **558**, 396–400 (2018).
52. Cornwall, C. E. et al. Global declines in coral reef calcium carbonate production under ocean acidification and warming. *Proc. Natl Acad. Sci. USA* **118**, e2015265118 (2021).
53. Rogers, K. et al. Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature* **567**, 91–95 (2019).
54. Woodroffe, C. D., Thom, B. G. & Chappell, J. Development of widespread mangrove swamps in mid-Holocene times in northern Australia. *Nature* **317**, 711–713 (1985).
55. Osland, M. J. et al. Migration and transformation of coastal wetlands in response to rising seas. *Sci. Adv.* **8**, eabo5174 (2022).
56. Cavanaugh, K. C. et al. Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. *Proc. Natl Acad. Sci. USA* **116**, 21602–21608 (2019).
57. IPCC. *Climate Change 2022: Mitigation of Climate Change* (eds Shukla, P. R. et al.) (Cambridge Univ. Press, 2022).
58. Garbe, J., Albrecht, T., Levermann, A., Donges, J. F. & Winkelmann, R. The hysteresis of the Antarctic ice sheet. *Nature* **585**, 538–544 (2020).
59. DeConto, R. M. et al. The Paris Climate Agreement and future sea-level rise from Antarctica. *Nature* **593**, 83–89 (2021).
60. Armstrong McKay, D. I. et al. Exceeding 1.5 °C global warming could trigger multiple climate tipping points. *Science* **377**, eabn7950 (2022).

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2023

Methods

Palaeo wetland response to RSLR

To estimate RSLR following the Last Glacial Maximum (Fig. 1), we use a revised numerical simulation of GIA[61], which adopts the ICE-6G global ice reconstruction from the Last Glacial Maximum to the present[62,63]. We use an ensemble of 300 combinations of rheological parameters in the GIA model to estimate RSL at 500-year time steps on a 512 × 260 global latitude × longitude grid, resulting in predictions of RSL at >130,000 points in space for each time step.

Post-glacial coastal habitat development and retreat prior to the Holocene are inferred from relict features that include the following: (1) drowned mangroves, tidal marshes and coral reefs, the remains of which have been found at around 90 m water depth[64], corresponding to meltwater pulse 1A (14.6–14.3 ka); and (2) relict features at around 50 m water depth[65,66], corresponding to a rapid rise in GMSL dating to 11.3–11.0 ka. Mangrove vertical development in relation to Holocene RSLR is based on 78 observations of the timing of the initiation of sustained mangrove peat development[12]. Evidence of post-glacial mangrove expansion is evident on the Sahul Shelf, Western Australia[67] and the Sunda Shelf, Southeast Asia[68] ~12–14.5 ka, a phase ceasing during meltwater pulse 1A (Fig. 1). A relatively brief (~300-year) period of mangrove expansion and vertical development prior to 9 ka is documented in the western Ganges–Brahmaputra Delta[69], and the Queensland continental shelf[70], locations of high sediment delivery at the time[69,70]. Our GIA modelling (Fig. 1) suggests RSLR dipped to around 6 mm yr^{-1} at this time. Mangroves in both sites were drowned during a period in which RSLR increased to circa 7 mm yr^{-1} ~9 ka. A pan-tropical expansion in mangrove development and sustained vertical adjustment[54,71–75] commenced from ~8.5 ka as RSLR declined[12] to <6 mm yr^{-1} according to GIA modelling (Fig. 1). A subset of these observations representative of the global dataset[12] are provided in Fig. 1, including Twin Cays, Belize[76]; Swan Key, FL, USA[77]; Pakhiralaya, Western Ganges, India[69]; Porto-Novo, Benin[78]; Mekong Delta, Cambodia[79]; Makoba Bay, Zanzibar[80]; Ord River, Western Australia[71]; and Mulgrave River, Queensland, Australia[81]. Reef island development commenced in the Pacific during the mid-Holocene corresponding to RSLR stabilization and fall. The example provided in Fig. 1 is Bewick Cay, Queensland, Australia[24].

Tidal marsh vulnerability to Holocene RSLR presented in Fig. 2 is based on the data from two studies utilizing multiple proxies across the UK[15] and the Mississippi Delta[16]. Holocene RSL data was compiled for 54 regions from Great Britain with the rate of RSL varying in relation to proximity to the centre of the Last Glacial Maximum British–Irish Ice Sheet[15]. RSLR rates estimated from GIA model predictions were compared to sea-level tendencies for 781 tidal marsh index points[15] (positive $n = 403$; negative $n = 360$; no tendency $n = 19$). For the Mississippi Delta, the Holocene RSL history was inferred from 72 sea-level index points, with marsh tendency assessed using 334 boreholes showing a well-defined Pleistocene–Holocene transition overlain by at least 2 m of sediment[16].

Contemporary wetland response to RSLR

Assessment of mangrove and tidal marsh vertical adjustment was conducted using the SET-MH technique. This globally distributed network of monitoring stations[82] combines a stable benchmark rod against which measurements of elevation change are made, with an artificial marker horizon introduced at the time of benchmark rod installation, against which sediment accretion is measured (Extended Data Fig. 1). Pins extended from a portable arm (the surface elevation table) extend to the marsh surface, measuring surface elevation change in relation to the base of the benchmark rod. Comparison with elevation gain can then be made against water level changes measured at nearby tide gauges[29].

This technique was previously used[29] to test how elevation gain at 477 SET-MH monitoring stations compared to RSLR changes measured over the same period. To this analysis (presented as Fig. 2e) we have added a mangrove SET-MH network of 190 SET-MH stations (Fig. 2f), the location of which are provided in Extended Data Table 2. These data combine published rates of elevation gain with new measurements reported here (Extended Data Table 2). RSLR for the period of SET-MH measurement was extracted from tide gauge records provided by the National Oceanic and Atmospheric Administration (https://tidesandcurrents.noaa.gov/sltrends/sltrends.html) and, for Australia, the Australian Baseline Sea Level Monitoring Project (http://www.bom.gov.au/oceanography/projects/abslmp/abslmp.shtml).

Contemporary habitat distribution

The contemporary distribution and extent of mangroves[83] (https://doi.org/10.34892/07vk-ws51), tidal marshes[84] (https://doi.org/10.34892/w2ew-m835) and coral reefs[85] (Figs. 1, 3 and 4) was accessed from the Ocean Data Viewer (https://data.unep-wcmc.org), hosted by the UN Environment World Conservation Monitoring Centre. An important caveat in relation to the representation of tidal marshes is the poor coverage of their possible extent at high northern latitudes. For Fig. 3, the coral reef dataset was complemented by additional data on the global distribution of atolls, which was sourced from the World Atolls database[86] (https://www.arcgis.com/home/item.html?id=1c18adf04d9e47669281061ff60167e1).

Surface water and marsh change analysis

Because mangrove canopy cover obscured surface water observations, we report changes in surface water occurrence, and conversion of wetland to open water only for tidal marshes. We used two earth-observation derived global datasets to estimate tidal marsh conversion to open water across the SET-MH monitoring network. The Global Tidal Wetland Change (GTWC) dataset[36] depicts losses and gains of tidal marshes, tidal flats and mangroves (collectively termed 'tidal wetlands') at 30-m resolution over a 20-yr period (1999-2019). The data were developed through a machine learning classification of more than 1.1 million Landsat scenes acquired over the global coastal zone since 1999. GTWC data layers include tidal wetland losses, gains, and the probability of occurrence of tidal wetlands for the first (1999) and last (2019) time steps of the analysis. The Global Surface Water dataset depicts the location and temporal distribution of surface water from 1984 to 2020 at 30-m resolution[35]. The data were generated from >4.4 million Landsat scenes by individually classifying each Landsat pixel into water and non-water using an expert system. Although the two datasets are developed using Landsat data, the datasets differ in their temporal spans (2 to 4 decades), methodological approaches to mapping change dynamics, post-processing methods and minimum mapping unit. We therefore used both datasets to estimate the extent of tidal marsh conversion to open water in relation to observed RSLR (Supplementary Data 1).

To estimate net tidal wetland change and the extent of conversion to open water at each SET-MH monitoring site, we developed a buffer feature around the SET installation with an area of 5 km^2. For global tidal wetland change, the area of losses and gains of each tidal wetland ecosystem type (tidal marshes, tidal flats and mangroves) was computed, yielding a net change estimate of tidal wetlands associated with each SET site. For global surface water, we used the water occurrence change intensity layer, which is computed as the absolute difference in the per pixel mean water occurrence between two distinct epochs[35] (1984–1999 and 2000–2020). The average surface water change in each SET buffer feature was computed (Supplementary Data 1).

The relationships between surface water and tidal wetland change versus contemporaneous RSLR and elevation deficit were tested using multiple linear regression. Predictive variables are provided in Extended Data Table 3, and consist of climatic, hydrological and edaphic properties associated with each SET-MH station, and are sourced from ref. 39. Potential collinearity of predictors was assessed using variance

inflation factor from the car package[87]. The variance inflation factor was found to be below the level usually considered problematic (3.22). The overall relative importance of the key predictors was assessed using random forest regression analyses[88], a machine learning approach which tallies the results of small classification trees (n = 20,000) while retaining a bootstrapped subset of all observations for out-of-bag (internal) error testing. Analyses were performed in R version 4.1.3 and presented as Extended Data Fig. 4b.

Island contraction and expansion

Data on island contraction or expansion (Extended Data Fig. 3) were sourced from recent assessments and reviews[37,40,89,90] (total island n = 872: Supplementary Data 2). We compared the proportion of islands showing areal contraction or expansion, binned at 1 mm yr^{-1} RSLR increments, using the rate of RSLR cited for each reef island in the manuscripts. Islands were considered stable if change was less than 3% of the original area, following ref. 37.

Ecosystem stability under RSLR

Contemporary marsh and mangrove resilience to RSLR was inferred from data from the globally distributed mangrove and tidal marsh SET-MH networks. The elevation surplus or deficit of each site was estimated by comparing the rate of tidal marsh surface elevation change recorded by the SET to rates of RSLR over the period of operation of the SET. RSLR was sourced from the National Oceanic and Atmospheric Administration's Laboratory for Satellite Altimetry (https://tidesandcurrents.noaa.gov/sltrends/). The elevation surplus/deficit of each SET site was categorized in Extended Data Fig. 2d,e as in surplus if surface elevation change exceeded the RSLR rate by 1 mm yr^{-1}, stable if surface elevation change was within ±1 mm yr^{-1} of the RSLR rate, or in deficit if the RSLR rate exceeded surface elevation change by 1 mm yr^{-1}. The stacked histograms in Extended Data Fig. 2d,e show the proportion of elevation budget categories in relation to RSLR rates (1 mm yr^{-1} bin size) at each tidal marsh (Extended Data Fig. 2d) and mangrove (Extended Data Fig. 2e) SET site.

The resilience of palaeo tidal marsh to RLSR is represented in Extended Data Fig. 2a,b for the UK and Mississippi Delta, respectively. A 'negative' sea-level tendency—indicating tidal marsh advance—is identified by decreasing marine influence (that is, regressive contact), whereas a 'positive' sea-level tendency—which indicates tidal marsh retreat—is identified by increasing marine influence (that is, transgressive contact) in sediment archives. In the example core (Extended Data Fig. 2a), the contact between an intertidal mud and tidal marsh peat, which represents a negative tendency and marsh advance, was dated to ~8,439–8,956 years ago. The thin accumulation of tidal marsh peat is overlain by an intertidal mud, representing a positive tendency and marsh retreat; this event was dated to 8,501–8,959 years ago. RSLR rates were estimated for the timing of these marsh advance and retreat events recorded in the stratigraphy using a GIA model. The stacked histogram (Extended Data Fig. 2a) shows the proportion of these events from sediment archives across the UK in relation to RSLR rates (0.5 mm yr^{-1} bin size). The facies succession identified in sediment cores from the Mississippi Delta (Extended Data Fig. 2b) were categorized based on the following criteria: a 'terrestrial' succession—indicating no evidence of marsh 'drowning'—is associated with the presence of terrestrial (marsh) mud or peat throughout the core and an absence of lagoonal facies; 'gradual drowning'—indicating marsh drowning that occurred over centuries—identified by at least a 30-cm-thick unit of marsh mud or peat occurring beneath lagoonal mud; 'rapid drowning'—indicating marsh drowning that occurred over about half a century—associated with less than a 30-cm-thick unit of marsh mud or peat occurring beneath lagoonal facies. The contact between marsh and lagoonal facies representing gradual or rapid marsh drowning was radiocarbon dated to determine the timing of the event, and RSLR rates at that time were estimated from an RSLR record obtained from compaction-free basal peats from the Mississippi Delta. The proportion of each type of facies succession is shown in comparison to estimated rates of RSLR (0.5 mm yr^{-1} bin size).

The 'initiation' of sustained mangrove accretion (Extended Data Fig. 2c) (at least 2 m of mangrove sediment) was radiocarbon dated and RSLR rates at that time interval were estimated from an ensemble of GIA model predictions[12]. The histogram shows the probability density (distribution) of initiation events in relation to RSLR rates (1 mm yr^{-1} bins).

We summarized the probability thresholds at which marsh or mangrove elevation deficit becomes likely ($P \geq 0.66$) or very likely ($P \geq 0.90$), adopting IPCC likelihood language[91]. To estimate the probability of a negative tendency (Fig. 2b,c) or elevation deficit (Fig. 2e,f) conditional on rates of RSLR, we follow ref. 15 by modelling the elevation budget or facies successions as binary response variables (elevation deficit or drowning, 1; elevation surplus or terrestrial, 0) in a Bayesian framework. We chose the bin widths for histograms and the number of segments in the Bayesian analysis by visual inspection for best fit. Details of the probabilistic analysis used to estimate the relationship between mangrove initiation and RSLR rates (Fig. 3f) can be found in ref. 4.

Sea-level rise projections

Sea-level rise projections (Figs. 3 and 4) were those used in the IPCC AR6 and were sourced from https://doi.org/10.5281/zenodo.5914710[42]. Sea-level rise scenarios to 2100 were converted to point shapefiles for the median, 17th and 83rd percentile projections for the following warming-level-based scenarios: 1.5 °C; 2.0 °C, 3.0 °C, 4.0 °C and 5.0 °C. The 17th–83rd percentile ranges are associated with the assessed IPCC likely range; the IPCC assessment is that there is at least a 66% chance that the true value will fall within this range. From the AR6 sea-level rise scenarios, sea-level rise rates at 2100 were converted to raster format (cell size 1 degree) for the median, 17th and 83rd percentile projections for the above-listed temperature-limited scenarios. All land-based pixels (defined as pixels where sea-level rise rates were zero for all percentiles of one temperature scenario) were converted to NoData.

Ecosystem exposure to projected RSLR

For Fig. 3, available polygons for tidal marshes, mangroves and coral reefs were converted to point files based on each polygon's centroid coordinates. Where polygon features consisted of multiple polygons, polygon features were split into single-polygon features before converting them to centroid points. All resulting polygon centroids were merged with the available point data for mangroves, tidal marshes and reef islands into a dataset containing 1,885,466 entries. To visualize the spatial variability of wetland exposure to local sea-level rise (Fig. 3a–d), local RSLR rates (incorporating vertical land movement)[42] were extracted from the median projections of the temperature-limited scenarios 1.5 °C, 2.0 °C, 3.0 °C and 4.0 °C and classified into the following RSLR rate exposure categories: <0 mm yr^{-1} (blue), 0–4 mm yr^{-1} (yellow), 4–7 mm yr^{-1} (orange) and >7 mm yr^{-1} (red).

To calculate proportional changes of exposure to local RSLR rates for all five temperature-limited scenarios (Fig. 3e–g), only the available polygons for salt marshes, mangroves and coral reefs were utilized, as those included accurate aerial information. As above, polygon data were converted to point files, based on their centroid locations, but to preserve the accurate aerial information multi-polygon features were not split up. All local RSLR rates of each scenario (five temperature scenarios, with three percentiles each) were extracted for each ecosystem category to calculate proportional exposure to RSLR rates <0 mm yr^{-1}, 0–4 mm yr^{-1}, 4–7 mm yr^{-1} and >7 mm yr^{-1}. For each temperature scenario, the respective uncertainty range was defined by the lower (17%) and upper (83%) percentiles respectively.

Modelling retreat potential

AR6 RSLR data up to 2100 were utilized to model the inland retreat space of coastal wetlands available for two RSLR scenarios: the 2 °C and 3 °C warming levels (Extended Data Fig. 6). The 3 °C warming level, representing the greater potential landward retreat, is also presented in Fig. 4. This modelling relies on the global coastal wetland model, which assumes inland retreat can occur where local population densities are below a pre-defined population density threshold and the coastal topography provides sufficiently flat inland areas[14].

AR6 RSLR data (RSLR between 2020 and 2100) were retrieved from https://doi.org/10.5281/zenodo.5914710[42] with a spatial resolution of 1 degree. Trajectories of RSLR for each coastal segment, the spatial unit that the global coastal wetland model is based on ref. 92, were derived from the data point located closest (Euclidean distance) to the center of the respective coastline segment. Inland retreat space was calculated as the area additionally inundated during mean high water spring conditions, under future RSLR scenarios, and expressed as percentage of current wetland extents[14]. High water spring levels were thereby assumed to rise at the same rate as mean sea level. Local topographical profiles were calculated based on global Shuttle Radar Topography Mission data[93] and on the method first presented in ref. 94.

Taking into account the widespread obstruction that human coastal infrastructure imposes on coastal wetland inland retreat[95] and assuming that the extent of obstruction is a function of population density, wetland inland retreat was accounted for only where population densities within the local 1-in-100 year floodplain are below a threshold of 20 people per km^2 as a best case of these scenarios, a threshold of 5 people per km^2 as a worst case scenario. This range has previously been estimated to represent current conditions for the existence of barriers to coastal wetland inland retreat[14]. Meanwhile, population density has been subjected to estimated population growth following the 'middle-of-the-road' shared socio-economic pathway (SSP2)[96]. We also modelled potential landward space available for ecosystem redistribution ignoring the potential impediment of population density, the no barriers scenario (Fig. 4).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data contributing to the analysis are contained in Supplementary Data 1 and Supplementary Data 2, available at https://doi.org/10.5281/zenodo.7787502[97].

61. Dendy, S., Austermann, J., Creveling, J. & Mitrovica, J. Sensitivity of Last Interglacial sea-level high stands to ice sheet configuration during Marine Isotope Stage 6. *Quat. Sci. Rev.* **171**, 234–244 (2017).
62. Argus, D. F., Peltier, W., Drummond, R. & Moore, A. W. The Antarctica component of postglacial rebound model ICE-6G_C (VM5a) based on GPS positioning, exposure age dating of ice thicknesses, and relative sea level histories. *Geophys. J. Int.* **198**, 537–563 (2014).
63. Peltier, W. R., Argus, D. & Drummond, R. Space geodesy constrains ice age terminal deglaciation: the global ICE-6G_C (VM5a) model. *J. Geophys. Res.* **120**, 450–487 (2015).
64. Humblet, M. et al. Late glacial to deglacial variation of coralgal assemblages in the Great Barrier Reef, Australia. *Global Planet. Change* **174**, 70–91 (2019).
65. Montaggioni, L. F. History of Indo-Pacific coral reef systems since the last glaciation: development patterns and controlling factors. *Earth Sci. Rev.* https://doi.org/10.1016/j.earscirev.2005.01.002 (2005).
66. Blanchon, P., Medina-Valmaseda, A. & Hibbert, F. D. Revised postglacial sea-level rise and meltwater pulses from Barbados. *Open Quat.* **7**, 87 (2021).
67. Nicholas, W. et al. Pockmark development in the Petrel Sub-Basin, Timor Sea, northern Australia: seabed habitat mapping in support of CO_2 storage assessments. *Cont. Shelf Res.* **83**, 129–142 (2014).
68. Hanebuth, T., Stattegger, K. & Grootes, P. M. Rapid flooding of the Sunda Shelf: a late-glacial sea-level record. *Science* **288**, 1033–1035 (2000).
69. Hait, A. K. & Behling, H. Holocene mangrove and coastal environmental changes in the western Ganga–Brahmaputra Delta, India. *Veg. Hist. Archaeobot.* **18**, 159–169 (2009).
70. Grindrod, J., Moss, P. & Van Der Kaars, S. Late Quaternary cycles of mangrove development and decline on the north Australian continental shelf. *J. Quat. Sci.* **14**, 465–470 (1999).
71. Thom, B. G., Wright, L. & Coleman, J. M. Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf-Ord river, Western Australia. *J. Ecol.* **63**, 203–232 (1975).
72. Carter, R., Johnson, D. & Hooper, K. Episodic post-glacial sea-level rise and the sedimentary evolution of a tropical continental embayment (Cleveland Bay, Great Barrier Reef shelf, Australia). *Aust. J. Earth Sci.* **40**, 229–255 (1993).
73. Hashimoto, T. R., Saintilan, N. & Haberle, S. G. Mid-Holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond River Estuary, New South Wales, Australia. *Geogr. Res.* **44**, 63–76 (2006).
74. Horton, B. P. et al. Holocene sea levels and palaeoenvironments, Malay–Thai Peninsula, Southeast Asia. *Holocene* **15**, 1199–1213 (2005).
75. Tanabe, S., Hori, K., Saito, Y., Haruyama, S. & Kitamura, A. Song Hong (Red River) delta evolution related to millennium-scale Holocene sea-level changes. *Quat. Sci. Rev.* **22**, 2345–2361 (2003).
76. McKee, K. L., Cahoon, D. R. & Feller, I. C. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecol. Biogeogr.* **16**, 545–556 (2007).
77. Khan, N. S. et al. Relative sea-level change in South Florida during the past ~5000 years. *Global Planet. Change* **216**, 103902 (2022).
78. Tossou, M., Akoègninou, A., Ballouche, A., Sowunmi, M. & Akpagana, K. The history of the mangrove vegetation in Bénin during the Holocene: a palynological study. *J. Afr. Earth. Sci.* **52**, 167–174 (2008).
79. Li, Z. et al. Mid-Holocene mangrove succession and its response to sea-level change in the upper Mekong River delta, Cambodia. *Quat. Res.* **78**, 386–399 (2012).
80. Woodroffe, S. A. et al. Radiocarbon dating of mangrove sediments to constrain Holocene relative sea-level change on Zanzibar in the southwest Indian Ocean. *Holocene* **25**, 820–831 (2015).
81. Crowley, G., Anderson, P., Kershaw, A. & Grindrod, J. Palynology of a Holocene marine transgressive sequence, lower Mulgrave River valley, north-east Queensland. *Austral. J. Ecol.* **15**, 231–240 (1990).
82. Webb, E. L. et al. A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. *Nat. Clim. Change* **3**, 458–465 (2013).
83. Spalding, M. *World Atlas of Mangroves* (Routledge, 2010).
84. Mcowen, C. J. et al. A global map of saltmarshes. *Biodivers. Data J.* **5**, e11764 (2017).
85. UNEP-WCMC, WorldFish Centre, WRI & TNC. *Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project. Version 4.1* (UNEP World Conservation Monitoring Centre Cambridge, 2021).
86. Goldberg, W. M. Atolls of the world: revisiting the original checklist. *Atoll Res. Bull.* https://doi.org/10.5479/si.0077-5630.610 (2016)
87. Fox, J. & Weisberg, S. *An R Companion to Applied Regression* 3rd edn (Sage, 2019).
88. Breiman, L. Random forests. *Mach. Learn.* **45**, 5–32 (2001).
89. Sengupta, M., Ford, M. R. & Kench, P. S. Shoreline changes in coral reef islands of the Federated States of Micronesia since the mid-20th century. *Geomorphology* **377**, 107584 (2021).
90. Hisabayashi, M., Rogan, J. & Elmes, A. Quantifying shoreline change in Funafuti Atoll, Tuvalu using a time series of Quickbird, Worldview and Landsat data. *GIScience Remote Sens.* **55**, 307–330 (2018).
91. Mastrandrea, M. D. et al. *Guidance Note for Lead Authors of the IPCC Fifth Assessment Report on Consistent Treatment of Uncertainties* (IPCC, 2010).
92. Vafeidis, A. T. et al. A new global database for assessing the vulnerability of coastal zones to sea-level rise. *J. Coast. Res.* **24**, 917–924 (2008).
93. Jarvis, A., Guévara, E., Reuter., H. I. & Nelson, A. D. Hole-filled SRTM for the globe, version 4. *SRTM 90m DEM Digital Elevation Database* http://srtm.csi.cgiar.org (2008).
94. Vafeidis, A. T. et al. Water-level attenuation in global-scale assessments of exposure to coastal flooding: a sensitivity analysis. *Nat. Hazards Earth Syst. Sci.* **19**, 973–984 (2019).
95. Enwright, N. M., Griffith, K. T. & Osland, M. J. Barriers to and opportunities for landward migration of coastal wetlands with sea-level rise. *Front. Ecol. Environ.* **14**, 307–316 (2016).
96. Fricko, O. et al. The marker quantification of the Shared Socioeconomic Pathway 2: a middle-of-the-road scenario for the 21st century. *Global Environ. Change* **42**, 251–267 (2017).
97. Saintilan, N. Supplementary data for Saintilan et al. 2023. *Zenodo* https://doi.org/10.5281/zenodo.7787502 (2023).

Acknowledgements We thank the authors of the IPCC projection for developing and making the sea-level rise projections available, multiple funding agencies for supporting the development of the projections, and the NASA Sea-Level Change Team for developing and hosting the IPCC AR6 Sea-Level Projection Tool. N.S. was supported by an Alexander Von Humboldt Research Award. R.E.K., G.G.G. and E.L.A. were supported by awards from the US National Aeronautics and Space Administration (80NSSC17K0698, 80NSSC20K1724 and JPL task 105393.509496.02.08.13.31) and National Science Foundation (ICER-1663807, ICER-2103754, OCE-1702587 and OCE-2002437). B.H. and T.A.S. were funded by the Ministry of Education Academic Research Fund MOE2019-T3-1-004, the National Research Foundation Singapore, and the Singapore Ministry of Education, under the Research Centres of Excellence initiative and the National Sea Level Programme Funding Initiative (Award USS-IF-2020-1), administered by the National Environment Agency, Singapore and supported by the National Research Foundation, Singapore. Any opinions, findings and conclusions or recommendations expressed in this material are those of the author(s) and do not reflect the views of the NRF, MND and NEA. T.E.T. was funded by the US National Science Foundation (OCE-0601814, EAR-1349311 and OCE-1502588). M.S. has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement no. 101037097

(REST-COAST project). C.L. was funded by the Australian Research Council award FL200100133. K.R. and C.W. were funded by the Australian Research Council Award DP210100739. The authors acknowledge PALSEA (Palaeo-Constraints on Sea-Level Rise), a working group of the International Union for Quaternary Sciences (INQUA) and Past Global Changes (PAGES), which in turn received support from the Swiss Academy of Sciences and the Chinese Academy of Sciences. This article is a contribution to HOLSEA (Geographic variability of Holocene sea level) and International Geoscience Program (IGCP) Project 725, 'Forecasting Coastal Change'. This work is Earth Observatory of Singapore contribution 537.

Author contributions N.S. conceived the project and led the writing. G.G.G. and R.E.K. provided sea-level projections. E.L.A. conducted modelling for Figs. 1 and 2. M.S. led the modelling and analysis leading to Figs. 3 and 4. T.A.S., N.S.K. and M.S. drafted figures. N.S., B.H., T.E.T., K.R., J.K., M.M.G., C.E.L., L.B.H., L.F. and C.D.W. contributed to the assessment of tidal wetland responses. N.S., C.P., S.A., N.S.K. and C.D.W. contributed to the assessment of coral reef and reef-top habitat responses. All authors contributed to manuscript editing.

Competing interests The authors declare no competing interests.

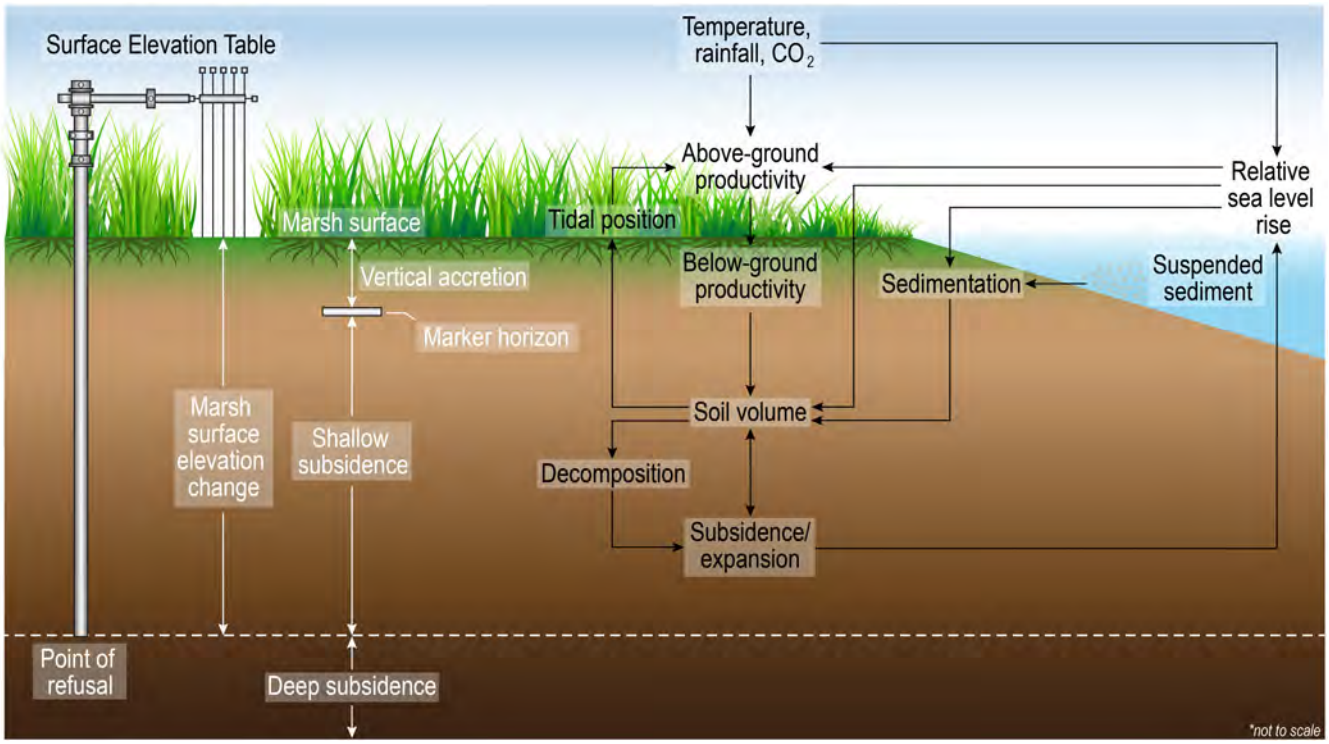
Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41586-023-06448-z.

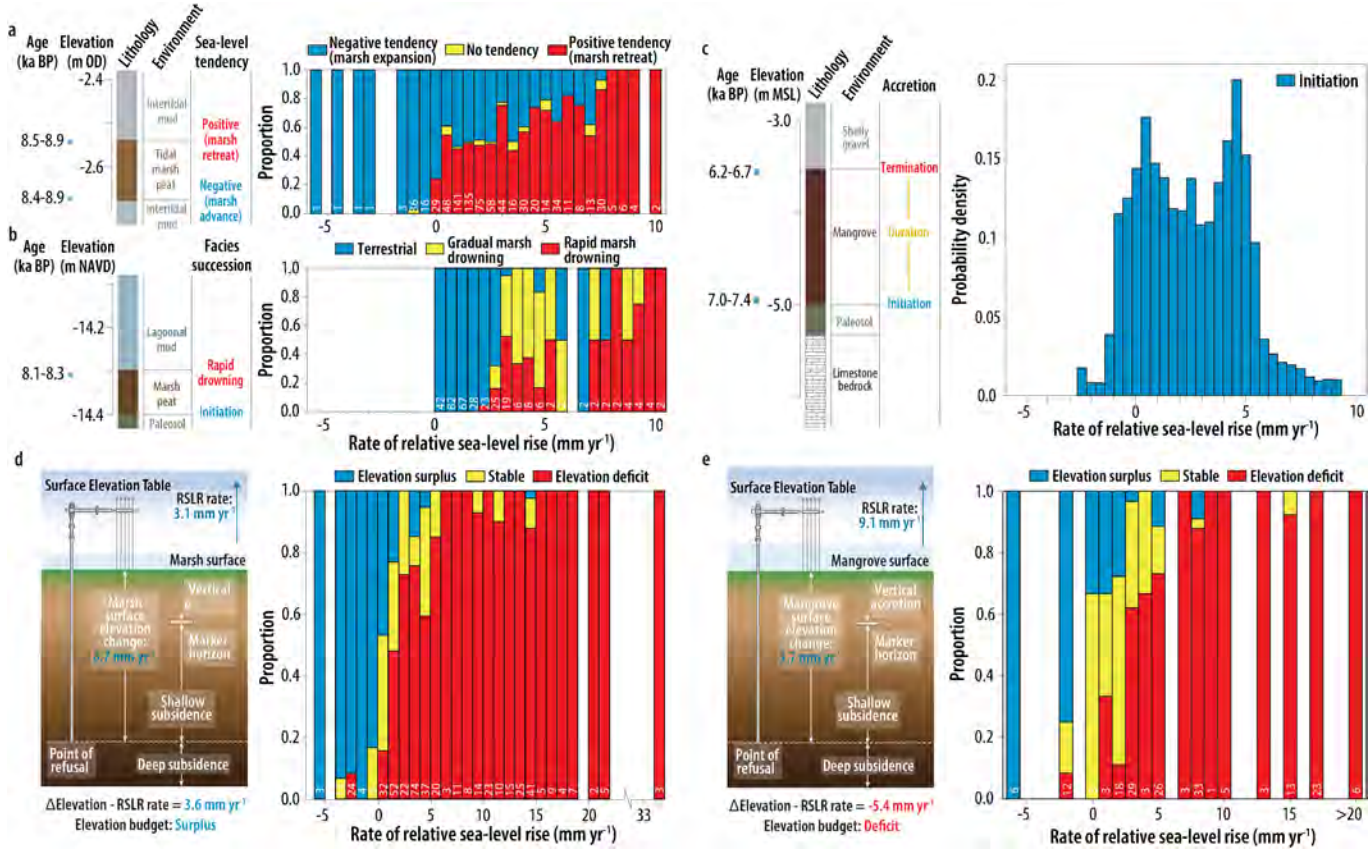
Correspondence and requests for materials should be addressed to Neil Saintilan.

Peer review information *Nature* thanks Ivan Haigh, Qiang He, Peter Herman and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer review reports are available.

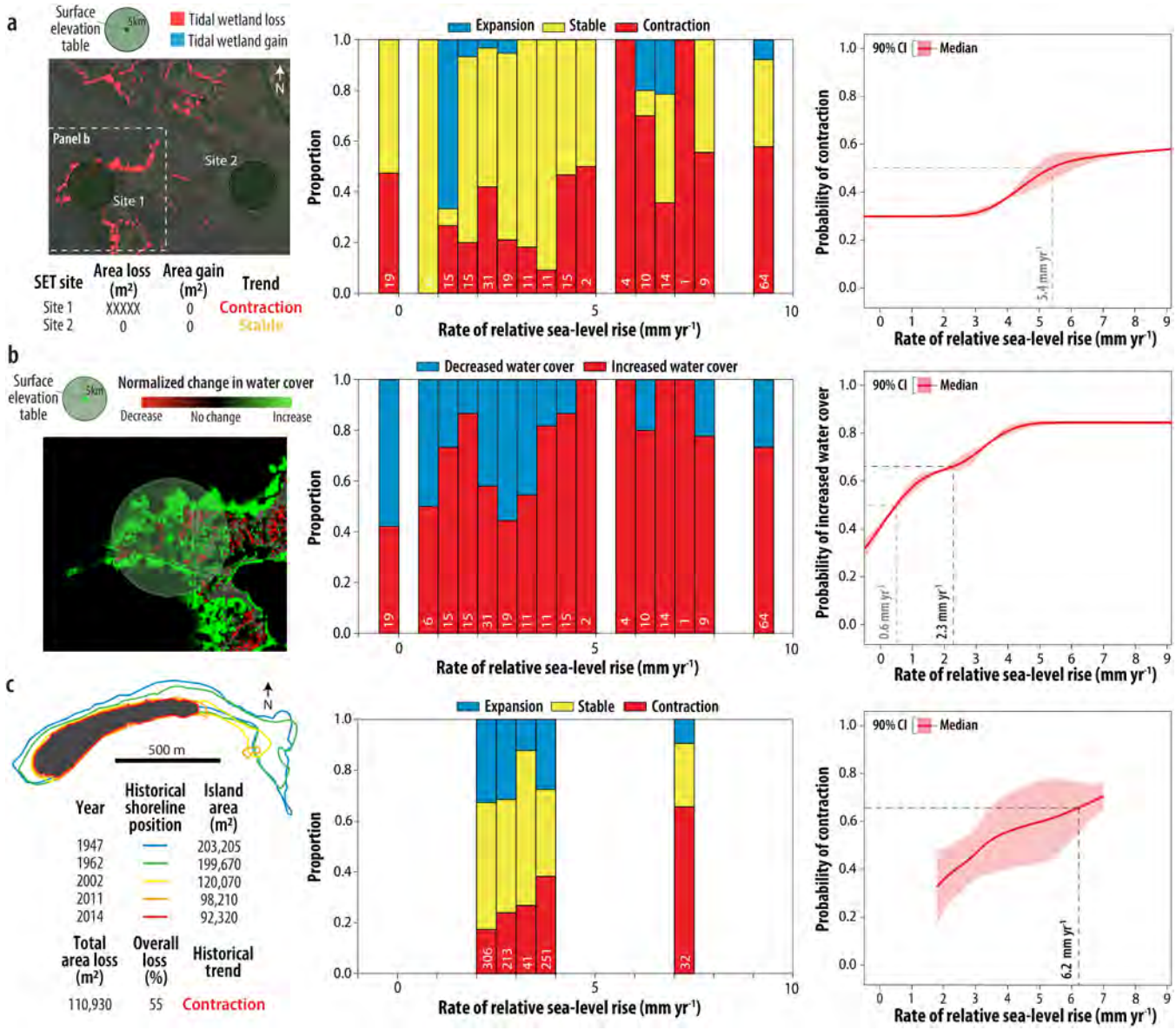
Reprints and permissions information is available at http://www.nature.com/reprints.



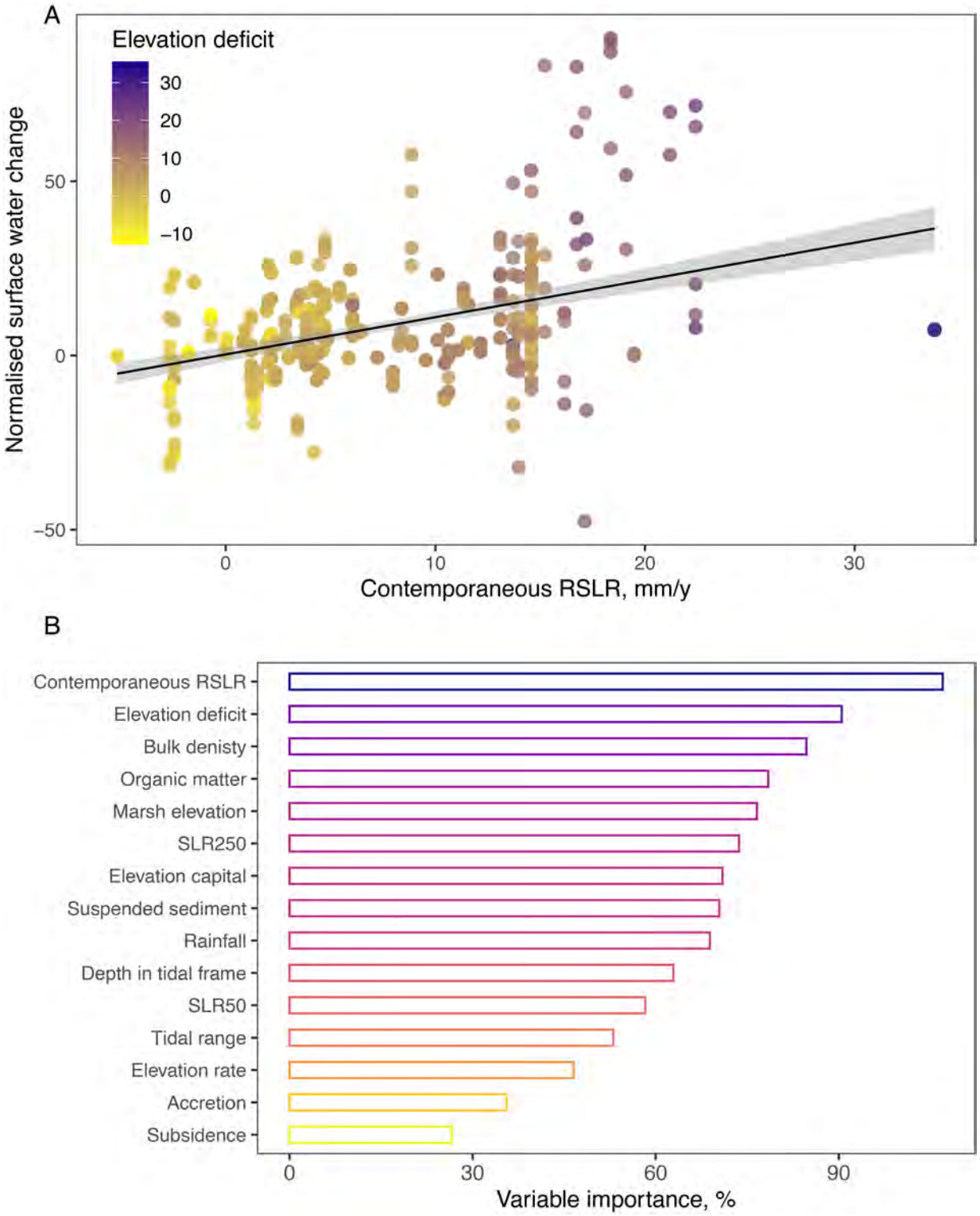
Extended Data Fig. 1 | Components of the Surface Elevation Table - Marker Horizon system. A benchmark rod driven to the point of refusal serves as a vertical benchmark against which tidal marsh/mangrove elevation gain or loss is measured. At the time of installation, an introduced horizon (feldspar or similar) is placed on the wetland surface, against which sediment and organic accretion is measured. These measurements allow for the inference of shallow subsidence, and the relation between elevation gain and RSLR.



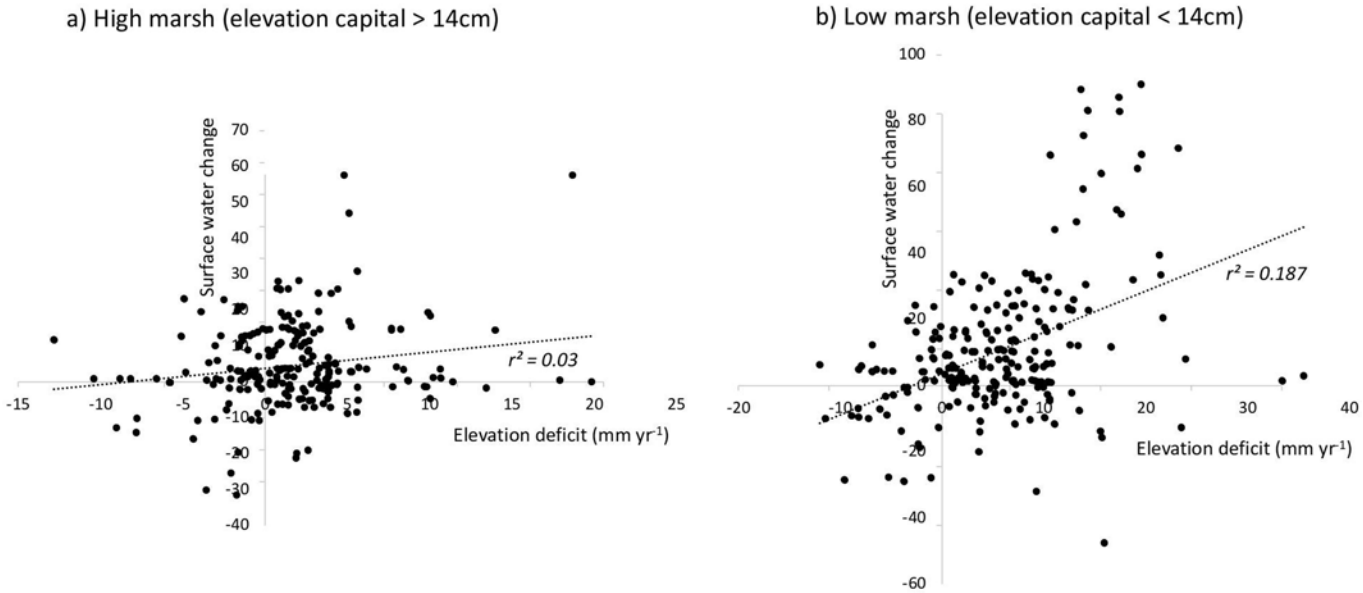
Extended Data Fig. 2 | Details of individual studies from which the probabilities of marsh and mangrove vertical adjustment to RSLR were inferred. (a) Analysis of tidal marsh retreat and advance recorded in sediment archives from across the United Kingdom[15]. (b) Analysis of marsh drowning recorded in sediment archives from the Mississippi Delta[16]. (c) Analysis of global mangrove accretion recorded in sediment archives from[12]. (d) Analysis of surface elevation tables (SET) from global tidal marshes[29]. (e) Analysis of surface elevation tables (SET) for mangrove SET sites in Extended Data Table 2. For a, b, d, and e probabilistic analysis shown in Fig. 2 follows[15] and[29], where the probability of an elevation deficit/surplus, marsh retreat/drowning, or rapid drowning/terrestrial succession was modelled as a binary response variable, and the relationship of this response with rates of RSLR was estimated in a Bayesian framework. Details of the probabilistic analysis used in e to estimate the relationship between mangrove initiation and RSLR rates (c) can be found in[12]. Numbers of observations for each RSLR increment are shown at the base of each column.



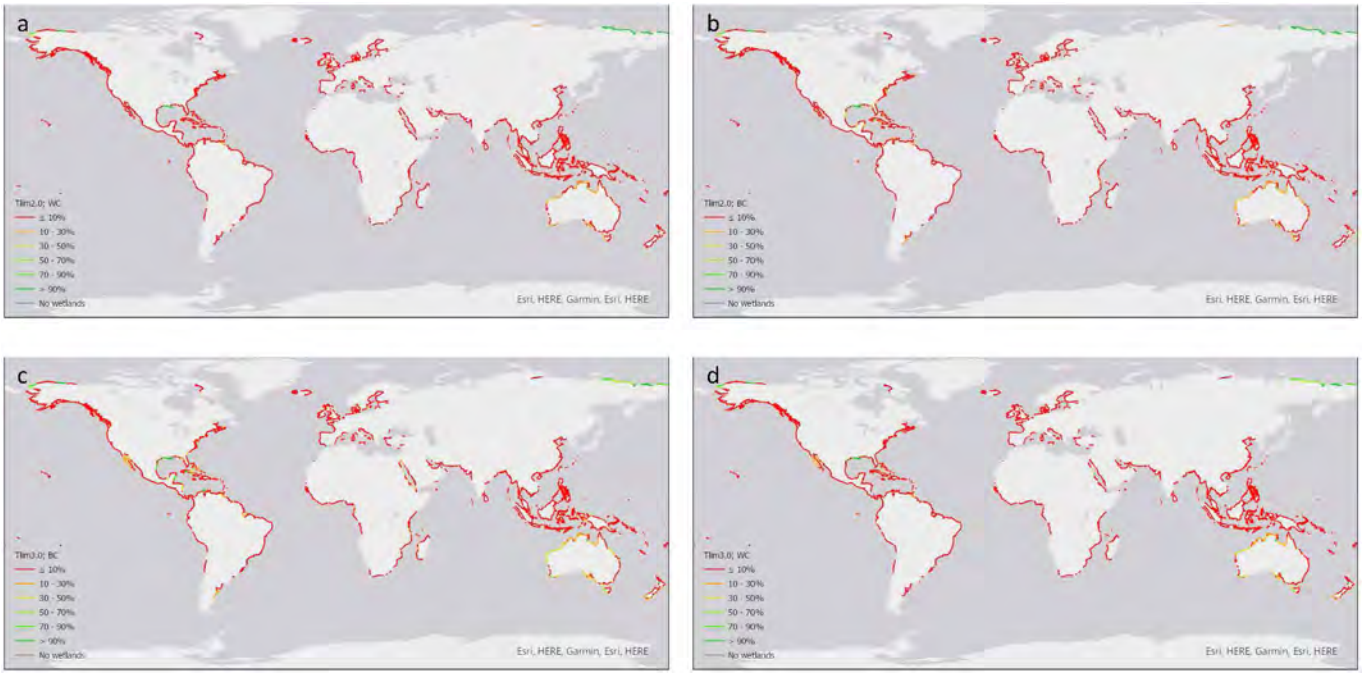
Extended Data Fig. 3 | Probability of conversion to open water with RSLR. Tidal marsh area change 1999-2019[36] within a 5 km^2 of tidal marsh SET-MH sites in relation to RSLR (a). Change in surface water occurrence at the tidal marsh SET-MH sites[29], comparing 20 years pre-2000 and post-2000[35] in relation to RSLR trends during the period of SET measurement[29] (b). Reef island planform change in relation to RSLR (c: area change and RSLR data from studies in Supplementary Information Data 2). Numbers of observations for each RSLR increment are shown at the base of each column. Image data in (a) are from Google Earth.



Extended Data Fig. 4 | Surface water area in tidal marshes increases with RSLR and elevation deficit. A: Normalised surface water change (change in the % occurrence of surface water) comparing the two decades pre-2000 and post-2000[35] at the tidal marsh SET-MH monitoring sites (n = 476)[29]. The presence of surface water increases with RLSR ($r^2 = 0.16$, $P<0.001$). Grey shading indicates the 95% confidence level interval for linear model predictions. B: Results of Random Forest analysis predicting the normalised surface water change at the SET-MH monitoring sites, based on predictive variables sourced from[29] (listed in Extended Data Table 3).



Extended Data Fig. 5 | Marsh elevation, elevation deficit and surface water change. Normalised surface water change (change in the % occurrence of surface water) comparing the two decades pre-2000 and post-2000[35] at the tidal marsh SET-MH monitoring sites[29], in relation to the deficit between elevation gain and RSLR. For marshes above the median marsh elevation of 14 cm above the lower limits of survival (a), the relationship is weak (linear regression $r^2 = 0.03$, $P = 0.009$; $n = 298$). For marshes below this median marsh elevation (b), normalised surface water change increases with the size of the elevation deficit (linear regression $r^2 = 0.187$, $P < 0.001$; $n = 231$). Elevation capital is the elevation of the marsh above the lower limits of survival, at which open water conversion would be expected.



Extended Data Fig. 6 | Inland retreat potential of existing mangrove and tidal marsh. Percentage of the current wetland area that could potentially be compensated for via wetland inland retreat until 2100, calculated for two sea-level rise scenarios. Median projections for 2.0 °C warming, allowing wetland retreat to a population threshold of (a) 5 people km^{-2} (worst case scenario, WC) and (b) 20 people km^{-2} (best case scenario, BC) Median projections for 3.0 °C warming, allowing wetland retreat to a population threshold of (c) 5 people km^{-2}; and (d) 20 people km^{-2}.

Extended Data Table 1 | Area (km², and proportion) of mangrove, tidal marsh and number of coral reefs exposed to various rates of RSLR under policy-relevant warming scenarios

Saltmarsh

SLR scenario	≤0 mm/yr	0-4 mm/yr	≥4 mm/yr	>4 mm/yr proportion	Uncertainty	>7 mm/yr proportion	Uncertainty	Avg. SLR	Global SLR
1.5°C,17%	126590	89612	6821	0.0306	0.31	0.0000	0.03	0.13	2.4
1.5°C,50%	67933	79732	75359	0.3379		0.0305		3.57	4.2
1.5°C,83%	1082	67513	154428	0.6924	0.35	0.3420	0.32	7.29	6.4
2.0°C,17%	74162	133715	15147	0.0679	0.58	0.0004	0.03	0.89	3.2
2.0°C,50%	67803	11045	144175	0.6465		0.0302		4.65	5.4
2.0°C,83%	829	4322	217872	0.9769	0.33	0.6616	0.63	8.9	8.2
3.0°C,17%	82210	72018	68796	0.3085	0.36	0.0000	0.39	2.09	5.2
3.0°C,50%	68112	5445	149467	0.6702		0.3939		6.65	7.8
3.0°C,83%	2597	2423	218003	0.9775	0.31	0.6931	0.30	11.88	11.8
4.0°C,17%	71682	9963	141379	0.6339	0.06	0.0462	0.62	3.68	7.4
4.0°C,50%	4765	63213	155046	0.6952		0.6647		8.63	10.2
4.0°C,83%	2573	1864	218587	0.9801	0.28	0.9786	0.31	14.42	14.8
5.0°C,17%	5691	5743	145646	0.9272	0.04	0.3561	0.61	5.05	8.8
5.0°C,50%	4765	273	152042	0.9679		0.9665		10.55	12.2
5.0°C,83%	2573	1864	152643	0.9718	0.004	0.9718	0.01	17.2	17.8

Mangrove

SLR scenario	≤0 mm/yr	0-4 mm/yr	≥4 mm/yr	>4 mm/yr proportion	Uncertainty	>7 mm/yr proportion	Uncertainty	Avg. SLR	Global SLR
1.5°C,17%	15939	128246	369	0.0026	0.81	0	0.03	0.13	2.4
1.5°C,50%	0	27377	117176	0.8106		0.0311		3.57	4.2
1.5°C,83%	0	0	144554	1.0000	0.19	0.7671	0.74	7.29	6.4
2.0°C,17%	6390	134704	3460	0.0239	0.97	0	0.32	0.89	3.2
2.0°C,50%	0	1399	143154	0.9903		0.3182		4.65	5.4
2.0°C,83%	0	0	144554	1.0000	0.01	1	0.68	8.9	8.2
3.0°C,17%	0	36252	108302	0.7492	0.25	0.0026	0.98	2.09	5.2
3.0°C,50%	0	0	144554	1.0000		0.9816		6.65	7.8
3.0°C,83%	0	0	144554	1.0000	0	1	0.02	11.88	11.8
4.0°C,17%	0	972	143582	0.9933	0.01	0.2161	0.78	3.68	7.4
4.0°C,50%	0	0	144554	1.0000		1		8.63	10.2
4.0°C,83%	0	0	144554	1.0000	0	1	0	14.42	14.8
5.0°C,17%	0	561	143992	0.9961	0.00	0.6466	0.35	5.05	8.8
5.0°C,50%	0	0	144554	1.0000		1		10.55	12.2
5.0°C,83%	0	0	144554	1.0000	0	1	0	17.2	17.8

Coral Reef

SLR scenario	≤0 mm/yr	0-4 mm/yr	≥4 mm/yr	>4 mm/yr proportion	Uncertainty	>7 mm/yr proportion	Uncertainty	Avg. SLR	Global SLR
1.5°C,17%	764429	131102	2521	0.0028	0.97	3.3406E-06	0.01	0.13	2.4
1.5°C,50%	0	21753	876300	0.9758		0.00556204		3.57	4.2
1.5°C,83%	0	0	898052	1.0000	0.02	0.97821284	0.97	7.29	6.4
2.0°C,17%	377	869497	28177	0.0314	0.97	0.00096097	0.04	0.89	3.2
2.0°C,50%	0	23	898028	1.0000		0.03749342		4.65	5.4
2.0°C,83%	0	0	898051	1.0000	0.00	0.99999777	0.96	8.9	8.2
3.0°C,17%	121	69083	828848	0.9229	0.08	0.00598964	0.99	2.09	5.2
3.0°C,50%	0	0	898051	1.0000		0.99189578		6.65	7.8
3.0°C,83%	0	0	898051	1.0000	0	1	0.01	11.88	11.8
4.0°C,17%	0	2907	895144	0.9968	0.00	0.06400527	0.94	3.68	7.4
4.0°C,50%	0	0	898051	1.0000		1		8.63	10.2
4.0°C,83%	0	0	898051	1.0000	0	1	0	14.42	14.8
5.0°C,17%	0	3031	895021	0.9966	0.00	0.12925212	0.87	5.05	8.8
5.0°C,50%	0	0	898051	1.0000		1		10.55	12.2
5.0°C,83%	0	0	898051	1.0000	0	1	0	17.2	17.8

Scenarios represented are the 1.5 °C, 2.0 °C, 3.0 °C, 4.0 °C, and 5.0 °C warming to 2080-2100 against the 1850-1900 baseline, reporting the 17th, 50th and 83rd percentile projections for each scenario. The average rate of RSLR for coastlines, and rate of global SLR are represented for each scenario as mm yr^{-1}.

Extended Data Table 2 | Location and timing of mangrove SET-MH measurements, with corresponding rate of RSLR and elevation gain

Region	Location, source	latitude, longitude	SET (n)	Start reading	End reading	RSLR**	Mean elevation change rate mm yr^{-1}(s.d.)
Florida, USA	Big Sable Creek[105] (Feher)	25.21, 81.14	1	1999	2021	9.04	0.65 (0.00)
Florida, USA	Biscayne Bay[105]	25.29, 80.37	2	2011	2020	7.48	1.38 (0.47)
Florida, USA	Lostmans River[105]	25.53, 81.18	1	1999	2021	7.48	5.54 (0.00)
Florida, USA	NE Florida Bay[105]	25.21, 80.42	12	1998	2019	1.72	2.43 (1.29)
Florida, USA	Rookery Bay[105]	25.58, 80.94	2	2001	2006	-1.86	0.46 (0.35)
Florida, USA	Rookery Bay[105]	25.58, 80.94	2	1997	2006	-1.84	12.78 (3.43)
Florida, USA	Rookery Bay[105]	25.58, 80.94	13	2015	2021	4.68	2.00 (4.77)
Florida, USA	Rookery Bay[105]	25.58, 80.94	1	1993	2017	1.31	2.48 (0.00)
Florida, USA	Rookery Bay[105]	25.58, 80.94	1	1994	2007	-2.28	9.04 (0.00)
Florida, USA	Rookery Bay[105]	25.58, 80.94	2	1993	2017	1.31	1.00 (1.24)
Florida, USA	Shark River[105]	25.32, 81.00	1	1998	2018	1.93	2.76 (0.00)
Florida, USA	Shark River[105]	25.32, 81.00	2	1998	2021	2.19	2.34 (0.71)
Florida, USA	Ten Thousand Is.[105]	25.85, 81.48	2	1998	2018	2.76	-0.82 (0.43)
Florida, USA	Ten Thousand Is.[105]	25.85, 81.48	1	2012	2020	4.71	3.08 (0.00)
Louisiana, USA	Port Fouchon[106]	29.10, 80.37	3	2006	2011	3.62	4.13 (0.23)
Belize	Twin Cays[84]	16.82, 88.10	3	2001	2004	2.0	-0.23 (3.94)
Victoria, Australia	French Island*	-38.30, 145.42	3	2000	2022	2.74	0.94 (0.74)
Victoria, Australia	Quail Island*	-38.23, 145.30	3	2000	2019	3.0	-2.59 (1.73)
Victoria, Australia	Rhyll*	-38.46, 145.28	3	2000	2019	3.0	-0.71 (0.90)
Victoria, Australia	Kooweerup*	-38.22, 145.41	2	2000	2022	2.74	1.06 (1.52)
NSW, Australia	Minnamurra*	-34.62, 150.84	3	2001	2011	0.47	1.4 (0.30)
NSW, Australia	Cararma Inlet*	-34.98, 150.77	3	2001	2020	3.88	2.18 (1.18)
NSW, Australia	Currambene Creek*	-35.01, 150.66	6	2001	2020	2.82	0.50 (0.76)
NSW, Australia	Homebush Bay*	-33.84, 151.07	6	2000	2020	5.4	2.76 (0.58)
NSW, Australia	Kooragang Island*	-32.84, 151.72	6	2002	2016	3.11	3.11 (1.09)
NSW, Australia	Kooragang Island[107]	-32.86, 151.71	3	2005	2008	12.68	3.00 (0.00)
NSW, Australia	Tweed River*	-28.18, 153.54	3	2000	2018	4.9	1.81 (0.83)
NSW, Australia	Berowra*	-33.62, 151.12	3	2002	2017	5.44	2.46 (2.10)
Queensland, Australia	Moreton Bay East*	-276.28,153.04	9	2007	2011	17.09	-11.31 (2.10)
Queensland, Australia	Moreton Bay West*	-27.43, 153.43	9	2007	2011	17.09	-15.37 (1.60)
Queensland, Australia	Daintree River*	-16.27, 145.40	5	2015	2021	17.18	2.98 (4.10)
Queensland, Australia	Daintree River*	-16.31, 145.42	7	2014	2021	15.06	0.92 (1.92)
Western Australia	Exmouth Gulf*	-22.49, 114.32	6	2011	2018	-6.54	-0.14 (0.18)
Northern Territory	Darwin Harbour*	-12.48, 130.91	6	2014	2021	15.13	7.01 (6.93)
Northern Territory	Darwin Harbour*	ł, 130.96	33	2016	2021	8.04	2.18 (5.97)
Micronesia	Yela River[108]	5.32, 162.93	3	1997	2004	29.23	-0.97 (1.93)
Micronesia	Utwe River[108]	5.28, 162.95	3	1997	2004	30.91	1.90 (1.50)
Micronesia	Pukusruk[108]	5.35, 163.02	1	1999	2004	-1.77	-2.33 (0.00)
Micronesia	Enipoas[108]	6.82, 158.21	3	1999	2004	-1.74	1.58 (0.65)
Micronesia	Sapwalap[108]	6.87, 158.30	3	1999	2004	-1.74	-0.74 (1.17)
New Zealand	Firth of Thames[109]	-37.21, 175.45	5	2008	2015	9.6	-6.10 (3.31)

*Original SET Data; **RSLR for the period of SET-MH measurements, from the nearest tide gauge.

Extended Data Table 3 | Identifiers and Variables used in the RF regression analysis (Data[29])

Accretion	Rate of accretion above the feldspar horizon (mm yr^{-1})
elevation.rate	Rate of elevation gain from the SET record (mm yr^{-1})
Subsidence	accretion - elevation.rate
SLR50	Local sea-level trend derived from nearest tide gauge: 0-50BP linear trend (mm yr^{-1})
RSLR.contemporaneous	RSLR for each site for the period of SET measurement. Linear trend (mm yr^{-1})
tidal.range	Difference between MHW and MLW (m)
marshElevation	Elevation of the SET-MH in relation to local datum (m)
elevCapital	Elevation of SET-MH in relation to modelled lowest marsh limits (cm)
elevDeficit	Elevation Deficit, defined as RSLR period of measure minus elevation rate. (mm yr^{-1})
bulkDensity	Bulk density of the upper 10 cm (dry, g cm^{-3})
Organic matter	Organic matter in the upper 10cm by weight (%)
Rainfall	Average annual rainfall (mm)
TSM.2011	MERIS-derived total suspended matter -average

Check for updates

Earth's Future

RESEARCH ARTICLE
10.1029/2020EF001901

Key Points:

- Wetland losses due to sea-level rise and reduced productivity of newly colonized areas limit soil carbon sequestration
- Focus on conservation of wetland vegetation is not necessarily the optimal option for soil carbon sequestration objectives
- Implementation of eco-geomorphic frameworks is of major importance for adequately quantifying projections of soil carbon stocks

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

S. G. Sandi and J. F. Rodriguez,
steven.sandirojas@newcastle.edu.au;
jose.rodriguez@newcastle.edu.au

Citation:

Sandi, S. G., Rodriguez, J. F., Saco, P. M., Saintilan, N., & Riccardi, G. (2021). Accelerated sea-level rise limits vegetation capacity to sequester soil carbon in coastal wetlands: A study case in southeastern Australia. *Earth's Future*, *9*, e2020EF001901. https://doi.org/10.1029/2020EF001901

Received 12 NOV 2020
Accepted 22 JUL 2021

Author Contributions:

Conceptualization: S. G. Sandi, J. F. Rodriguez, P. M. Saco, N. Saintilan
Investigation: S. G. Sandi
Methodology: S. G. Sandi, J. F. Rodriguez, P. M. Saco, G. Riccardi
Supervision: J. F. Rodriguez, P. M. Saco
Visualization: S. G. Sandi
Writing – original draft: S. G. Sandi

© 2021. The Authors. Earth's Future published by Wiley Periodicals LLC on behalf of American Geophysical Union. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Accelerated Sea-Level Rise Limits Vegetation Capacity to Sequester Soil Carbon in Coastal Wetlands: A Study Case in Southeastern Australia

S. G. Sandi[1], J. F. Rodriguez[1], P. M. Saco[1], N. Saintilan[2], and G. Riccardi[3]

[1]Centre for Water Security and Environmental Sustainability (CWSES) and School of Engineering, The University of Newcastle, Callaghan, NSW, Australia, [2]Department of Environmental Sciences, Macquarie University, Sydney, NSW, Australia, [3]Department of Hydraulics and Research Council of National University of Rosario (CIUNR), National University of Rosario, Rosario, Argentina

Abstract Estimates of global carbon stocks in coastal wetlands reveal that these are some of the most efficient carbon-sequestering environments in the world, which has prompted a renewed interest in conservation and restoration programs as an opportunity for greenhouse gas abatement. Accumulation of carbon in coastal wetlands is linked to diverse factors such as the type of vegetation, geomorphic setting, and sediment supply. Feedbacks between these factors and the tidal flow conditions drive the dynamics of carbon accumulation rates. Climate change-induced sea-level rise has been shown to increase the vulnerability to submergence of saltmarsh and mangroves in coastal wetlands, even if accommodation and landward colonization are possible. These potential losses of wetland vegetation combined with the reduced productivity of newly colonized areas will directly affect the capacity of the wetlands to sequester carbon from sediments and root growth. Here, we implement an eco-geomorphic model to simulate vegetation dynamics, soil carbon accumulation, and changes in soil carbon stock for a restored mangrove-saltmarsh wetland experiencing accelerated sea-level rise. We evaluate model outcomes for existing conditions and two different management scenarios aimed at mitigating sea-level rise effects and conserve wetland vegetation. Even though some management measures can result in partial conservation of wetland vegetation, they do not necessarily result in the best option for soil carbon capture. Our results suggest that accelerated sea-level can trigger accelerated wetland colonization resulting in wetland areas with limited opportunities for soil carbon capture from sediment and root mineralization, an issue that has not been considered in previous studies.

Plain Language Summary Coastal wetlands are environments with a high capacity to transfer carbon from the atmosphere and accumulate it in the soil. Recently, there has been significant interest in promoting conservation and restoration of wetlands as a means to reduce carbon in the atmosphere. Carbon accumulation depends on the complex interaction between tides, vegetation and sediments. Vegetation produces organic matter and slows down the flows which allow sediments to deposit increasing the surface elevation. Because of rapid sea-level rise as a result of climate change, coastal wetlands areas are increasingly vulnerable to submergence. Wetland vegetation will colonize new areas inland to compensate for these losses, but this colonization may be limited by human-made infrastructure. Vegetation losses and limited colonization will result in vegetation with less capacity to accumulate soil carbon. Here, we use a model to study the effects of sea-level rise on vegetation and soil carbon accumulation. We apply the model to a restored mangrove-saltmarsh wetland considering different management scenarios during rapid sea-level rise. Our results suggest that management strategies must integrate the processes described here as management practices can lead to newly colonized vegetation with limited opportunities to accumulate soil carbon.

1. Introduction

Mangroves and saltmarshes are recognized to be some of the most carbon-rich environments found throughout the world (Donato et al., 2011; Ouyang & Lee, 2014). In these coastal environments, carbon stocks (also known as blue carbon) are stored in the form of underlying sediments, the living plant biomass, and the non-living plant biomass (J. Howard et al., 2014). Different processes including carbon gas emissions, litter

Writing – review & editing: J. F. Rodriguez, P. M. Saco, N. Saintilan, G. Riccardi

fall, sediment entrapment, and dead root mineralization drive the dynamics of soil carbon accumulation in coastal wetlands. Over time, carbon is slowly buried in the soil, which leads to the rich carbon soils underneath the wetlands. Changes in land use of coastal wetlands have occurred over centuries and the effective removal of mangrove and saltmarsh has contributed to accelerated depletion of soil carbon stocks in the form of gas emissions to the atmosphere (Atwood et al., 2017; Lovelock et al., 2011, 2017; Pendleton et al., 2012). This occurs because once wetland vegetation is removed and the land use is converted to other uses (aquaculture, agriculture, shrimp ponds, industrial use, timber harvest, and urban development), sediments are destabilized and or exposed to oxygen which leads to increased microbial activity and gas emissions.

Studies in recent years have addressed the importance of mangrove and saltmarsh conservation as a means to reduce gas emissions (Adame et al., 2018; Macreadie, Nielsen, et al., 2017; Rogers, Macreadie, et al., 2019). Many of these studies have concentrated on estimating current carbon stocks and current rates of gas emissions (Atwood et al., 2017; Donato et al., 2011; Macreadie, Ollivier, et al., 2017; Ouyang & Lee, 2014; Pendleton et al., 2012; Thorhaug et al., 2019), as well as understanding the variability of carbon stocks and the processes that drive the accumulation of carbon (Abbott et al., 2019; Kelleway, Saintilan, et al., 2017; Kusumaningtyas et al., 2019; Morris et al., 2016; Ouyang et al., 2017; Pérez et al., 2018; Roner et al., 2016). The effects of sea-level rise on carbon sequestration dynamics and current stocks have only recently started to be considered (Breithaupt et al., 2020; Rogers, Kelleway, et al., 2019; Watanabe et al., 2019) and initial findings seem to indicate potential increases in carbon accumulation by the end of the century, at least in some scenarios of increased CO_2 emissions (Krauss et al., 2017; Wang et al., 2019).

The full effects of sea-level rise on soil carbon accumulation, however, remain uncertain (Kirwan & Mudd, 2012; Lovelock & Reef, 2020). In coastal wetlands, particularly in mangroves and saltmarsh, complex eco-geomorphic feedbacks between sediment transport, water flow, and vegetation strongly affect the dynamics of the system. Models that can include these feedbacks, especially between vegetation and soil processes (Kirwan & Megonigal, 2013; Kirwan et al., 2016; Saco & Rodríguez, 2013) and hydraulic effects (Alizad, Hagen, Morris, Bacopoulos, et al., 2016; Lentz et al., 2016; Passeri et al., 2015), are of major importance for adequately representing the dynamics of the wetland and potential changes in the future (Passeri et al., 2015; Rodríguez et al., 2017). For instance, mangrove landward colonization under contemporary sea-level rise rates can result in increased blue carbon sequestration of wetlands due to the higher carbon sequestration capacity of mangroves compared to other vegetation (Kelleway et al., 2016; Krauss et al., 2017; Lamont et al., 2020); however, under future rates of sea-level rise wetland losses due to submergence are expected (Craft et al., 2009; Kirwan et al., 2016; Lovelock et al., 2015; Ward et al., 2016), which can balance out or surpass carbon sequestration gains due to landward colonization. In addition, the presence of human-made structures within the wetlands (Rodríguez et al., 2017; Sandi et al., 2018) and barriers to wetland colonization (Schuerch et al., 2018) limit the capacity for wetlands to adapt to future sea-level rise. More importantly, rapid retreat and colonization triggered by accelerated changes in sea level may not allow vegetation to mature, resulting in newly colonized areas with different vegetation structure, affecting the soil carbon accumulation dynamics (Krauss et al., 2017). The inclusion of soil carbon dynamics in an eco-geomorphic modeling context allows us to track wetland accretion, retreat, and transgression, which can then be used to estimate the potential vulnerability of soil carbon stocks and carbon accumulation rates in coastal wetlands.

The issue of future soil carbon sequestration potential of coastal wetlands is of extreme importance for wetland restoration projects. For centuries, the imposition of levee banks has isolated wetlands from tidal inundation and facilitated their conversion to agricultural land. A recognition of the habitat values of wetlands and their declining extent across the globe has prompted the "de-embankment" and managed realignment of saltmarshes in the UK Essex and Norfolk coastlines (Mossman et al., 2012), the Baltic Sea saltmarshes in northern Germany (Hofstede, 2019), and other initiatives driven by the EU Habitats Directive. Similar restoration projects in North America and Australia have been funded through compensatory habitat schemes, with tidal reinstatement facilitating the restoration of the vegetative and hydrological requirements of bird and fish habitat (Boys & Pease, 2017; Elphick et al., 2015). Increasingly, tidal reinstatement is seen as a leading opportunity for greenhouse gas abatement, providing a financial incentive to the restoration of "blue carbon" ecosystems (Kelleway et al., 2020; Kroeger et al., 2017; Sheehan et al., 2019). The long-term success

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

of these projects will depend on how wetlands respond to sea-level rise, both in terms of the extent of vegetated habitat and in the continuity and efficacy of ecosystem services, including soil carbon sequestration. In these restored systems, the nature of entrance conditions, particularly the hydrodynamic constraints imposed at the point of levee removal, may prove to be a critically important determinant of end-points, both in terms of habitat extent and the volume of soil carbon sequestered. These two restoration objectives (i.e., optimal habitat restoration and optimal soil carbon sequestration) may not be mutually attainable, as it is often assumed.

Here we extend an eco-geomorphic model of coastal wetlands that simulates hydrodynamic and vegetation processes (Rodríguez et al., 2017; Sandi et al., 2018) to incorporate soil carbon processes. This simulation approach integrates a detailed hydrodynamic model that fully integrates attenuation effects due to natural and human-made features, vegetation response based on their preference to hydrodynamic conditions, and bio-geomorphic accretion (Kirwan et al., 2010; Morris et al., 2002). We apply this model to a wetland in the Hunter Estuary, Australia, where tidal flows have been reinstated. Restoration of the wetland has provided important habitat areas for shorebirds, but predictions of future losses of wetland vegetation under sea-level rise have prompted analysis of management alternatives based on inlet control (Rodríguez et al., 2017; Sandi et al., 2018). We estimate the current stock of soil carbon based on measurements at the site (Howe et al., 2009) and we simulate changes in the soil carbon stock under sea-level rise by accounting accreted carbon and contributions from biomass production via root mineralization as well as potential carbon losses under three different management scenarios: (a) no tidal gate control, (b) tidal gate at a fixed elevation, and (c) tidal gate at an elevation changing with SLR. In all management, scenarios surrounding earthworks and embankments impede landward colonization.

1.1. Study Area

This research focuses on Area E, an enclosed rehabilitated wetland site situated in Kooragang Island, New South Wales, Australia, ~10.5 km from the mouth of the Hunter River (Figure 1a) with a total area of 1.24 km^2. Wetlands of the Hunter Estuary are of major importance for migratory shorebirds. In the past, many areas of the estuary including Kooragang Island (Figure 1) were drained using a series of levees and culverts to make the land suitable for cattle grazing, logging and industrial use. In the 1990s, tidal flows were reinstated in Area E to restore wetland areas (Williams et al., 2000). Reinstatement of tidal conditions promoted landward colonization of estuarine communities and allowed mangroves to colonize shallow mudflats, tidal pools and low elevation saltmarsh habitats (Howe et al., 2010). This type of mangrove vegetation transgression has been reported for many other sites in NSW (Saintilan & Williams, 1999; Saintilan et al., 2014) and it can lead to a general loss of wetland biodiversity (Kelleway, Cavanaugh, et al., 2017).

The site includes most of the estuarine habitats present in the Hunter Estuary (Howe et al., 2010), including mudflats, tidal pools, mangroves and saltmarsh. Mangrove forests are composed of Grey Mangrove (*Avicennia marina*) and saltmarshes are dominated by Beaded Samphire (*Sarcocornia quinqueflora*) and Marine Couch (*Sporobolous virginicus*). The study area receives flows directly from the South Arm of the Hunter River where the hydrodynamics are dominated by the tidal regime as runoff flows coming from the Hunter River are comparatively small. The tidal regime follows a semi-diurnal tidal cycle with a tidal range of about 1.6 m.

In Australia, mangrove commonly occupies the lower elevations of the upper intertidal zone and saltmarsh is usually found at higher elevations (Rogers & Krauss, 2019). On occasions, such as the case of Area E, mudflats can be present in the lowermost areas of the intertidal range. The human-made structures within and surrounding Area E limit accommodation, that is, the vertical and lateral space available for fine sediments to accumulate and be colonized by wetland vegetation. This poses a threat to saltmarsh as mangroves are expected to continue encroaching on the saltmarsh areas in the future (Rodríguez & Howe, 2013). At the same time, submergence of wetland vegetation under sea-level rise is also expected to occur (Rodríguez et al., 2017; Sandi et al., 2018).

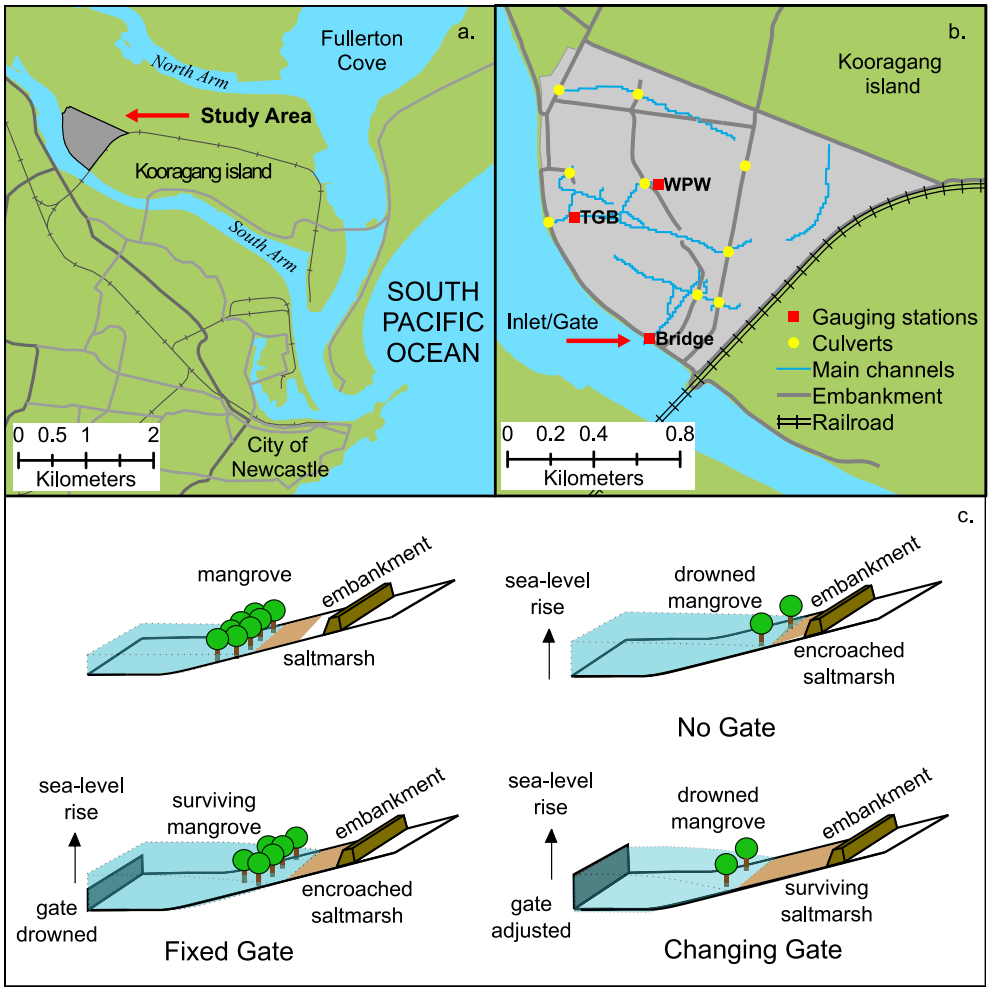


Figure 1. Location the study area (a), and details of the site configuration including internal and surrounding infrastructure and drainage network (b), schematic of the different control scenarios (c). Earthworks and embankments impede landward colonization. Sea-level rise corresponds approximately to projections after 100 years.

2. Materials and Methods

In order to simulate potential effects of sea-level rise on the soil carbon of Area E, we first estimate the recent soil carbon stock based on-site measurements. We then investigate the potential changes in the soil carbon stock by simulating the eco-geomorphic feedbacks between vegetation, tidal regime, and sediment accretion under sea-level rise using the methodology developed by Rodríguez et al. (2017) and Sandi et al. (2018). This allows estimating the changes in vegetated areas of mangrove and saltmarsh as well as the changes in surface elevation due to bio-geomorphic accretion. We also account for changes in the biomass productivity that contributes to the soil carbon. We then incorporate specific rates of change in the soil carbon to represent potential carbon losses arising from root mineralization and vegetation loss.

This eco-geomorphic approach includes different models operating at different timescales. First, a spatially distributed hydrodynamic model provides a detailed long-term description of the tidal regime that drives the establishment and decline of mangrove and saltmarsh. The vegetation distribution is coupled with a bio-geomorphic accretion model used to update the topography. Both vegetation distribution and changes in surface elevations are re-incorporated into the hydrodynamic model to provide feedback directly into the simulation through updated hydraulic resistance and topography. For simulating sea-level rise, the input water levels, surface elevation change, and vegetation characteristics are updated according to the sea-level rise projection every 20 years (see Section 2.5).

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Once changes in vegetation and surface elevation are estimated, the changes in soil carbon stock are calculated by considering the sequestered carbon through organic sediment deposition obtained as a fraction of the simulated accreted soil and also including inputs from dead root mineralization. If vegetation is lost due to submergence, we assume that aboveground biomass productivity is lost, and a fraction of the belowground biomass production becomes soil carbon, but the capacity to continue accumulating soil carbon is lost. Potential changes of carbon in living biomass are not accounted for, but changes in the vegetation are tracked in all simulations.

We implement our modeling approach to assess the potential effects of sea-level rise in the soil carbon stock of the wetland and sequestering capacity under different management scenarios using inlet control. We first consider a scenario with no control at the inlet in Fish Fry Creek (Figure 1b), which represents a baseline scenario. The other two scenarios are considered by introducing a hydraulic control gate at the Fish Fry Creek inlet. This control gate has been proposed to limit mangrove encroachment on saltmarsh, one of the main consequences of sea-level rise that compromises shorebird habitat (Howe et al., 2010; Rodríguez & Howe, 2013). We consider a fixed gate scenario with a level of 0.35 m above Australian Height Datum (mAHD) and a rising gate scenario with the gate level starting at 0.35 mAHD and gradually rising the gate level following the rising sea-level. Similar control scenarios were implemented by Sandi et al. (2018) to assess the effectiveness of the control structures in preserving bird habitat. The gate produces attenuations to the tidal regime, only allowing the tide levels above the gate level to enter the wetland. The gate also has the effect of increasing inundation duration of mangrove areas, limiting mangrove encroachment. Earthworks and embankments impede landward colonization. In the fixed gate scenario, the gate eventually becomes drowned and attenuation effects are reduced so mangrove can encroach on saltmarsh (Figure 1c), but in the rising gate scenario the attenuation of the tidal input is maintained, which continues limiting mangrove encroachment and promotes saltmarsh survival (Figure 1c).

2.1. Hydrodynamic Model

The flow regime is modeled with a quasi-2D hydrodynamic model, developed for describing wetting and drying processes in floodplain systems (Riccardi, 2000) affected by flow resistance. The model structure is based on an interconnected cells scheme and uses simplified versions of the shallow flow equations to determine the water depths in the wetland. Full dynamic equations are used for channel flow, but for slow floodplain flows, in which inertial effects can be neglected, a diffusive wave simplification is used, speeding up computations. The model includes formulations to simulate flow through culverts, embankments, earthworks and control gates. The simulated domain is discretized into a 10 m resolution squared grid with a total of 13,543 cells. Boundary conditions at the wetland entrance (Fish Fry Creek and Wader Creek inlets in Figure 1b) consist of water surface elevations in the Hunter estuary. The resulting differential equation system is solved with a two-dimensional finite differences scheme using a Gauss-Seidel iteration method where the Courant-Friedrichs-Lewy celerity condition is used for stability of the model. Calibration and model testing has been previously presented by Rodríguez et al. (2017) and Sandi et al. (2018) (see the supporting information for comparison plots and performance indicators).

Previous models of soil carbon dynamics do not consider the effects of flow resistance, tidal attenuation or human-made structures. For comparison purposes, we also run simplified calculations considering that the flow dynamics in the wetland are unaffected by structures or vegetation. Water levels in all points of the wetland are considered the same as the water level of the tidal data at the inlet. We refer to this as the "bathtub approach" and it is strictly a simplification of the flow dynamics. Vegetation and accretion are estimated the same way as in the hydrodynamic approach. Recent literature advocates for a shift from using bathtub approaches to models that can include non-linear responses of the vegetation to hydrodynamics and coastal morphology (Passeri et al., 2015). Bathtub models can underestimate coastal wetland vulnerability, resulting in less wetland submergence from simulations (Rodríguez et al., 2017). This can have significant implications in the simulation of sequestered soil carbon, so we use the results of the bathtub model to explore the magnitude of soil carbon accumulation in comparison to a hydrodynamic approach. Results of wetland vegetation extent, biomass productivity, and accretion using the bathtub model are presented in the supporting information.

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2.2. Vegetation

We simulate the vegetation by first calculating spatially distributed time-aggregated variables of the tidal regime from the hydrodynamic simulations. Rules for vegetation establishment can be described by suitable ranges of depth below mean high tide (D) and the ratio of inundated time over total time or hydroperiod (H) (D'Alpaos et al., 2007; Kirwan & Murray, 2007; Kirwan et al., 2010). Here, values of D and H were obtained integrating spring tide results from 1 year of continuous hydrodynamic simulations as in Rodríguez et al. (2017) and Sandi et al. (2018). During spring tides, water levels and inundation extent are more pronounced and become critical for vegetation establishment and survival in the upper intertidal frame (Howe, 2008).

Mangrove establishment is strongly influenced by hydroperiod (Woodroffe et al., 2016). Soils regularly inundated, such as those in estuarine environments, can experience an accumulation of phytotoxins (McKee, 1993; Youssef & Saenger, 1998) or undergo conditions of limited oxygen availability for root uptake (McKee, 1996), thus mangrove species require a minimum period of time for soils to be well aerated and for pneumatophores to obtain enough oxygen. The dominant mangrove species in the site (*Avicennia marina*) is sensitive to spring-tide hydroperiod, and a suitable range $0.1 < H < 0.5$ was adopted based on data collected on site (Howe, 2008). A similar hydroperiod range for *Avicennia marina* was assumed by van Maanen et al. (2015) for simulating evolution of mangroves in sandy tidal embankments. The range selected by van Maanen et al. (2015) is based on observation of the position of *Avicennia marina* on the intertidal range (Clarke & Myerscough, 1993). This range of hydroperiod is also consistent with simulated data from Crase et al. (2013), for *Rhizophora stylosa*, a mangrove species that occupies a similar position in the tidal range in tropical locations. Though hydroperiod drives mangrove establishment, mangroves are capable of colonizing areas with a wide range of inundation frequencies as other drivers affect suitability conditions necessary for mangroves to grow (Krauss et al., 2008). We also impose a secondary constraint in terms of D and we assume that mangrove propagule establishment is restricted by high soil salinity conditions that will occur under very low values of D (Saintilan et al., 2009). A restriction of $D > 0.2$ m was considered for mangrove suitability conditions.

In Area E, the typical height of dominant saltmarsh species is close to 25 cm; therefore, a limit of $D < 0.25$ m was set for saltmarsh suitability as D that cover the plants completely will drown saltmarsh and result in hypoxia, restricting their establishment (Morris et al., 2002). For saltmarsh, a limit for hydroperiod ($H < 0.8$) was also included to represent that saltmarsh would not establish in areas that are almost permanently inundated. Finally, saltmarsh was assumed to be outcompeted by mangrove in wetland areas with adequate conditions for both species, as reported in previous work (Saintilan et al., 2014).

The vegetation model was tested by comparing the simulated vegetation distribution against a vegetation map obtained by combining RTK GPS data and a ground-truthed high-resolution aerial photography for the year 2007 (Howe, 2008). The simulated vegetation is obtained by running the hydrodynamic and vegetation models using as input the tidal information of 2007 from a nearby gauging station (see the supporting information for comparison maps and performance indicators).

2.3. Eco-Geomorphic Accretion Model

In order to include changes in soil surface elevation for long-term projections of sea-level rise, a previous methodology based on saltmarshes in the United States was adapted (Kirwan et al., 2010; Morris et al., 2002). Our model calculates the surface elevation change over time (dE/dt) at each point in the wetland and includes the contribution of suspended sediment deposition and biomass accretion:

$$\frac{dE}{dt} = \mathrm{SSC}\left(q + kB\right)D \tag{1}$$

where SSC is the suspended sediment concentration q is a depositional parameter that represents the rate at which sediment settles in the absence of vegetation, k represents the efficiency of specific vegetation to trap sediment as well as changes in elevation from organic matter accumulation, and B is the aboveground biomass production. For aboveground biomass production we use the formulation of Morris et al. (2002), where B increases with D until it reaches an optimum value, beyond which biomass production decreases:

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1
Simulated Aboveground Biomass for Saltmarsh, Simulated Carbon Stock in Biomass and Calculated Soil Carbon Stock in Area E

	Mangrove	Saltmarsh	Mudflat and tidal pools
Simulated aboveground biomass	(Mg ha^{-1})	(Mg ha^{-1})	
	8.09 ± 4.07	8.24 ± 1.37	
Carbon content	(MgC ha^{-1})	(MgC ha^{-1})	(MgC ha^{-1})
Aboveground biomass	3.80 ± 1.92	3.87 ± 0.64	
Belowground biomass	3.11 ± 1.35	1.40 ± 0.23	
Soil carbon (1 m depth)	110.58 ± 35.53	156.55 ± 40.28	74.45 ± 22.69

Note. Values of average biomass, aboveground, and belowground carbon in biomass represent the spatial average of simulated data.

$$B = aD + bD^2 + c \tag{2}$$

The parameters a, b, and c are determined empirically from site data and are different for saltmarsh and mangrove. Equation 2 satisfies the ecological principle that the vegetation is distributed over a range of tolerance values from different stressors depth (Morris et al., 2002), which in this case is D. In areas with lower D, plants are smaller which means lower biomass production whereas in areas with higher D plants are larger, but there is more competition leading to reduced access to resources and less dense vegetation. Because of this, there should be an intermediate range of flooding where biomass production has the highest values. We calibrated the parameters in Equations 1 and 2 using simulated values of D, accretion rate data collected in the study area (Rogers et al., 2013), and in the absence of biomass production measurements, we adopted biomass values collected in the Georges River for the same dominant vegetation, that is, saltmarsh and young mangroves less than 15 years old (Kelleway et al., 2016). In the study area, tallest saltmarsh are located at lower elevations so it is assumed that biomass increases as to a maximum value of D, similarly to observations of saltmarsh in South Carolina (Morris et al., 2002). For mangroves, average B was set to the average simulated value of D as it is assumed that small trees will establish in less inundated areas with low D and also more competition will occur in more inundated areas with high D, leading to less productivity. We assume the initial values of biomass production to be the same as the initial biomass to estimate the initial living biomass carbon stock (Table 1). However, because Equation 2 allows to estimate primary production but not woody biomass accumulation we do not compute carbon stocks in living biomass over the whole simulation period (see Section 2.4.2). Instead, we only consider the cumulative contribution of biomass to the soil carbon via root mineralization, which is calculated as a fraction of the belowground biomass primary production (see Section 2.4.1).

The value of SSC is spatially variable and we have assumed a relationship based on measurements from Howe (2008) in which SSC decreases linearly with D from a maximum constant value SSC_{max} at the inlet (37 g m^{-3}). The same relationship was applied by Rodríguez et al. (2017) and Sandi et al. (2018):

$$\frac{SSC}{SSC_{max}} = 0.55D + 0.32 \tag{3}$$

with D in meters. Previous research has used physically based transport equations for SSC (Breda et al., 2021; D'Alpaos et al., 2007) or an exponential decay formulation with distance to tidal channels (D'Alpaos et al., 2007; Kirwan & Guntenspergen, 2010; Kirwan & Murray, 2008). Because of the complex flow paths within our study area, implementing a physically based or distance-based model was impractical due to the computational requirements.

The eco-geomorphic accretion model does not consider erosion. Fluvial erosion has not been identified as an important process in the study area for long-term simulations as the stream network has remained stable for many years (Howe, 2008) and episodic storm events have shown reworking of sediments in the vegetated areas rather than net erosion (Rogers et al., 2013). It is assumed that flow within the wetland is slow and

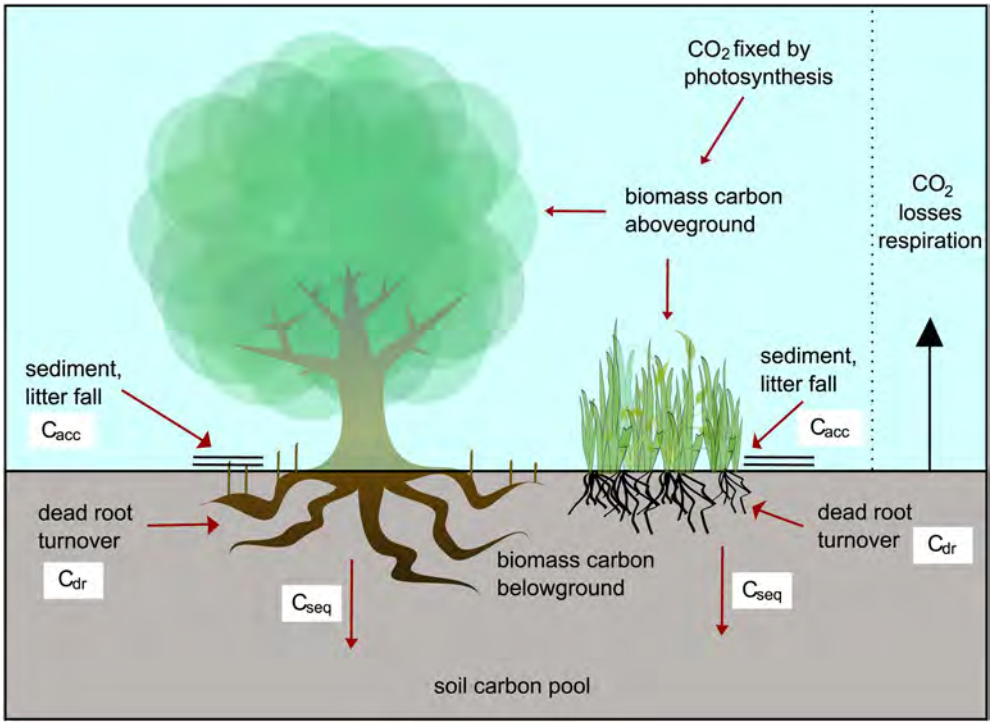


Figure 2. Conceptual carbon sequestration cycle at the site. C_{acc}: accreted carbon, C_{dr}: dead root turnover carbon, C_{seq}: sequestered carbon (sum of C_{acc} and C_{dr}).

vegetation stabilizes sediment and prevents erosion. Erosion by wind waves is limited by the small size of permanent pools and shading effects of infrastructure under current conditions (Howe, 2008), but may become more important as sea-level rises and permanent water pools increase their size (Carniello et al., 2011; Leonardi et al., 2016). However, it is likely that wetland submergence due to the limited accretion capacity of the attenuated system will still be the dominant mechanism of wetland loss during sea-level rise (Ravens et al., 2009) as opposed to erosion.

The calibration of the eco-geomorphic accretion model consisted in obtaining the parameters that produced the best match of the results of Equation 1 with local data comprising a 10-year record (2002–2012) of surface elevation changes derived from surface elevation tables (to ± 1.4 mm) (Howe et al., 2009; Rogers et al., 2013). The calibrated parameters of the eco-geomorphic accretion model (q and k in Equation 1 and a, b, and c in Equation 2) are presented in the supporting information.

2.4. Soil Carbon Model

Our conceptual model of soil carbon sequestration processes is presented in Figure 2. The soil carbon stock receives carbon inputs from sediments and litter fall in the topsoil surface layer and from dead root turnover along the soil profile. Part of the soil carbon originating from dead roots is potentially lost by mineralization in the form of gas emissions or dissolved carbon. Our assessment of soil carbon dynamics under sea-level rise considers the organic carbon deposited in the soil due to bio-geomorphic accretion and potential changes in living biomass which translate on buried carbon from root mineralization and carbon losses due to biomass losses and root mineralization.

2.4.1. Soil Carbon Stock

The soil carbon stock of a wetland is the sum of all carbon in the soil. We first estimate the contemporary soil carbon stock of Area E considering only the sum of carbon contained in the top 1 m layer of the soil which is standard for a carbon stock inventory (J. Howard et al., 2014). Also, soil carbon profiles in Kooragang Island show that the majority of the carbon are within this layer (DPI, 2008; Saintilan et al., 2013)

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

and decreases exponentially with depth. This estimate of soil carbon stock is a baseline for comparison, but environmental history is also key in soil carbon accumulation and may not directly reflect the contemporary vegetation (Kelleway, Saintilan, et al., 2017), especially in the case of mangroves as they were recently established in the study area.

Soil carbon densities (ρ_{sd}) in Area E were obtained for the top 20 cm of the top soil layer of different vegetated and non-vegetated areas by extracting 45 different soil cores (Howe et al., 2009) (see Supporting Information S1). Mean organic soil carbon densities were 0.0406 ± 0.010 MgC m^{-3} ($n = 19$) for saltmarsh, 0.0287 ± 0.009 MgC m^{-3} ($n = 9$) for mangrove, and 0.0193 ± 0.006 MgC m^{-3} ($n = 8$) for unvegetated tidal pools and mudflats. Synthetic organic carbon profiles were then estimated to a depth of 1 m using an exponential relationship obtained from carbon profiles in Kooragang Island (see Supporting Information S1):

$$\rho'_{sd} = k_0 \cdot e^{-\lambda \cdot z} \tag{4}$$

where ρ'_{sd} is the projected soil carbon density at a depth z in meters from the surface, k_0 is a constant adjusted to the carbon density of the top soil layer (ρ_{sd}) and λ is a decay constant equal to 3.5.

2.4.2. Carbon in Biomass

Organic biomass carbon was obtained by first calculating the biomass productivity above and belowground and then converting the living biomass to carbon. We calculate aboveground biomass production using Equation 2 which is then converted to aboveground biomass carbon productivity rate (C_{ab}) using a carbon content factor F_1:

$$C_{ab} = F_1 \cdot B \tag{5}$$

We used the same value $F_1 = 0.47$ for mangrove and saltmarsh as recommended by Kauffman and Donato (2012) and J. Howard et al. (2014) and in line with biomass carbon content measurements by Owers et al. (2018) in the region of our study area. A similar aboveground biomass carbon content factor was reported for *Spartina alterniflora* saltmarsh in South America (Negrin et al., 2012).

Calculation of carbon produced in belowground biomass follows a similar process to aboveground biomass. To estimate belowground biomass production, we convert B (Equation 2) to belowground biomass by adopting an aboveground/belowground biomass factor F_2. The belowground biomass carbon production rate (C_{bb}) is then computed using a third factor F_3 of carbon content:

$$C_{bb} = F_2 \cdot F_3 \cdot B \tag{6}$$

For mangrove, the value of F_2 is considered to be variable, as observations of mangrove in the region have shown increasing F_2 with increased soil salinity (Saintilan, 1997, 1998). Here, we consider that F_2 increases from 0.5 to 2.0 with decreasing D (accounting for salinity increases) following a power law. This means that areas with lower D are more saline and the F_2 factor is higher. For F_3, we follow J. Howard et al. (2014), who proposes a value of $F_3 = 0.39$ for mangrove based on Jaramillo et al. (2003). For saltmarsh, values of $F_2 = 0.5$ and $F_3 = 0.34$ were selected as recommended by J. Howard et al. (2014) based on Duarte (1990).

The initial living biomass carbon stock (Table 1) is assumed to be equal to the sum of biomass production rates (C_{ab} and C_{bb}) at the beginning of the simulation when there are newly established mangroves and saltmarsh in the study site. However, biomass carbon stocks are not computed over time as our model does not compute the accumulation of woody biomass in mangroves.

2.4.3. Soil Carbon Accumulation Rates

We compare the capacity of the wetland to sequester soil carbon between the three different control scenarios by estimating the carbon accumulation rate per area (C_{seq}). We define this rate as the sum of the accreted carbon rate and the rate of carbon buried from dead root decomposition:

$$C_{seq} = C_{acc} + C_{dr} \tag{7}$$

We calculate the accreted carbon rates (C_{acc}) in each cell of our model by multiplying the surface elevation change (Equation 1) by the top soil organic carbon density:

$$C_{acc} = \rho sd \cdot \frac{dE}{dt} \quad (8)$$

This accreted carbon is added to the soil carbon stock. The carbon produced in the living biomass is represented by C_{ab} and C_{bb} (Equations 5 and 6), and it is recalculated every 20 years, at time when we update tidal levels, soil surface elevation, vegetation distribution, and biomass production due to sea-level rise. Turnover of carbon stored in roots originating from belowground biomass production (C_{bb}) is added annually over time to the soil carbon stock. Most of the mineralized carbon from dead roots is lost as pore water or gas emissions, but a considerable amount remains buried in the soil. Ouyang et al. (2017) estimate that dead root burial accounts for 24%–29% of the annual sequestered carbon in mangroves and 77.9% of the annual carbon sequestered in saltmarsh. The rate at which carbon is buried in the soil as a result of dead root decomposition C_{dr} is calculated as:

$$C_{dr} = C_{bb} \cdot P_{dr} \cdot \left(1 - k_d\right) \quad (9)$$

where P_{dr} is the dead root productivity rate with values of 0.22 year^{-1} for mangrove and 0.67 year^{-1} for saltmarsh and k_d is the root decay rate, with values of 0.493% year^{-1} for mangrove and 0.434% year^{-1} for saltmarsh (Alongi, 2014; Bouillon et al., 2008; Ouyang et al., 2017).

Initial soil carbon accumulation rates are different for the gate-controlled scenarios as the inclusion of a gate affects the distribution of the vegetation.

In addition, we do not explicitly calculate potential inputs of soil carbon originating from aboveground dead biomass; however, carbon inputs from litter fall and suspended organic matter are included in the accreted carbon which comes from bio-geomorphic accretion (Equation 1).

2.4.4. Potential Carbon Losses

For comparison of potential carbon losses between scenarios, we consider different processes of carbon loss when vegetation is submerged or replaced due to sea-level rise. In our assessment, changes in vegetation are quantified every 20 years, so we also estimate potential carbon losses every 20 years. We assume if vegetation is submerged or replaced by another vegetation, the carbon not mineralized from belowground biomass will be lost. We also consider that there are no losses from carbon stored in the soil when vegetation is submerged because we assume that the soil will remain relatively undisturbed during this process (Krauss et al., 2018; Negandhi et al., 2019). When vegetation survives 20 years under sea-level rise, the fraction of carbon not mineralized from dead root biomass is added to the potential carbon losses annually over time. Cumulative potential carbon losses are converted into CO_2 to represent greenhouse gases emissions, assuming all emissions occur as CO_2, although carbon losses can also occur in the form of CH_4 or carbon dissolved in water. Similarly, the cumulative sequestered carbon estimated by our model will be converted to CO_2, as this will represent the potential greenhouse gases burial in the study area under each scenario.

Different practices that lead to wetland vegetation losses, such as wetland conversion to grazing, aquaculture, shrimp ponds or other land uses, can lead to significant losses of soil carbon because soils are highly disturbed as part of these practices (Atwood et al., 2017). In this research, only vegetation losses due to sea-level rise are considered, and future carbon losses originating from wetland conversion should receive special considerations.

2.5. Sea-Level Rise Projections

To calculate the future potential dynamics of the soil carbon stocks, we consider an accelerated rate of sea-level rise the next 100 years following the RCP8.5 scenario of the IPCC Fifth Assessment Report (Church et al., 2013). We considered increasing rates of sea-level rise from 4 mm yr^{-1} in recent time up to 11 mm yr^{-1} by the end of the century. The rates of sea-level rise are increased every 20 years, at the time where the tidal input, surface elevations, and characteristics of the vegetation are updated and integrated into the hydrodynamic model to simulate feedback effects. Similarly, Alizad, Hagen, Morris, Bacopoulos, et al. (2016) and Alizad, Hagen, Morris, Medeiros, et al. (2016) implemented a methodology where rates of sea-level rise were increased in time-steps for simulations of saltmarsh in the Florida panhandle. Their time-steps were

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

shorter than ours (5–10 years), but this was because their rates of sea-level rise were larger. The initial rate of sea-level rise in our study site was corroborated with data from the Hexham Bridge gauging station located 1 km upstream of the wetland site. Changes in the amplitude of the tidal series were not considered as the same data from the Hexham bridge show no change in the amplitude over the last 10 years. We limit the analysis to the RCP8.5 scenario because is the scenario where more changes in vegetation would be expected, which means it can provide the highest contrast of soil carbon sequestration for the control scenarios in our simulation period. Recently updated projections of sea-level rise from the IPCC Special Report on the Ocean and Cryosphere in a Changing Climate also use the RCP8.5 scenario (Oppenheimer et al., 2019). The latest projections show higher rates of sea-level rise in comparison to the IPCC Fifth Assessment Report, but our assumed values are within the likely range of the latest projections.

3. Results

3.1. Initial Soil Carbon Stock

Our estimate of the soil carbon stock in the top 1 m layer shows that the largest soil carbon per unit area corresponds to saltmarsh (Table 1). The soil carbon content per area in saltmarsh areas is 40% higher than in mangroves and 120% higher than in mudflats. As saltmarsh also covers the largest vegetated area in Area E at the beginning of the simulations, the total soil carbon stock of saltmarsh is also the largest in the site. The simulated living biomass carbon stock (above and below ground) of saltmarsh per area is 5.27 MgC ha^{-1} and only accounts for 3% of the total carbon stock, as the soil carbon stock is 157 MgC ha^{-1} (Table 1). In mangroves, the living biomass carbon stock per area represents 5% of the total carbon stock as the simulated living biomass carbon stock per area is 6.91 MgC ha^{-1} and the soil carbon stock is 111 MgC ha^{-1}. These results are consistent with measured carbon content in newly colonized mangroves less than 15 years old (Kelleway et al., 2016) and saltmarsh areas in the region (Macreadie, Ollivier, et al., 2017), however, it must be noted that carbon in aboveground biomass of mature mangroves can reach values 10 times higher than our simulated results (Kauffman et al., 2020; Kelleway et al., 2016; Serrano et al., 2019). Though we estimate rates of biomass production, our approach does not allow for accumulation of mangrove woody biomass, therefore, biomass carbon stocks are not calculated over time, only the contributions of belowground biomass to the soil carbon (C_{dr}). The total soil carbon stock of Area E amounts to 13,300 MgC. We use this value as the initial soil carbon stock in the wetland.

3.2. Projections of Biomass Production and Accretion

Figures 3 and 4 show model results for the three scenarios in terms of soil accretion (Figure 3) and vegetation distribution (Figure 4). In the scenario with no-gate control, saltmarsh vegetation losses at the end of the simulation period are the most significant. Saltmarsh areas are able to cope with effects of sea-level rise for the first 40 years, but then there is a rapid decline due to submergence and mangrove encroachment, with a net loss of 40 ha of saltmarsh after 60 years (Figures 3a and 4f). By the end of the simulation period, our results show a potential net loss of 60 ha of saltmarsh in the no-gate scenario (Figures 3a and 4i). Conversely, mangroves are able to encroach on saltmarsh and establish in other locations of Area E which results in an increase of 20 ha of mangrove areas over the first 80 years of simulation; however, this gain in mangrove areas is lost after 100 years due to mangrove submergence (Figures 3a and 4i). Despite saltmarsh areas showing a significant decrease in our simulations with no-gate control, the average productivity of aboveground biomass does not show a significant change over the simulation period, as the estimated saltmarsh aboveground biomass values are between 8.2 and 9.6 Mg ha^{-1} $year^{-1}$ (Figure 3d). Average accretion rates in saltmarsh areas increase from 1.3 to 2.3 mm $year^{-1}$ over the first 80 years of simulation and decrease at the end of the simulation (Figure 3g). For mangrove, despite an almost linear increase in area over the first 80 years with no-gate control (Figures 3d and 3g), there is more variation in the average productivity of aboveground biomass and average accretion rates than in saltmarsh. The initial average aboveground biomass productivity for mangrove is 8.1 Mg ha^{-1} $year^{-1}$, which decreases after 20 years when newly colonized mangrove establish in areas of lower D which leads to mangroves with lower biomass productivity (Figure 3d). At the end of the simulation, there is an increase in the average aboveground mangrove biomass productivity, likely due to limited accommodation which precludes the establishment of newly colonized mangrove. The remaining mangrove areas have higher D values than in previous years, resulting in higher

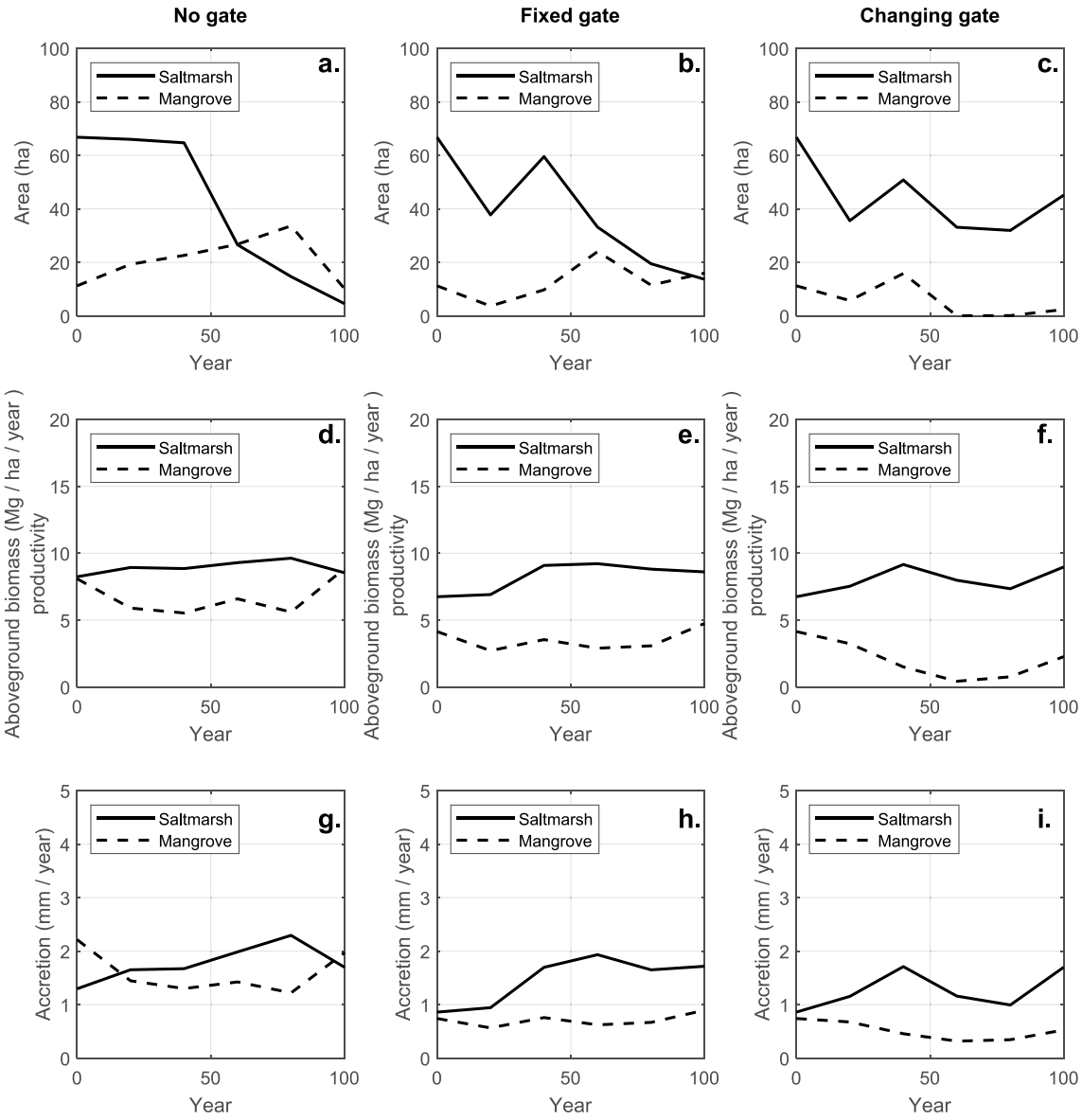


Figure 3. Simulated changes in vegetation extent in ha (a–c), aboveground biomass production in Mg ha^{-1} year^{-1} (d–f), and accretion rates in mm year^{-1} (g–i) under different control scenarios.

average aboveground biomass. Accretion rates in mangrove areas show a similar trend to the aboveground biomass. Initial average accretion rate for mangrove is 2.2 mm year^{-1}, which decreases to values between 1.2 and 1.4 mm year^{-1} between 20 and 80 years and increases at the end of the simulation period (Figure 3g).

The inclusion of gate control in the wetland to limit mangrove encroachment on saltmarsh also promotes an initial decrease of saltmarsh in the upper areas of the wetland as a result of tidal attenuation. For our calculations of initial biomass productivity, initial accretion rates, and soil carbon sequestration with gate conditions, we used the estimated vegetation distribution just after the installation of the gate (Figure 4b) which differs from the initial vegetation distribution without the gate (Figure 4a). Our estimates show that after 20 years, gate control could potentially lead to a decrease in 30 ha of saltmarsh areas (Figures 3b, 3c, 4d and 4e). In the scenario with fixed gate control, mangrove encroachment on saltmarsh is limited in the first 40 years, but eventually, mangrove encroaches on saltmarsh areas after 60 years and both mangrove and saltmarsh are submerged toward the end of the simulation period (Figures 3e, 4g and 4j). During the first 20 years, average aboveground biomass production and average accretion rates in saltmarsh are lower in

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

10.1029/2020EF001901

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

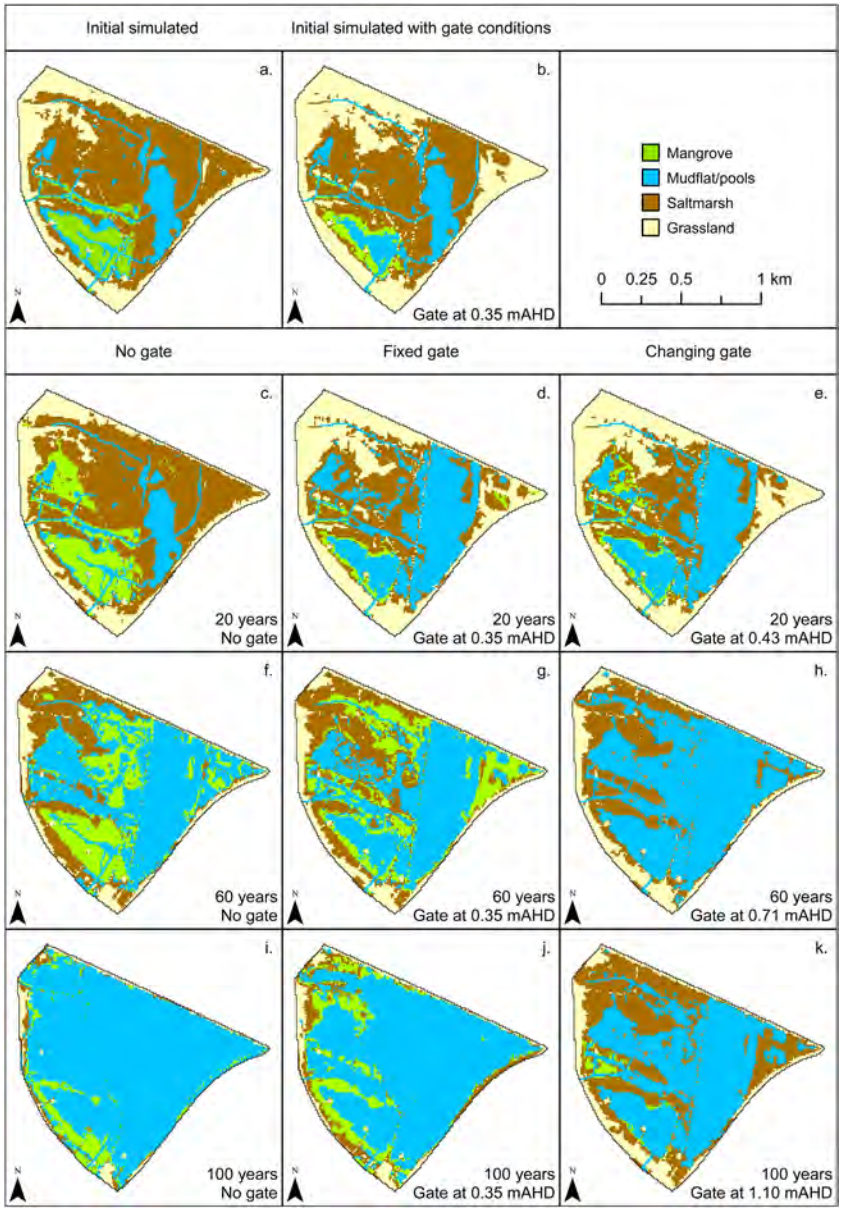


Figure 4. Changes in vegetation distribution. Simulated initial vegetation distribution with no-gate control (a), and gate control (b). Simulated vegetation distribution after 20, 60, and 100 years with no-gate control (c, f, i), fixed gate control (d, g, j), and changing gate control (e, h, k). Note: Adapted from Sandi et al. (2018). Gate levels are presented in relationship to the current Australian Height Datum (AHD).

the scenario with fixed gate control than the scenario with no-gate, but after 40 years values are in a similar range (8.6–9.2 Mg ha^{-1} year^{-1} and 1.7–2.9 mm year^{-1}) (Figures 3e and 3h). This suggests that as sea level rises the initial effects of hydraulic control from the fixed gate have less influence on the dynamics of the vegetation and accretion. In mangrove, areas variation of average aboveground biomass production and average accretion rates for the scenario with fixed gate control (Figures 3e and 3h) have similar trends to the scenario with no-gate (Figures 3d and 3g); however, magnitudes are around 50% lower than in the no-gate control scenario as the gate promotes the submergence of the mangrove in areas of high D early in the simulation and newly colonized mangrove is established in areas of low D, leading to lower biomass production and lower accretion rates (Equations 1 and 2).

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

In the scenario with changing gate conditions, attenuation of the tidal regime promotes the establishment of saltmarsh areas at the end of the simulation period and the almost complete exclusion of mangroves after 60 years (Figures 3c and 4h). Under the changing gate control scenario, hydraulic attenuation also produces lower average aboveground biomass production and average accretion rates in saltmarsh after 60 and 80 years, but increases at the end of the simulation (Figures 3f and 3i). In mangroves, average aboveground biomass productivity decreases from the initial value of 8.1 to 0.4 Mg·ha^{-1} year^{-1} and average accretion rates decrease from 0.7 to 0.3 mm year^{-1} after 60 years. Mangrove areas with changing gate conditions are very small after 60 years and do not significantly contribute to the vegetation dynamics of Area E (Figures 3c, 4h and 4k).

3.3. Projection of Soil Carbon Accumulation Rates

Soil carbon accumulation rates show that higher rates per area occur under the no-gate control scenario for both saltmarsh and mangrove (Figures 5a and 5g). For saltmarsh, our estimates show an initial average soil carbon accumulation rate per area of 1.0 MgC ha^{-1} year^{-1} which increases to a maximum of 1.6 MgC ha^{-1} year^{-1} after 80 years (Figure 5a). In terms of the total soil carbon accumulation rates, initially, saltmarsh areas accumulate 70.6 MgC year^{-1} which increases to 82.3 MgC year^{-1} after 20 years and significantly reduces to 37.3 MgC year^{-1} after 60 years and to 5.6 MgC year^{-1} after 100 years (Figures 5d, 6c, 6f and 6i). This decrease in the soil carbon accumulation rates occurs as saltmarsh is lost from submergence and mangrove encroachment (Figure 4). The initial average soil carbon accumulation rate per area in mangroves is 1.0 MgC ha^{-1} year^{-1} which decreases to 0.7 MgC ha^{-1} year^{-1} after 20 years and remains low for most of the simulation period (Figure 5g). The initial total soil carbon accumulation rate for mangrove is 11.0 MgC year^{-1}, which reaches a maximum of 21.7 MgC year^{-1} after 80 years and decreases to 10.0 MgC year^{-1} after 100 years (Figure 5j). The majority of the remaining vegetated areas at the end of the no-gate control simulation are mangrove areas (Figure 4i), so in this scenario mangrove accounts for the majority of the soil carbon accumulation of the wetland after 100 years. However, by that point, the capacity for soil carbon sequestering of the site has reduced by 80% from the initial values given the vegetation loss (Figures 4i and 6i).

In the scenarios with gate control, soil carbon accumulation rates per area are lower than in the no-gate control scenario as attenuation from hydraulic control limits both biomass productivity and accretion (Figures 5b, 5c, 5h and 5i). The objective of the gate is to limit mangrove establishment, but also causes some initial saltmarsh area loss. With the introduction of the gate, the initial average soil carbon accumulation rate per area in saltmarsh is 0.8 MgC ha^{-1} year^{-1} (Figures 5b and 5c) and for mangrove is 0.5 MgC ha^{-1} year^{-1} (Figures 5h and 5i). The initial total soil carbon accumulation rate for saltmarsh decreases to 42.9 MgC year^{-1} with the inclusion of the gate (Figures 5e and 5f) and to 2.5 MgC year^{-1} for mangrove (Figures 5k and 5l). Soil carbon sequestered from mangrove is significant in the fixed control scenario after 60 years (Figure 5k), when effects from the gate are less pronounced and newly colonized mangrove encroaches on saltmarsh. In the fixed gate scenario, soil carbon sequestered from mangrove areas contributes to more than 13% of the total sequestered soil carbon near the end of the simulation period (Figure 5k). In the scenario with changing gate control, the total soil carbon sequestration from mangroves contributes to less than 5% of the sequestered soil carbon over the whole simulation period (Figure 5l). At the end of the simulation, the combined total soil carbon accumulation rate of both mangrove and saltmarsh is of 15.6, 25.7, and 58.0 MgC year^{-1} for the scenarios with no-gate, fixed gate and changing gate control respectively.

3.4. Changes in Soil Carbon Stock

Sequestered soil carbon originating from soil carbon sequestration rates (Figure 5) as well as potential carbon losses are converted to CO_2 to represent potential greenhouse gases burial and emissions on the study area for all scenarios (see Section 2.4.4). Figure 7 shows the change in soil carbon stock (in MgC) as a result of cumulative CO_2 burial and CO_2 emissions (in $MgCO_2$). All control scenarios show steady rates of potential carbon loss (CO_2 emissions) that are much lower than the sequestered soil carbon (CO_2 burial) resulting in a net increase of carbon stock (in MgC) over the years (Figure 7). In the scenario with no-gate control, CO_2 burial rate decreases after 60 years, when saltmarsh vegetation is significantly lost due to submergence and mangrove encroachment occurs (Figure 7a). The total soil carbon stock in the site reaches

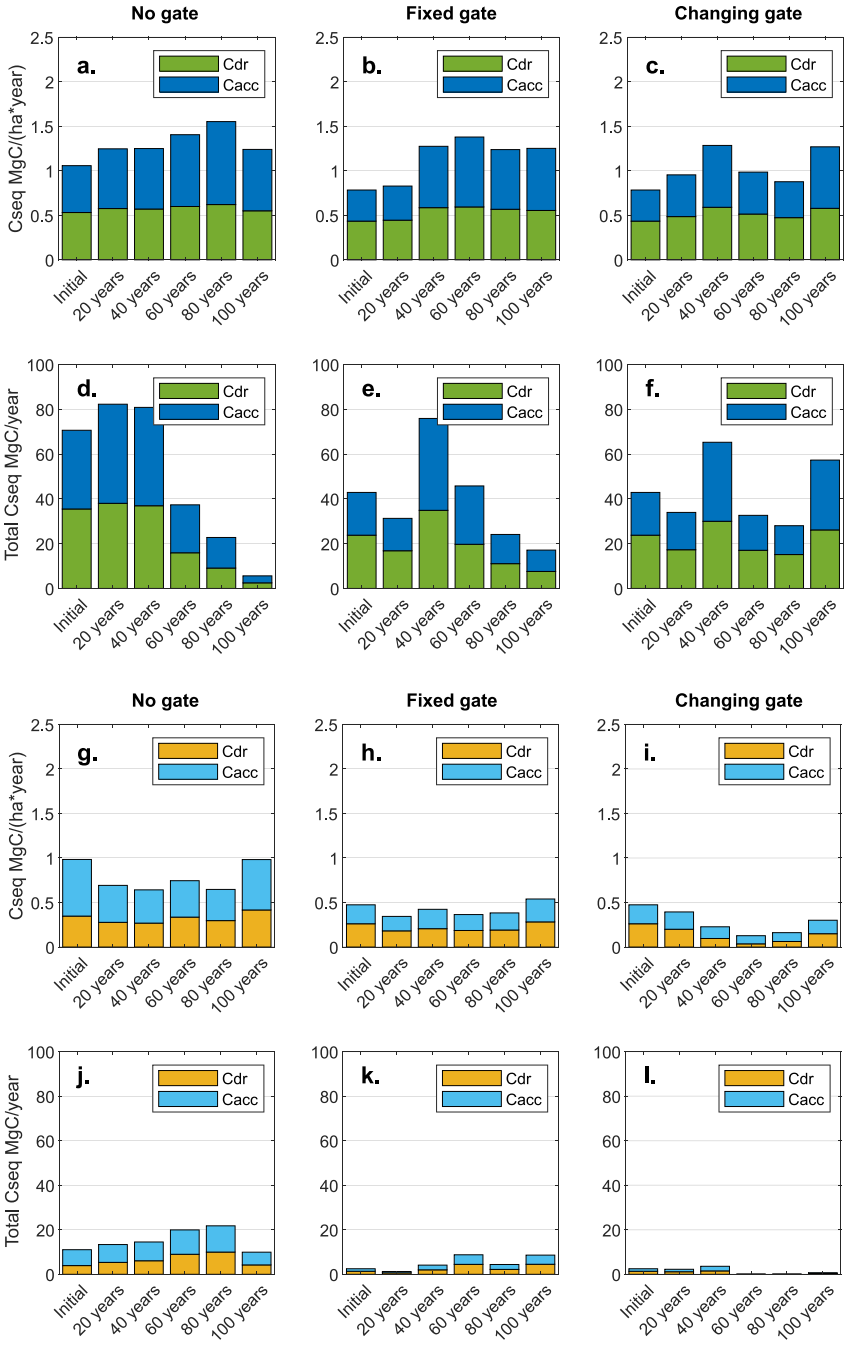


Figure 5. Average soil carbon sequestration rates per area (MgC ha^{-1} $year^{-1}$) from soil accretion (C_{acc}) and root decomposition (C_{dr}) for saltmarsh (a–c), and total carbon sequestration rates (MgC $year^{-1}$) for saltmarsh (d–f) under different management scenarios. Average carbon sequestration rates per area (MgC ha^{-1} $year^{-1}$) from soil accretion (C_{acc}) and root decomposition (C_{dr}) for mangrove (g–i), and total carbon sequestration rates (MgC $year^{-1}$) for mangrove (j–l) under different management scenarios.

~20,800 MgC after 100 years under no-gate conditions, with a net soil carbon gain of 56% of the initial stock. In the scenarios with gate control, submergence and transition to grassland occurs early in the simulations due to the effects of the gate, which reduces the capacity for CO_2 burial (Figure 7a). The total soil carbon stocks reach values of 18,100 MgC and 17,500 MgC under the fixed gate and changing gate control scenarios respectively (Figure 7c). These correspond to net soil carbon gains of 36% and 32% at the end of

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

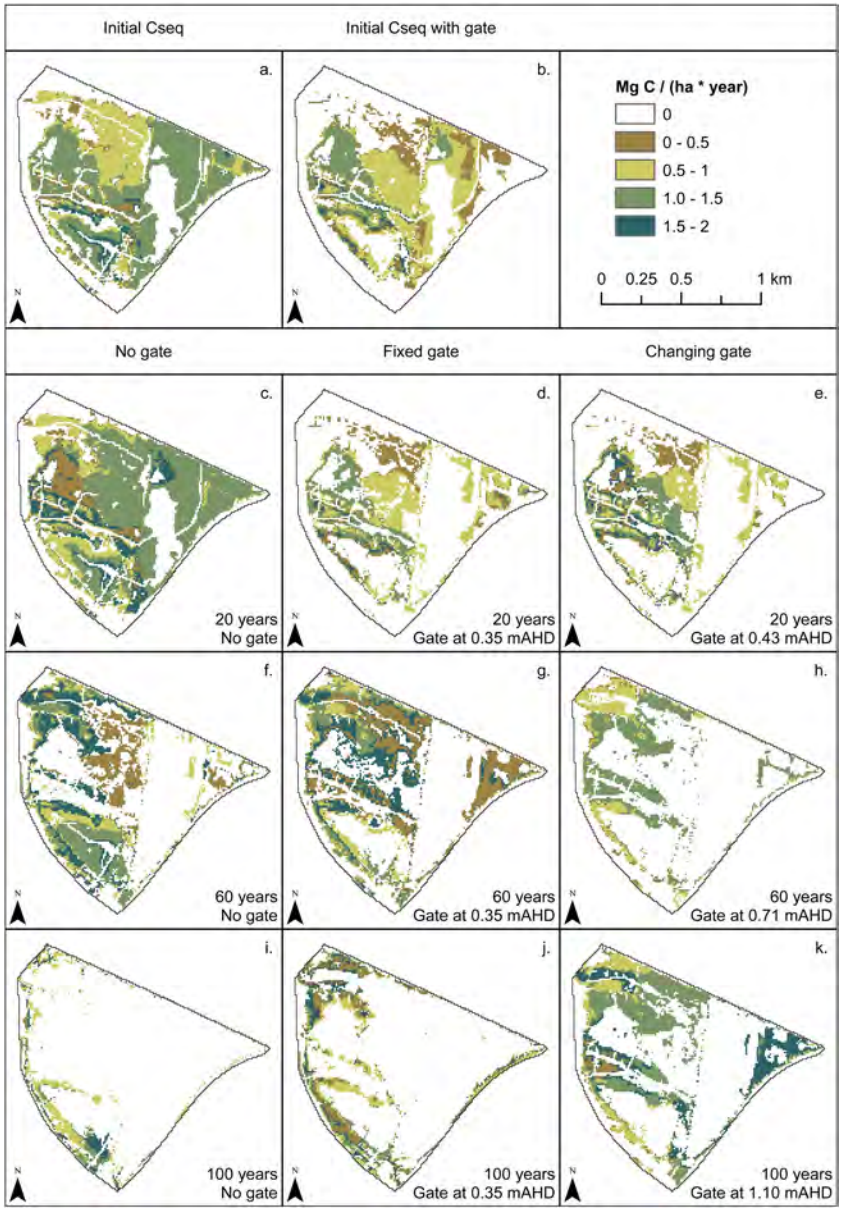


Figure 6. Changes in soil carbon accumulation rates per area (MgC ha^{-1} $year^{-1}$). Estimated initial carbon accumulation rates per area with no-gate control (a), and gate control (b). Simulated carbon accumulation rates per area after 20, 60, and 100 years with no-gate control (c, f, i), fixed gate control (d, g, j), and changing gate control (e, h, k). Gate levels are presented in relationship to the current Australian Height Datum (AHD).

the simulation period, around 20% less than the scenario with no-gate control. Both gated scenarios have the same dynamics of soil carbon stock.

For comparison, we also estimated soil carbon burial and carbon emissions using a simpler bathtub approach. In the bathtub model simulation, mangrove vegetation encroaches on saltmarsh very early in the simulation, there is little vegetation submergence at the end of the simulation period and accretion rates are much higher than the hydrodynamic model simulations (Figure S6). The trends of cumulative CO_2 burial and CO_2 emissions are similar over the first 60 years of simulation, but by using the bathtub approach, the estimated cumulative CO_2 burial is grossly over predicted at the end of the simulation (Figure 7a), resulting in a total soil carbon stock of ~25,300 MgC after 100 years (Figure 7c), which is 1.2 times the values expected using the hydrodynamic approach. Cumulative CO_2 emissions also show higher magnitudes using the

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

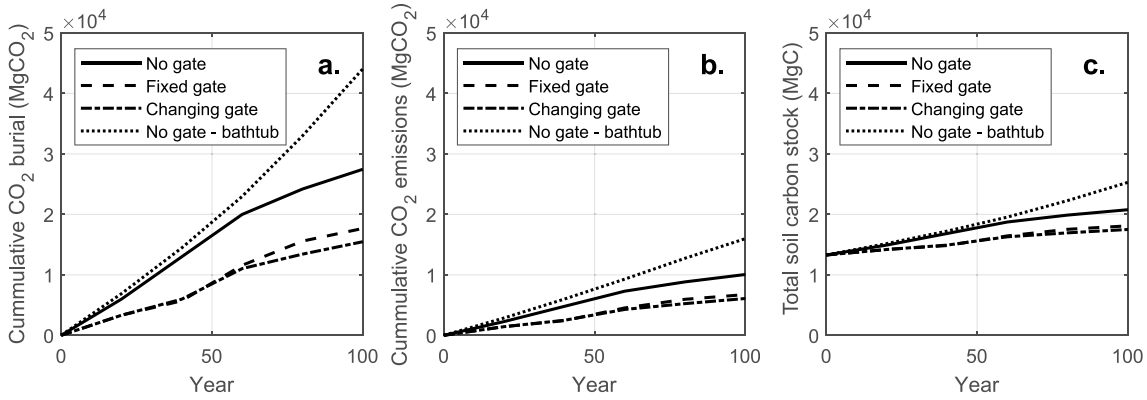


Figure 7. Soil carbon dynamics in Area E under different control scenarios. Cumulative CO_2 burial (a), CO_2 emissions (b), and total soil carbon stock (c).

bathtub approach at the end of the simulation. After 60 years of simulation, soil carbon burial and emissions are less in the hydrodynamic model than the bathtub model because most vegetation drowns.

4. Discussion

Soil carbon sequestration in estuarine and coastal wetlands produces some of the most carbon-rich soils in the world. Knowledge of the previous conditions, as well as analysis of the historic environmental processes, are important when estimating soil carbon budgets because the variations of the carbon along the soil profile are the result of different environmental conditions over time (Kelleway, Saintilan, et al., 2017). In our study area, the majority of the area was covered by saltmarsh since before the 1950s (Williams et al., 2000), but mangroves only established at the site after tidal flows were reinstated during the 1990s (Howe et al., 2010). Because of this, the saltmarsh at the site is well established while mangroves are relatively less mature. Our estimate of the soil carbon stock in saltmarsh (157 MgC ha^{-1}) is consistent with estimates of soil carbon stocks in Australian saltmarshes (165 MgC ha^{-1}) estimated by Macreadie, Ollivier, et al. (2017) and (168 MgC ha^{-1}) estimated by Serrano et al. (2019). Our estimate of the soil carbon stock for mangroves (111 MgC ha^{-1}) reflects the age since establishment as it is lower than estimates of mangrove soil carbon stocks collated by Serrano et al. (2019) for Australian mangroves (251 MgC ha^{-1}). Estimates soil carbon stocks for Australian mangroves are generally lower than other estimates in the Indo Pacific region (783 MgC ha^{-1} on average) (Donato et al., 2011); however, the data reported by Donato et al. (2011) includes a wide range of mangrove species, soils (ranging from <0.5 m to deep >3 m), and the environmental history was not taken into account. Our estimate of the soil carbon stock in mangroves is consistent with belowground soil carbon stocks reported for mangroves between 0 and 15 years of age (Kelleway et al., 2016), which is roughly the age of the mangroves at the site at the initial time of the simulations.

Our estimated initial average soil carbon sequestration rate per area (C_{seq}) for saltmarsh is 1.0 MgC ha^{-1} $year^{-1}$, which is in between values reported by Serrano et al. (2019) (0.39 MgC ha^{-1} $year^{-1}$), Macreadie, Ollivier, et al. (2017) (0.55 MgC ha^{-1} $year^{-1}$) and Ouyang and Lee (2014) (2.75 MgC ha^{-1} $year^{-1}$) for Australian saltmarshes, and lower that global values reported for saltmarsh (1.51 MgC ha^{-1} $year^{-1}$) (Duarte et al., 2005). In our calculations, half of the saltmarsh carbon accumulation rates originate from soil accretion (Figure 5a), which results in 0.5 MgC ha^{-1} $year^{-1}$, very close to the value of soil carbon accumulation rate reported by Macreadie, Ollivier, et al. (2017). The remaining half of the soil carbon accumulation rate in our calculations originates from dead root turnover (Figure 5a), which was not included by Macreadie, Ollivier, et al. (2017) or Serrano et al. (2019). For mangrove, our estimate of the initial average soil carbon sequestration rate per area (C_{seq}) is 1.0 MgC ha^{-1} $year^{-1}$ which is lower than values reported by Saintilan et al. (2013) (2.56 MgC ha^{-1} $year^{-1}$), Serrano et al. (2019) (1.26 MgC ha^{-1} $year^{-1}$), and above the mean value reported by Lovelock et al. (2014) (0.76 MgC ha^{-1} $year^{-1}$). For mangrove, one-third of the soil carbon accumulation rates originates from dead root turnover and the remaining two-thirds are the result of accretion (Figure 5g). Lovelock et al. (2014) argued that their low rates of soil carbon sequestration in mangroves may be related to the exclusion of the contribution from roots throughout the soil profile in their estimates. Our

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

estimates of soil carbon accumulation rates integrate turnover from dead roots as part of the calculations as opposed to only increases of the top soil layer. Lamont et al. (2020) suggest substantial carbon sequestration in deeper soils originating from dead roots turnover.

Analysis of the model results for the three scenarios of management via tidal inlet control reflects the strong influence of flow conditions on the vegetation distribution and extent and the resulting aboveground biomass production. Scenarios with tidal regimes affected by gate control show an overall initial decrease in aboveground biomass production and changes in the spatial distribution of saltmarsh vegetation compared to the no-gate scenario due to increased hydrodynamic attenuation. Consequently, different spatial changes on the soil carbon accumulation rates occur across the site and over time for different scenarios (Figure 6). In the scenario with no-gate control saltmarsh is rapidly displaced by mangrove encroachment, reducing its soil carbon accumulation rates. In the gate-controlled scenarios, the initial soil carbon accumulation rates for saltmarsh are lower than in the no-gate scenario due to the reduced inundation levels, and continue to be lower for the first 40 years of simulation (Figure 5). In the changing gate scenario, mangrove establishment is limited and saltmarsh vegetation is promoted at the end of the simulation, resulting in an increase in soil carbon accumulation rates. Under no-gate scenario, the initial mangrove areas at the lower end of the tidal frame remain for most of the simulation period reaching mature age (Figure 4), but they become submerged at the end of the simulation period. As sea-level rise occurs, mangroves can colonize new areas with low D, which translates into newly colonized mangroves with lower biomass production rates, but still capable of sequestering considerable soil carbon via root decomposition (C_{dr}) (Figure 5). With the inclusion of the inlet control gate, the initial mangrove areas completely disappear (due to drowning) early in the simulation (Figure 4), resulting in less initial capacity to sequester soil carbon (Figure 5) and also in a reduction of future capacity as those mangrove areas do not reach a mature age. In the fixed gate scenario, newly colonized mangroves with lower biomass get established in other areas of the wetland as sea level rises, but the mangrove spatial distribution changes frequently (Figure 4) resulting in ephemeral wetland areas due to short-term establishment and die-off of mangroves. This is also reflected in the results showing less soil carbon accumulation rates in the fixed gate control scenario than the scenario with no-gate (Figure 5). In the changing gate scenario, mangrove establishment is limited for all the simulation period, so only saltmarsh contributes to soil carbon sequestration. Importantly, our model does not only simulate the spatial distribution of the vegetation, but also provides estimates of carbon accumulation rates that are spatially varied and consistent with expected vegetation structures and age.

Previous estimates of the effects sea-level rise on the soil carbon sequestration of saltmarsh environments suggest that carbon burial might increase in the first half of the century, followed by a decrease toward the end of the century (Kirwan & Mudd, 2012). This is consistent with our findings as there is a decrease in the rate of CO_2 burial (Figure 7a) and a decrease in the capacity of the wetland for soil carbon accumulation under no-gate control (Figures 5d and 5j), mostly as a result of vegetation submergence after 60 years, but also due to the fact that new vegetation areas have less biomass productivity and less capacity for soil carbon accumulation from accretion and dead root turnover. Though current projections of sea-level rise show continuous increases in sea-level rise rates over the next century, historical records show that these rates have varied over different timescales, indicating more rapid acceleration in some decades and less rapid acceleration in others. Over millennia, global trends of sea-level rise have also accelerated and decelerated, leading to coastal wetland retreat and expansion. Analysis of paleo-records linking sea-level rise rates with capacity of vegetation to initiate accretion show widespread submergence occurs in coastal wetlands when sea-level rise rates surpass 7 mm/year (Horton et al., 2018; Saintilan et al., 2020; Törnqvist et al., 2020). In our simulations, this rate of sea-level rise occurs after 60 years when the widespread loss of vegetation is likely to occur. Landward colonization and further accommodation in the study site is not possible due to the embankments surrounding it. This accommodation might alleviate the significant reduction in carbon accumulation rates induced by vegetation submergence (Lovelock & Reef, 2020); however, topography and anthropogenic barriers commonly limit accommodation in many other sites and regions. In the cases where vegetation could be able to colonize landwards, the wetland might also be unable to adapt vertically if accelerated sea-level rise continues and surpasses the 7 mm/year threshold derived from paleo-records. Under more attenuated conditions (scenarios with gate control), the capacity of the study area for CO_2 burial decreases (Figure 7), but the wetland has higher rates of soil carbon accumulation at the end of the simulation period (Figures 6j and 6k) as more vegetation is able to survive. Despite these higher rates, the final soil

Table 2
Trade-Off Between Wetland Vegetation Loss and Soil Carbon Stock Gains

Control	Percent wetland survival (%)		Percent increase in soil carbon stock (%)	
No gate	More habitat loss	19	More carbon gain	56
Fixed gate		38		36
Rising gate	Less habitat loss	61	Less carbon gains	32

carbon stocks are significantly lower than in the no-gate scenario (Figure 7c) and the newly established vegetation might not be able to adapt if accelerated sea-level rise continues beyond the period of analysis.

Due to the complex eco-geomorphic interactions between water, sediments and vegetation, the planning of coastal wetland rehabilitation and wetland creation should incorporate detailed modeling under sea-level rise and management scenarios. In our simulations, we have included three simplistic hydraulic control conditions and we found that there is a trade-off between strategies that guarantee the survival of the wetland and the total soil carbon sequestered. In the no-gate control scenario, the wetland was able to sequester more soil carbon by the end of the simulation than in the gate-controlled scenarios even when high emissions occurred following vegetation submergence (Table 2). In the gate-controlled scenarios, the presence of more vegetation than for the no-gate scenario leads to more habitat provision toward the end of the simulation; however, the newly colonized vegetation has lower aboveground biomass productivity due to the restrictions to the tidal regime and hydraulic attenuation and therefore there is less total soil carbon gains in the gate-controlled scenarios (Table 2). The scenario with changing gate control has the highest soil carbon sequestering capacity at the end of the simulation period, but it has the lowest soil carbon gains of the three management scenarios (Table 2). These results have significant implications for the management of coastal wetlands. Currently, coastal wetland accounting, wetland creation, wetland rehabilitation and wetland protection frameworks have identified the significance of wetland conservation for emission reduction programs such as REDD+ (Adame et al., 2018; Cameron et al., 2019; Rogers, Macreadie, et al., 2019). Rehabilitated wetlands have shown great capacity to sequester soil carbon at rates similar or higher than those of natural wetlands (Cameron et al., 2019) and created wetlands seem to be able to cope with the effects of sea-level rise under current conditions and the more conservative emissions scenarios (Krauss et al., 2017). However, predictions under future sea-level rise rely on assumptions of soil carbon sequestration capacity remaining at current levels and simplified inundation formulations that do not account for local wetland features. These assumptions are particularly restrictive for predictions using scenarios of high CO_2 emissions and accelerated sea-level rise, in which important changes to the wetland vegetation structure and spatial distribution are predicted to occur faster than for any contemporary observational period. Therefore, implementation of a detailed modeling framework like the one developed here and projections of vegetation changes and soil carbon sequestration under sea-level rise can help evaluating management strategies to obtain the best outcomes for habitat provision and soil carbon sequestration.

Other effects of climate change on vegetation and soil carbon dynamics are less obvious and harder to integrate into modeling frameworks. For example, increased temperature and drought effects can lead to increased forest mortality, but higher CO_2 concentrations can alleviate some of these effects through CO_2 fertilization (Liu et al., 2017). Furthermore, in mangrove-saltmarsh wetlands increased CO_2 may affect competition between mangrove (C_3 photosynthetic path) and saltmarsh (C_3 and C_4 photosynthetic path) species (R. J. Howard et al., 2018; McKee & Rooth, 2008). Mangrove encroachment on saltmarsh might decline due to increased resource competition (McKee & Rooth, 2008) as salinity can be a larger driver for mangrove encroachment than increases in CO_2 (Ball et al., 1997; Reef et al., 2015). In turn, saltmarsh C_3 species have been reported to have a larger increase in biomass in response to CO_2 fertilization than C_4 saltmarsh species (Arp et al., 1993), although Ratliff et al. (2015) did not find the differences to be significant. As the saltmarsh species in our study area are both C_3 (*Sarcocornia quinqueflora*) and C_4 (*Sporoboulus virginicus*), it is possible that increased CO_2 may favor a shift to *Sarcocornia* dominance, and an increase on saltmarsh biomass productivity and accretion capacity. This suggests that effects of increased CO_2 in the atmosphere might contribute to more soil carbon burial from saltmarsh than what our estimates indicate. The magnitude of the increase in soil carbon burial is uncertain, as biomass productivity increase due to CO_2 fertilization estimates vary widely and maybe limited by nitrogen availability (Ratliff et al., 2015). Additionally, it must be noted that saltmarsh and mangroves occur along a continuum from sediment-rich to sediment-poor environments, where organic soil contribution from plants has a major role in the accretion and survival of the latter (Cahoon et al., 2020). Because of this, accretion, survival and soil carbon sequestration capacity

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

in mangrove-saltmarsh wetlands that receive considerable amounts of sediment may not benefit as much from biomass productivity increases, but there could be significant benefits for sediment-poor wetlands.

Findings presented here show detailed calculation of different processes contributing to soil carbon accumulation. Dynamics of total carbon budgets, however, must include blue carbon stored in aboveground and belowground biomass stocks which our eco-geomorphic approach does not provide. Even though in our case most of the carbon is stored in the soil (95%), carbon stored in aboveground biomass can be a significant fraction of the total carbon stock, in particular for mangroves. For example, in *Avicennia spp,* this fraction can be up to 25% of the total carbon budget considering the top 1 m layer of the soil (Kauffman et al., 2020). In Australian ecosystems, mangrove aboveground biomass carbon is around 20% of the total carbon budget in temperate and subtropical climate regions and up to 44% in tropical climates (Serrano et al., 2019). In our approach, we focus on the soil carbon and use calculations of aboveground biomass productivity in terms of the inundation descriptor D (Equation 2), for both saltmarsh and mangroves, each with their respective calibrated parameters. More complex relationships can be developed based on formulations for individual mangrove tree growth (Chen & Twilley, 1998; van Maanen et al., 2015), but they require the definition of a larger number of parameters than Equation 2.

5. Summary and Conclusions

Although blue carbon ecosystems have been the focus of several research in recent years, the impacts of accelerated sea-level rise on the future of coastal wetlands, particularly their capacity for soil carbon accumulation remains uncertain. Current understanding of coastal wetland processes suggests that future tidal reinstatement, wetland restoration and landward colonization induced by sea-level rise present an opportunity for potential gains of soil carbon. However, estimates of the magnitude of future soil carbon gains often rely on assumptions of sequestration capacity remaining at current levels, uniform wetland inundation levels (i.e., bathtub approach), and availability of upland areas for wetland transgression into existing less productive ecosystems.

Our results, using an eco-geomorphic model that includes soil carbon processes, show that under accelerated sea-level rise the combined effects of rapid vegetation retreat and colonization affected by local wetland features produces a shift to newly colonized vegetation that have lower capacity for soil carbon accumulation. Results using the model with uniform wetland inundation levels (bathtub) grossly over predicts (by 60%) the accumulated soil carbon burial at the end of the 100-year simulation period.

Our baseline scenario, assuming no inlet control post wetland restoration, shows the highest total soil carbon accumulated at the end of the simulation period, but also the highest decrease in soil carbon accumulation capacity with respect to initial values due to vegetation submergence and resulting newly colonized vegetation. In the other two scenarios, inlet control (a common management strategy) is used to manage sea-level rise effects and conserve vegetation and bird habitat, but early disappearance of mature mangrove vegetation and establishment of newly colonized vegetation decreases soil carbon accumulation rates which results in 20% less of the soil carbon sequestered in the baseline scenario. The capacity for soil carbon accumulation at the end of the simulation is higher in the controlled scenarios as more vegetated areas survive submergence, but it is likely that this capacity will decrease if accelerated sea-level rise continues.

These results highlight the importance of implementing an eco-geomorphic modeling framework to study the dynamics of soil carbon in coastal wetlands. The implementation of management strategies needs to not only aim at preserving wetland areas and habitat, but also to provide conditions to preserve vegetation with significant capacity for soil carbon accumulation.

Data Availability Statement

Full description of the carbon model parameters has been provided in text and supporting information. This research uses hydrodynamic and vegetation simulation data from a previously developed model by Rodríguez et al. (2017) and Sandi et al. (2018). These data have been made available at https://doi.org/10.4211/hs.db2cc5d068c04a2da47496c7265d3025.

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Acknowledgments
P. M. Saco acknowledges support from the Australian Research Council (grant DP140104178 and Future Fellowship grant FT140100610). The authors sincerely thank the reviewers, whose comments and suggestions helped improved and clarify this manuscript.

References

Abbott, K. M., Elsey-Quirk, T., & DeLaune, R. D. (2019). Factors influencing blue carbon accumulation across a 32-year chronosequence of created coastal marshes. *Ecosphere*, *10*(8), e02828. https://doi.org/10.1002/ecs2.2828

Adame, M. F., Najera, E., Lovelock, C. E., & Brown, C. J. (2018). Avoided emissions and conservation of scrub mangroves: Potential for a blue carbon project in the Gulf of California, Mexico. *Biology Letters*, *14*(12), 20180400. https://doi.org/10.1098/rsbl.2018.0400

Alizad, K., Hagen, S. C., Morris, J. T., Bacopoulos, P., Bilskie, M. V., Weishampel, J. F., & Medeiros, S. C. (2016). A coupled, two-dimensional hydrodynamic-marsh model with biological feedback. *Ecological Modelling*, *327*(Supplement C), 29–43. https://doi.org/10.1016/j.ecolmodel.2016.01.013

Alizad, K., Hagen, S. C., Morris, J. T., Medeiros, S. C., Bilskie, M. V., & Weishampel, J. F. (2016). Coastal wetland response to sea-level rise in a fluvial estuarine system. *Earth's Future*, *4*(11), 483–497. https://doi.org/10.1002/2016ef000385

Alongi, D. M. (2014). Carbon cycling and storage in mangrove forests. *Annual Review of Marine Science*, *6*(1), 195–219. https://doi.org/10.1146/annurev-marine-010213-135020

Arp, W. J., Drake, B. G., Pockman, W. T., Curtis, P. S., & Whigham, D. F. (1993). Interactions between C_3 and C_4 salt marsh plant species during four years of exposure to elevated atmospheric CO_2. *Vegetatio*, *104/105*, 133–143. https://doi.org/10.1007/bf00048149

Atwood, T. B., Connolly, R. M., Almahasheer, H., Carnell, P. E., Duarte, C. M., Ewers Lewis, C. J., et al. (2017). Global patterns in mangrove soil carbon stocks and losses. *Nature Climate Change*, *7*(7), 523–528. https://doi.org/10.1038/nclimate3326

Ball, M. C., Cochrane, M. J., & Rawson, H. M. (1997). Growth and water use of the mangroves Rhizophora apiculata and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO_2. *Plant, Cell & Environment*, *20*(9), 1158–1166. https://doi.org/10.1046/j.1365-3040.1997.d01-144.x

Bouillon, S., Borges, A. V., Castañeda-Moya, E., Diele, K., Dittmar, T., Duke, N. C., et al. (2008). Mangrove production and carbon sinks: A revision of global budget estimates. *Global Biogeochemical Cycles*, *22*(2). https://doi.org/10.1029/2007gb003052

Boys, C. A., & Pease, B. (2017). Opening the floodgates to the recovery of nektonic assemblages in a temperate coastal wetland. *Marine and Freshwater Research*, *68*(6), 1023–1035. https://doi.org/10.1071/mf15445

Breda, A., Saco, P. M., Sandi, S. G., Saintilan, N., Riccardi, G., & Rodríguez, J. F. (2021). Accretion, retreat and transgression of coastal wetlands experiencing sea-level rise. *Hydrology and Earth System Sciences*, *25*, 769–786. https://doi.org/10.5194/hess-25-769-2021

Breithaupt, J. L., Smoak, J. M., Bianchi, T. S., Vaughn, D. R., Sanders, C. J., Radabaugh, K. R., et al. (2020). Increasing rates of carbon burial in southwest Florida coastal wetlands. *Journal of Geophysical Research: Biogeosciences*, *125*(2), e2019JG005349. https://doi.org/10.1029/2019jg005349

Cahoon, D. R., McKee, K. L., & Morris, J. T. (2020). How plants influence resilience of salt marsh and mangrove wetlands to sea-level rise. *Estuaries and Coasts*, *44*, 883–898. https://doi.org/10.1007/s12237-020-00834-w

Cameron, C., Hutley, L. B., Friess, D. A., & Brown, B. (2019). Community structure dynamics and carbon stock change of rehabilitated mangrove forests in Sulawesi, Indonesia. *Ecological Applications*, *29*(1), e01810. https://doi.org/10.1002/eap.1810

Carniello, L., D'Alpaos, A., & Defina, A. (2011). Modeling wind waves and tidal flows in shallow micro-tidal basins. *Estuarine, Coastal and Shelf Science*, *92*(2), 263–276. https://doi.org/10.1016/j.ecss.2011.01.001

Chen, R., & Twilley, R. R. (1998). A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. *Journal of Ecology*, *86*(1), 37–51. https://doi.org/10.1046/j.1365-2745.1998.00233.x

Church, J. A., Clark, P. U., Cazenave, A., Gregory, J. M., Jevrejeva, S., Levermann, A., et al. (2013). Sea level change. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, et al. (Eds.), *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change* (pp. 1137–1216). Cambridge University Press.

Clarke, P. J., & Myerscough, P. J. (1993). The intertidal distribution of the grey mangrove (Avicennia marina) in southeastern Australia: The effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. *Australian Journal of Ecology*, *18*(3), 307–315. https://doi.org/10.1111/j.1442-9993.1993.tb00458.x

Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., et al. (2009). Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Frontiers in Ecology and the Environment*, *7*(2), 73–78. https://doi.org/10.1890/070219

Crase, B., Liedloff, A., Vesk, P. A., Burgman, M. A., & Wintle, B. A. (2013). Hydroperiod is the main driver of the spatial pattern of dominance in mangrove communities. *Global Ecology and Biogeography*, *22*(7), 806–817. https://doi.org/10.1111/geb.12063

D'Alpaos, A., Lanzoni, S., Marani, M., & Rinaldo, A. (2007). Landscape evolution in tidal embayments: Modeling the interplay of erosion, sedimentation, and vegetation dynamics. *Journal of Geophysical Research*, *112*(F1). https://doi.org/10.1029/2006JF000537

Donato, D. C., Kauffman, J. B., Murdiyarso, D., Kurnianto, S., Stidham, M., & Kanninen, M. (2011). Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, *4*(5), 293–297. https://doi.org/10.1038/ngeo1123

DPI, N. (2008). *Acid sulfate soils priority investigations for the lower Hunter River Estuary*. Port Stephens.

Duarte, C. M. (1990). Seagrass nutrient content. *Marine Ecology Progress Series*, *67*, 201–207. https://doi.org/10.3354/meps067201

Duarte, C. M., Middelburg, J. J., & Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, *2*(1), 1–8. https://doi.org/10.5194/bg-2-1-2005

Elphick, C. S., Meiman, S., & Rubega, M. A. (2015). Tidal-flow restoration provides little nesting habitat for a globally vulnerable saltmarsh bird. *Restoration Ecology*, *23*(4), 439–446. https://doi.org/10.1111/rec.12194

Hofstede, J. L. A. (2019). On the feasibility of managed retreat in the Wadden Sea of Schleswig-Holstein. *Journal of Coastal Conservation*, *23*(6), 1069–1079. https://doi.org/10.1007/s11852-019-00714-x

Horton, B. P., Shennan, I., Bradley, S. L., Cahill, N., Kirwan, M., Kopp, R. E., & Shaw, T. A. (2018). Predicting marsh vulnerability to sea-level rise using Holocene relative sea-level data. *Nature Communications*, *9*(1), 2687. https://doi.org/10.1038/s41467-018-05080-0

Howard, J., Hoyt, S., Isensee, K., Telszewski, M., & Pidgeon, E. (2014). *Coastal blue carbon: Methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses*.

Howard, R. J., Stagg, C. L., & Utomo, H. S. (2018). Early growth interactions between a mangrove and an herbaceous salt marsh species are not affected by elevated CO_2 or drought. *Estuarine, Coastal and Shelf Science*, *207*, 74–81. https://doi.org/10.1016/j.ecss.2018.03.026

Howe, A. J. (2008). *Hydrodynamics, geomorphology and vegetation of estuarine wetlands in the Hunter, Australia: Implications for migratory shorebird high tide roost availability* (PhD thesis). University of Newcastle.

Howe, A. J., Rodríguez, J. F., & Saco, P. M. (2009). Surface evolution and carbon sequestration in disturbed and undisturbed wetland soils of the Hunter Estuary, southeast Australia. *Estuarine, Coastal and Shelf Science*, *84*(1), 75–83. https://doi.org/10.1016/j.ecss.2009.06.006

Howe, A. J., Rodriguez, J. F., Spencer, J., MacFarlane, G. R., & Saintilan, N. (2010). Response of estuarine wetlands to reinstatement of tidal flows. *Marine and Freshwater Research*, *61*(6), 702–713. https://doi.org/10.1071/mf09171

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Jaramillo, V. J., Kauffman, J. B., Rentería-Rodríguez, L., Cummings, D. L., & Ellingson, L. J. (2003). Biomass, carbon, and nitrogen pools in Mexican tropical dry forest landscapes. *Ecosystems*, *6*(7), 609–629. https://doi.org/10.1007/s10021-002-0195-4

Kauffman, J. B., Adame, M. F., Arifanti, V. B., Schile-Beers, L. M., Bernardino, A. F., Bhomia, R. K., et al. (2020). Total ecosystem carbon stocks of mangroves across broad global environmental and physical gradients. *Ecological Monographs*, *90*(2), e01405. https://doi.org/10.1002/ecm.1405

Kauffman, J. B., & Donato, D. C. (2012). Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests (Vol. 86). CIFOR.

Kelleway, J. J., Cavanaugh, K., Rogers, K., Feller, I. C., Ens, E., Doughty, C., & Saintilan, N. (2017). Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Global Change Biology*, *23*(10), 3967–3983. https://doi.org/10.1111/gcb.13727

Kelleway, J. J., Saintilan, N., Macreadie, P. I., Baldock, J. A., Heijnis, H., Zawadzki, A., et al. (2017). Geochemical analyses reveal the importance of environmental history for blue carbon sequestration. *Journal of Geophysical Research: Biogeosciences*, *122*(7), 1789–1805. https://doi.org/10.1002/2017jg003775

Kelleway, J. J., Saintilan, N., Macreadie, P. I., Skilbeck, C. G., Zawadzki, A., & Ralph, P. J. (2016). Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Global Change Biology*, *22*(3), 1097–1109. https://doi.org/10.1111/gcb.13158

Kelleway, J. J., Serrano, O., Baldock, J. A., Burgess, R., Cannard, T., Lavery, P. S., et al. (2020). A national approach to greenhouse gas abatement through blue carbon management. *Global Environmental Change*, *63*, 102083. https://doi.org/10.1016/j.gloenvcha.2020.102083

Kirwan, M. L., & Guntenspergen, G. R. (2010). Influence of tidal range on the stability of coastal marshland. *Journal of Geophysical Research*, *115*(F2). https://doi.org/10.1029/2009JF001400

Kirwan, M. L., Guntenspergen, G. R., D'Alpaos, A., Morris, J. T., Mudd, S. M., & Temmerman, S. (2010). Limits on the adaptability of coastal marshes to rising sea level. *Geophysical Research Letters*, *37*(23). https://doi.org/10.1029/2010GL045489

Kirwan, M. L., & Megonigal, J. P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*, *504*(7478), 53–60. https://doi.org/10.1038/nature12856

Kirwan, M. L., & Mudd, S. M. (2012). Response of salt-marsh carbon accumulation to climate change. *Nature*, *489*, 550. https://doi.org/10.1038/nature11440

Kirwan, M. L., & Murray, A. B. (2007). A coupled geomorphic and ecological model of tidal marsh evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(15), 6118–6122. https://doi.org/10.1073/pnas.0700958104

Kirwan, M. L., & Murray, A. B. (2008). Ecological and morphological response of brackish tidal marshland to the next century of sea level rise: Westham Island, British Columbia. *Global and Planetary Change*, *60*(3–4), 471–486. https://doi.org/10.1016/j.gloplacha.2007.05.005

Kirwan, M. L., Temmerman, S., Skeehan, E. E., Guntenspergen, G. R., & Fagherazzi, S. (2016). Overestimation of marsh vulnerability to sea level rise. *Nature Climate Change*, *6*(3), 253–260. https://doi.org/10.1038/nclimate2909

Krauss, K. W., Cormier, N., Osland, M. J., Kirwan, M. L., Stagg, C. L., Nestlerode, J. A., et al. (2017). Created mangrove wetlands store belowground carbon and surface elevation change enables them to adjust to sea-level rise. *Scientific Reports*, *7*(1), 1030. https://doi.org/10.1038/s41598-017-01224-2

Krauss, K. W., Demopoulos, A. W. J., Cormier, N., From, A. S., McClain-Counts, J. P., & Lewis, R. R. (2018). Ghost forests of Marco Island: Mangrove mortality driven by belowground soil structural shifts during tidal hydrologic alteration. *Estuarine, Coastal and Shelf Science*, *212*, 51–62. https://doi.org/10.1016/j.ecss.2018.06.026

Krauss, K. W., Lovelock, C. E., McKee, K. L., López-Hoffman, L., Ewe, S. M. L., & Sousa, W. P. (2008). Environmental drivers in mangrove establishment and early development: A review. *Aquatic Botany*, *89*(2), 105–127. https://doi.org/10.1016/j.aquabot.2007.12.014

Kroeger, K. D., Crooks, S., Moseman-Valtierra, S., & Tang, J. (2017). Restoring tides to reduce methane emissions in impounded wetlands: A new and potent blue carbon climate change intervention. *Scientific Reports*, *7*(1), 11914. https://doi.org/10.1038/s41598-017-12138-4

Kusumaningtyas, M. A., Hutahaean, A. A., Fischer, H. W., Pérez-Mayo, M., Ransby, D., & Jennerjahn, T. C. (2019). Variability in the organic carbon stocks, sources, and accumulation rates of Indonesian mangrove ecosystems. *Estuarine, Coastal and Shelf Science*, *218*, 310–323. https://doi.org/10.1016/j.ecss.2018.12.007

Lamont, K., Saintilan, N., Kelleway, J. J., Mazumder, D., & Zawadzki, A. (2020). Thirty-year repeat measures of mangrove above- and below-ground biomass reveals unexpectedly high carbon sequestration. *Ecosystems*, *23*(2), 370–382. https://doi.org/10.1007/s10021-019-00408-3

Lentz, E. E., Thieler, E. R., Plant, N. G., Stippa, S. R., Horton, R. M., & Gesch, D. B. (2016). Evaluation of dynamic coastal response to sea-level rise modifies inundation likelihood. *Nature Climate Change*, *6*(7), 696–700. https://doi.org/10.1038/nclimate2957

Leonardi, N., Ganju, N. K., & Fagherazzi, S. (2016). A linear relationship between wave power and erosion determines salt-marsh resilience to violent storms and hurricanes. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(1), 64–68. https://doi.org/10.1073/pnas.1510095112

Liu, Y., Parolari, A. J., Kumar, M., Huang, C.-W., Katul, G. G., & Porporato, A. (2017). Increasing atmospheric humidity and CO_2 concentration alleviate forest mortality risk. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(37), 9918–9923. https://doi.org/10.1073/pnas.1704811114

Lovelock, C. E., Adame, M. F., Bennion, V., Hayes, M., O'Mara, J., Reef, R., & Santini, N. S. (2014). Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of South East Queensland, Australia. *Estuaries and Coasts*, *37*(3), 763–771. https://doi.org/10.1007/s12237-013-9702-4

Lovelock, C. E., Atwood, T., Baldock, J., Duarte, C. M., Hickey, S., Lavery, P. S., et al. (2017). Assessing the risk of carbon dioxide emissions from blue carbon ecosystems. *Frontiers in Ecology and the Environment*, *15*(5), 257–265. https://doi.org/10.1002/fee.1491

Lovelock, C. E., Cahoon, D. R., Friess, D. A., Guntenspergen, G. R., Krauss, K. W., Reef, R., et al. (2015). The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature*, *526*(7574), 559–563. https://doi.org/10.1038/nature15538

Lovelock, C. E., & Reef, R. (2020). Variable impacts of climate change on blue carbon. *One Earth*, *3*(2), 195–211. https://doi.org/10.1016/j.oneear.2020.07.010

Lovelock, C. E., Ruess, R. W., & Feller, I. C. (2011). CO_2 efflux from cleared mangrove peat. *PLoS One*, *6*(6), e21279. https://doi.org/10.1371/journal.pone.0021279

Macreadie, P. I., Nielsen, D. A., Kelleway, J. J., Atwood, T. B., Seymour, J. R., Petrou, K., et al. (2017). Can we manage coastal ecosystems to sequester more blue carbon? *Frontiers in Ecology and the Environment*, *15*(4), 206–213. https://doi.org/10.1002/fee.1484

Macreadie, P. I., Ollivier, Q. R., Kelleway, J. J., Serrano, O., Carnell, P. E., Ewers Lewis, C. J., et al. (2017). Carbon sequestration by Australian tidal marshes. *Scientific Reports*, *7*(1), 44071. https://doi.org/10.1038/srep44071

McKee, K. L. (1993). Soil physicochemical patterns and mangrove species distribution-reciprocal effects? *Journal of Ecology*, *81*(3), 477–487. https://doi.org/10.2307/2261526

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

McKee, K. L. (1996). Growth and physiological responses of Neotropical mangrove seedlings to root zone hypoxia. *Tree Physiology*, *16*(11–12), 883–889. https://doi.org/10.1093/treephys/16.11-12.883

McKee, K. L., & Rooth, J. E. (2008). Where temperate meets tropical: Multi-factorial effects of elevated CO_2, nitrogen enrichment, and competition on a mangrove-salt marsh community. *Global Change Biology*, *14*(5), 971–984. https://doi.org/10.1111/j.1365-2486.2008.01547.x

Morris, J. T., Barber, D. C., Callaway, J. C., Chambers, R., Hagen, S. C., Hopkinson, C. S., et al. (2016). Contributions of organic and inorganic matter to sediment volume and accretion in tidal wetlands at steady state. *Earth's Future*, *4*(4), 110–121. https://doi.org/10.1002/2015ef000334

Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B., & Cahoon, D. R. (2002). Responses of coastal wetlands to rising sea level. *Ecology*, *83*(10), 2869–2877. https://doi.org/10.1890/0012-9658(2002)083[2869:ROCWTR]2.0.CO;2

Mossman, H. L., Davy, A. J., & Grant, A. (2012). Does managed coastal realignment create saltmarshes with 'equivalent biological characteristics' to natural reference sites? *Journal of Applied Ecology*, *49*(6), 1446–1456. https://doi.org/10.1111/j.1365-2664.2012.02198.x

Negandhi, K., Edwards, G., Kelleway, J. J., Howard, D., Safari, D., & Saintilan, N. (2019). Blue carbon potential of coastal wetland restoration varies with inundation and rainfall. *Scientific Reports*, *9*(1), 4368. https://doi.org/10.1038/s41598-019-40763-8

Negrin, V., Villalobos, A., González Trilla, G., Botté, S., & Marcovecchio, J. (2012). Above and belowground biomass and nutrient pools of Spartina alterniflora (smooth cordgrass) in a South American salt marsh. *Chemistry and Ecology*, *28*(4). https://doi.org/10.1080/02757540.2012.666529

Oppenheimer, M., Glavovic, B. C., Hinkel, J., van de Wal, R., Magnan, A. K., Abd-Elgawad, A., et al. (2019). Sea level rise and implications for low-lying islands, coasts and communities. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, et al. (Eds.), *IPCC special report on the ocean and cryosphere in a changing climate*.

Ouyang, X., & Lee, S. Y. (2014). Updated estimates of carbon accumulation rates in coastal marsh sediments. *Biogeosciences*, *11*(18), 5057–5071. https://doi.org/10.5194/bg-11-5057-2014

Ouyang, X., Lee, S. Y., & Connolly, R. M. (2017). The role of root decomposition in global mangrove and saltmarsh carbon budgets. *Earth-Science Reviews*, *166*, 53–63. https://doi.org/10.1016/j.earscirev.2017.01.004

Owers, C. J., Rogers, K., & Woodroffe, C. D. (2018). Spatial variation of above-ground carbon storage in temperate coastal wetlands. *Estuarine, Coastal and Shelf Science*, *210*, 55–67. https://doi.org/10.1016/j.ecss.2018.06.002

Passeri, D. L., Hagen, S. C., Medeiros, S. C., Bilskie, M. V., Alizad, K., & Wang, D. (2015). The dynamic effects of sea level rise on low-gradient coastal landscapes: A review. *Earth's Future*, *3*(6), 159–181. https://doi.org/10.1002/2015EF000298

Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., et al. (2012). Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS One*, *7*(9), e43542. https://doi.org/10.1371/journal.pone.0043542

Pérez, A., Libardoni, B. G., & Sanders, C. J. (2018). Factors influencing organic carbon accumulation in mangrove ecosystems. *Biology Letters*, *14*(10), 20180237. https://doi.org/10.1098/rsbl.2018.0237

Ratliff, K. M., Braswell, A. E., & Marani, M. (2015). Spatial response of coastal marshes to increased atmospheric CO_2. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(51), 15580–15584. https://doi.org/10.1073/pnas.1516286112

Ravens, T. M., Thomas, R. C., Roberts, K. A., & Santschi, P. H. (2009). Causes of salt marsh erosion in Galveston Bay, Texas. *Journal of Coastal Research*, *2009*, 265–272. https://doi.org/10.2112/07-0942.1

Reef, R., Winter, K., Morales, J., Adame, M. F., Reef, D. L., & Lovelock, C. E. (2015). The effect of atmospheric carbon dioxide concentrations on the performance of the mangrove Avicennia germinans over a range of salinities. *Physiologia Plantarum*, *154*(3), 358–368. https://doi.org/10.1111/ppl.12289

Riccardi, G. (2000). A cell model for hydrological-hydraulic modeling. *Journal of Environmental Hydrology*, *8*.

Rodríguez, J. F., & Howe, A. (2013). Estuarine wetland ecohydraulics and migratory shorebird habitat restoration. In I. Maddock, A. Harby, P. Kemp, & P. Wood (Eds.), *Ecohydraulics: An integrated approach* (pp. 375–394). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118526576.ch22

Rodríguez, J. F., Saco, P. M., Sandi, S., Saintilan, N., & Riccardi, G. (2017). Potential increase in coastal wetland vulnerability to sea-level rise suggested by considering hydrodynamic attenuation effects. *Nature Communications*, *8*, 16094. https://doi.org/10.1038/ncomms16094

Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., et al. (2019). Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. *Nature*, *567*(7746), 91–95. https://doi.org/10.1038/s41586-019-0951-7

Rogers, K., & Krauss, K. W. (2019). Moving from generalisations to specificity about mangrove-saltmarsh dynamics. *Wetlands*, *39*(6), 1155–1178. https://doi.org/10.1007/s13157-018-1067-9

Rogers, K., Macreadie, P. I., Kelleway, J. J., & Saintilan, N. (2019). Blue carbon in coastal landscapes: A spatial framework for assessment of stocks and additionality. *Sustainability Science*, *14*(2), 453–467. https://doi.org/10.1007/s11625-018-0575-0

Rogers, K., Saintilan, N., Howe, A. J., & Rodríguez, J. F. (2013). Sedimentation, elevation and marsh evolution in a southeastern Australian estuary during changing climatic conditions. *Estuarine, Coastal and Shelf Science*, *133*, 172–181. https://doi.org/10.1016/j.ecss.2013.08.025

Roner, M., D'Alpaos, A., Ghinassi, M., Marani, M., Silvestri, S., Franceschinis, E., & Realdon, N. (2016). Spatial variation of salt-marsh organic and inorganic deposition and organic carbon accumulation: Inferences from the Venice lagoon, Italy. *Advances in Water Resources*, *93*, 276–287. https://doi.org/10.1016/j.advwatres.2015.11.011

Saco, P. M., & Rodríguez, J. F. (2013). 2.14 Modeling ecogeomorphic systems. In J. F. Shroder (Ed.), *Treatise on geomorphology* (pp. 201–220). Academic Press. https://doi.org/10.1016/b978-0-12-374739-6.00038-5

Saintilan, N. (1997). Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. *Marine and Freshwater Research*, *48*(2), 147–152. https://doi.org/10.1071/mf96079

Saintilan, N. (1998). Above- and below-ground biomass of mangroves in a sub-tropical estuary. *Marine and Freshwater Research*, *48*(7), 601–604. https://doi.org/10.1071/MF97009

Saintilan, N., Khan, N. S., Ashe, E., Kelleway, J. J., Rogers, K., Woodroffe, C. D., & Horton, B. P. (2020). Thresholds of mangrove survival under rapid sea level rise. *Science*, *368*(6495), 1118–1121. https://doi.org/10.1126/science.aba2656

Saintilan, N., Rogers, K., Mazumder, D., & Woodroffe, C. (2013). Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. *Estuarine, Coastal and Shelf Science*, *128*(Supplement C), 84–92. https://doi.org/10.1016/j.ecss.2013.05.010

Saintilan, N., Rogers, K., & McKee, K. (2009). Salt marsh-mangrove interactions in Australasia and the Americas. In G. M. E. Perillo, E. Wolanski, D. R. Cahoon, & M. M. Brinson (Eds.), *Coastal wetlands—An integrated ecosystem Approach*. Elsevier Science.

Saintilan, N., & Williams, R. J. (1999). Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography*, *8*(2), 117–124. https://doi.org/10.1046/j.1365-2699.1999.00133.x

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., & Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*, *20*(1), 147–157. https://doi.org/10.1111/gcb.12341

Sandi, S. G., Rodríguez, J. F., Saintilan, N., Riccardi, G., & Saco, P. M. (2018). Rising tides, rising gates: The complex ecogeomorphic response of coastal wetlands to sea-level rise and human interventions. *Advances in Water Resources*, *114*, 135–148. https://doi.org/10.1016/j.advwatres.2018.02.006

Schuerch, M., Spencer, T., Temmerman, S., Kirwan, M. L., Wolff, C., Lincke, D., et al. (2018). Future response of global coastal wetlands to sea-level rise. *Nature*, *561*(7722), 231–234. https://doi.org/10.1038/s41586-018-0476-5

Serrano, O., Lovelock, C. E., Atwood, B. T., Macreadie, P. I., Canto, R., Phinn, S., et al. (2019). Australian vegetated coastal ecosystems as global hotspots for climate change mitigation. *Nature Communications*, *10*(1), 4313. https://doi.org/10.1038/s41467-019-12176-8

Sheehan, L., Sherwood, E. T., Moyer, R. P., Radabaugh, K. R., & Simpson, S. (2019). Blue carbon: An additional driver for restoring and preserving ecological services of coastal wetlands in Tampa Bay (Florida, USA). *Wetlands*, *39*(6), 1317–1328. https://doi.org/10.1007/s13157-019-01137-y

Thorhaug, A. L., Poulos, H. M., López-Portillo, J., Barr, J., Lara-Domínguez, A. L., Ku, T. C., & Berlyn, G. P. (2019). Gulf of Mexico estuarine blue carbon stock, extent and flux: Mangroves, marshes, and seagrasses: A North American hotspot. *Science of the Total Environment*, *653*, 1253–1261. https://doi.org/10.1016/j.scitotenv.2018.10.011

Törnqvist, T. E., Jankowski, K. L., Li, Y.-X., & González, J. L. (2020). Tipping points of Mississippi Delta marshes due to accelerated sea-level rise. *Science Advances*, *6*(21), eaaz5512. https://doi.org/10.1126/sciadv.aaz5512

van Maanen, B., Coco, G., & Bryan, K. R. (2015). On the ecogeomorphological feedbacks that control tidal channel network evolution in a sandy mangrove setting. *Proceedings of the Royal Society A: Mathematical, Physical & Engineering Sciences*, *471*(2180). https://doi.org/10.1098/rspa.2015.0115

Wang, F., Lu, X., Sanders, C. J., & Tang, J. (2019). Tidal wetland resilience to sea level rise increases their carbon sequestration capacity in United States. *Nature Communications*, *10*(1), 5434. https://doi.org/10.1038/s41467-019-13294-z

Ward, R. D., Friess, D. A., Day, R. H., & MacKenzie, R. A. (2016). Impacts of climate change on mangrove ecosystems: A region by region overview. *Ecosystem Health and Sustainability*, *2*(4), e01211. https://doi.org/10.1002/ehs2.1211

Watanabe, K., Seike, K., Kajihara, R., Montani, S., & Kuwae, T. (2019). Relative sea-level change regulates organic carbon accumulation in coastal habitats. *Global Change Biology*, *25*(3), 1063–1077. https://doi.org/10.1111/gcb.14558

Williams, R. J., Watford, F. A., & Balashov, V. (2000). *Kooragang wetland rehabilitation project: History of changes to estuarine wetlands of the lower Hunter River*. Cronulla.

Woodroffe, C. D., Rogers, K., McKee, K. L., Lovelock, C. E., Mendelssohn, I. A., & Saintilan, N. (2016). Mangrove sedimentation and response to relative sea-level rise. *Annual Review of Marine Science*, *8*, 243–266. https://doi.org/10.1146/annurev-marine-122414-034025

Youssef, T., & Saenger, P. (1998). Photosynthetic gas exchange and accumulation of phytotoxins in mangrove seedlings in response to soil physico-chemical characteristics associated with waterlogging. *Tree Physiology*, *18*(5), 317–324. https://doi.org/10.1093/treephys/18.5.317

23284277, 2021, 9, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2020EF001901 by Macquarie University, Wiley Online Library on [25/06/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Cambridge Prisms: Coastal Futures

www.cambridge.org/cft

The present, past and future of blue carbon

Kerrylee Rogers[1], Jeffrey J. Kelleway[1] and Neil Saintilan[2]

[1]School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW 2522, Australia and [2]School of Natural Sciences, Macquarie University, North Ryde, NSW 2109, Australia

Review

Cite this article: Rogers K, Kelleway JJ and Saintilan N (2023). The present, past and future of blue carbon. *Cambridge Prisms: Coastal Futures*, **1**, e30, 1–18
https://doi.org/10.1017/cft.2023.17

Received: 23 December 2022
Revised: 09 May 2023
Accepted: 25 May 2023

Keywords:
Blue carbon; Climate adaptation; Coastal wetlands; Sea-level rise; Coastal habitats

Corresponding author:
Kerrylee Rogers;
Email: kerrylee@uow.edu.au

Abstract

Blue carbon is identified as a natural climate solution as it provides multiple ecosystem services, including climate mitigation, adaptation, and other co-benefits. There remain ongoing challenges for blue carbon as a natural climate solution, particularly as blue carbon ecosystems are at risk from climate change. Concepts of uniformitarianism were applied to consider how the present and past behaviour of blue carbon ecosystems can inform decision-makers of blue carbon risks. Climate change may increase the capture and storage of blue carbon in the short to medium term; this is largely due to negative feedbacks between elevated atmospheric carbon dioxide and temperature, and supplemented by natural processes of sediment supply and accumulation. Opportunities for retreat and increasing carbon storage as sea levels rise are likely to be greater where sea level has a longer history of relative stability, largely in the Southern Hemisphere. Landward retreat will be crucial where millennia of sea-level rise have limited the capacity for in situ blue carbon additionality; this may be thwarted by highly developed coastal zones and coastal squeeze effects. Negative feedbacks may fail under higher emissions, greater warming and rates of sea-level rise exceeding ~5–7 mm $yr.^{-1}$; this tipping point may be surpassed within the next century under a high emissions scenario. Retreat of blue carbon ecosystems to higher elevations where they are afforded protection from the effects of sea-level rise will be critical for blue carbon additionality. Carbon markets are prepared to incentivise restoration of blue carbon ecosystems as they adapt to climate change; however, knowledge gaps remain, particularly regarding the behaviour of blue carbon ecosystems in the global south. Given the momentum in blue carbon research, scientists and practitioners are well placed to continue addressing blue carbon risks.

Impact statement

The role of coastal ecosystems in sequestering atmospheric carbon has been demonstrated and efforts are underway to leverage this service for climate change mitigation. Focussing largely on mangroves and saltmarshes, this paper applies concepts of uniformitarianism to consider how the present behaviour of blue carbon ecosystems (BCEs), and their response to varying sea level and climate change in the past, provides knowledge of BCE futures. There is evidence BCEs are being modified by climate change, and losses are compounded by ongoing clearance and degradation. Consequently, atmospheric warming, sea-level rise and human modifications have important implications for greenhouse gas fluxes from BCEs. Observations of the response of BCEs to sea-level rise indicate some capacity to adapt by accumulating mineral and organic material and increasing substrate elevations. Contributions of organic matter to substrates as sea level rises, coupled with landward retreat of BCEs to maintain their intertidal position, bolsters capacity to sequester atmospheric carbon within substrates and biomass. However, evidence of the response of mangroves and saltmarshes to sea-level rise over the Holocene indicate a threshold for adaptation that is exceeded when sea-level rises at ~5–7 mm $yr.^{-1}$. This rate of sea-level rise is anticipated to be surpassed by the end of the 21st century unless deep cuts to atmospheric carbon concentrations occur rapidly. Accordingly, the fate of BCEs remains uncertain. However, it is probable mangrove forests and saltmarshes high in the tidal frame will transition towards lower tidal positions as sea level rises and may survive for some time, offering some confidence when trading carbon with a 25-year permanence timeframe. Landward retreat will be critical for blue carbon additionality, and this will require concerted management to minimise coastal squeeze and preserve BCE services. This uncertainty should be accommodated when considering the permanence of blue carbon in financial markets.

© The Author(s), 2023. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (http://creativecommons.org/licenses/by/4.0), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

Introduction

Blue carbon is a collective term referring to the carbon associated with marine and coastal ecosystems, and includes all fluxes and stores that are biologically driven (Bindoff et al., 2019). Similar to carbon sequestered in terrestrial forests, blue carbon has piqued the interest of practitioners seeking to mitigate climate change by enhancing carbon storage within natural

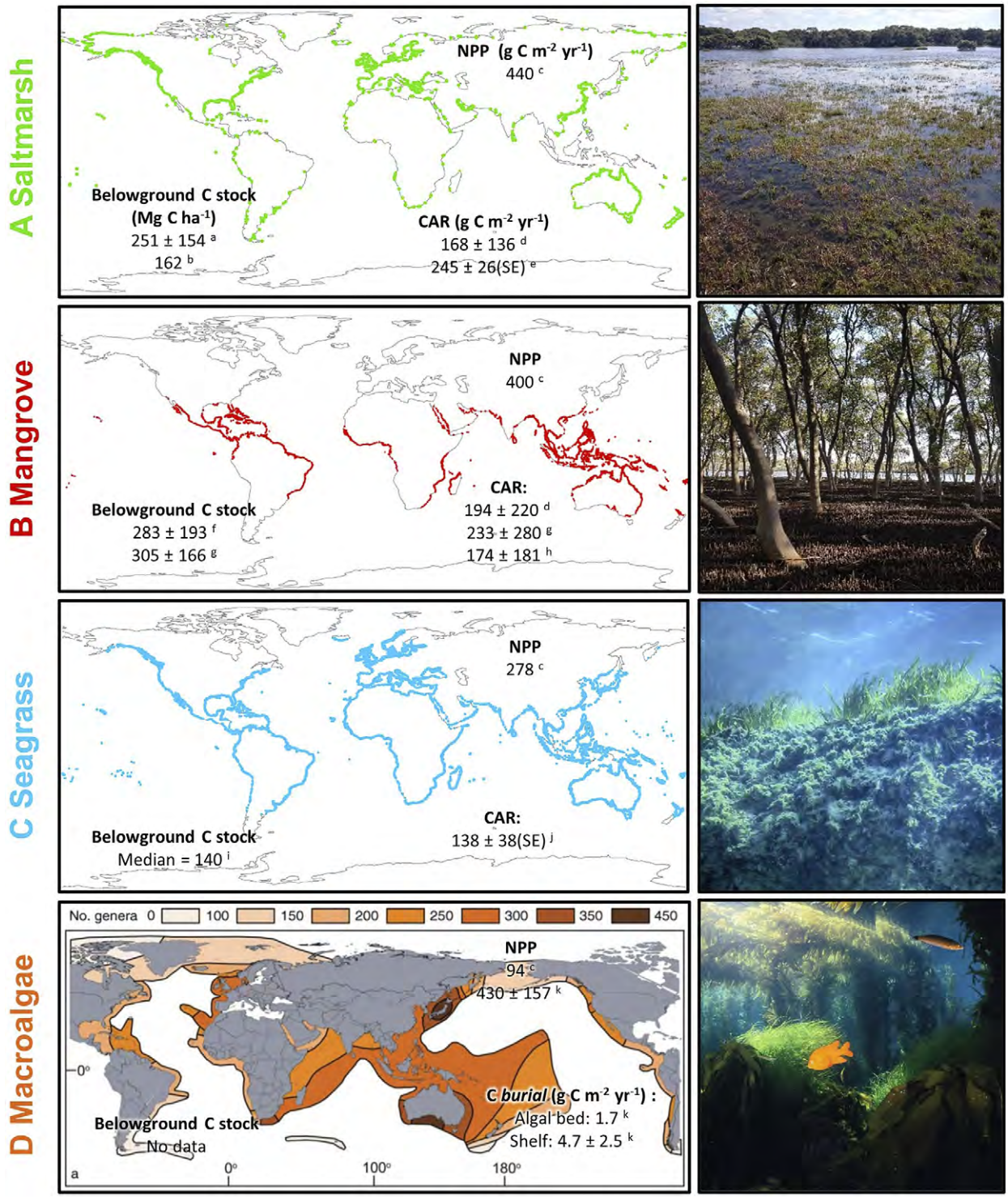


Figure 1. Global mapped distribution and existing estimates of carbon cycling parameters of (A) saltmarsh and (B) mangrove; (C) modelled distribution of seagrass; and (D) genus richness of benthic marine macroalgae. All values are global mean values ±1 standard deviation (where available) unless otherwise specified. Belowground carbon stocks are estimated to 1 m depth. CAR = (surface) carbon accumulation rate; NPP = net ecosystem primary productivity; SE = 1 standard error. Note that for macroalgae, CAR is replaced by estimates of carbon burial in situ (i.e. in algal beds) and exported particulate organic carbon buried in shelf sediments. Map data sources: saltmarsh (Mcowen et al., 2017); mangrove (Bunting et al., 2018); seagrass (Jayathilake and Costello, 2018); macroalgae (Kerswell, 2006). Carbon data sources: a (Rogers et al., 2019a); b (Pendleton et al. 2012a); c (Duarte and Cebrian, 1996); d (Wang et al., 2021); e (Ouyang and Lee, 2014); f (Atwood et al., 2017); g; h (Alongi, 2012); i; j (McLeod et al., 2011); k (Krause-Jensen and Duarte, 2016).

ecosystems and improving the provision of ecosystem services (Macreadie et al., 2021). This interest is based on the high carbon storage potential of many blue carbon ecosystems (BCEs), a potential that is reported to be much higher on a unit area basis than other ecosystem-based climate solutions (Donato et al., 2011; Pendleton et al., 2012; Duarte et al., 2013). BCEs are typically vegetated with mangroves, saltmarshes (also termed tidal marshes) and seagrasses, and to a lesser extent macroalgae, cyanobacteria and supratidal

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

forests (Duarte et al., 2013; Raven, 2018; Bindoff et al., 2019; Lovelock and Duarte, 2019) (Figure 1). Carbon is drawn from the atmosphere via photosynthesis and stored within living biomass at a concentration of 40–50% of the mass, a value that is reasonably consistent among plants (Ma et al., 2018). Blue carbon is partitioned into above- and below-ground biomass and the soil carbon pool. Above-ground biomass is typically estimated from allometric equations, initially derived from destructive measurements that relate vegetation structure to mass (Thursby et al., 2002; Komiyama et al., 2008; Radabaugh et al., 2017), or by applying remote sensing techniques to extrapolate spatial relationships (Pham et al., 2019; Sani et al., 2019). The below-ground component is somewhat more difficult to quantify as substrates contain both living biomass and dead organic material that has accumulated over decades to thousands of years, as evident from radiocarbon dating of BCEs (Horton et al., 2018; Saintilan et al., 2020; Sefton et al., 2021).

The enhanced capacity for storage is dependent upon rates of carbon addition exceeding loss of carbon via the decomposition of organic material, and there is increasing agreement that this should also exceed in situ carbonate production (Saderne et al., 2019). High net primary production from in situ vegetation underpins the supply of organic matter to substrates, mostly from root material (Saintilan et al., 2013; Xiong et al., 2018). However, organic matter transported on tides can also become trapped and sequestered into substrates, and there is an increasing need to discriminate the varying role of autochthonous and allochthonous sources (Saintilan et al., 2013; Canuel and Hardison, 2016; Van de Broek et al., 2018; Macreadie et al., 2019). Periodic inundation by saline tidal waters creates anaerobic conditions in saturated substrates that supress microbial activity and slow the decomposition of sequestered organic material (Duarte et al., 2013; Spivak et al., 2019). Addition of mineral sediments supplied by tides serves to trap sequestered organic material (Spivak et al., 2019) and saline substrates hamper methanogenic processes (Poffenbarger et al., 2011). While greenhouse gas emissions are not fully supressed (Rosentreter et al., 2018), the general outcome is physicochemical conditions that favour slow decomposition of organic material, long-term preservation of a portion of fixed carbon within substrates, and limited release of powerful greenhouse gases (e.g. methane and nitrous oxide) to the atmosphere (McKee et al., 2007; McLeod et al., 2011; Kroeger et al., 2017). Storage may be further enhanced when coastal processes operate to ensure that space within substrates for carbon storage continues to be available, and this appears to be strongly influenced by rates of sediment supply, sedimentation, and coastal evolution in the context of changing sea levels (Rogers et al., 2019a). Together these conditions mean that BCEs can store orders of magnitude more carbon within their substrates than other terrestrial ecosystems, estimated to be in the order of 0.4–6.5 Pg. C in the upper 1 m of saltmarsh substrates globally, 9.4–10.4 Pg. C for mangrove forest substrates and 4.2–8.4 Pg. C for seagrass substrates (Duarte et al., 2013).

Estimates of carbon storage in BCEs are typically determined based on their current distribution. At the coarsest level, a central measure (e.g. mean, median) of carbon concentration is multiplied by BCE extent to estimate carbon storage in various components (above- and below-ground biomass, soil carbon pool) (Howard et al., 2014). As can be seen in Figure 1 such projections to a global scale will be subject to large uncertainties associated with the high variability, across multiple spatial scales, in estimates within each ecosystem type; spatial biases in data availability also influence confidence in global projections.

In spite of this increasing recognition of spatial and temporal variation in carbon storage, it is probable that additional soil organic carbon originating from BCEs is preserved within coastal floodplains and on continental shelfs where conditions are now no longer favourable for BCEs, but where long-term preservation may have occurred over millennia as coastal landscapes evolved (Hanebuth et al., 2000; Grindrod, 2002; Rogers et al., 2019b). Additionally, there is also an imprint of direct human impacts on BCEs, with losses largely due to land cover change and gains largely due to restoration activities leading to a net decline in tidal wetland extent (inclusive of tidal flats, mangrove forests and tidal marshes) of ~4,000 km^2 between 1999 and 2019 (Murray et al., 2022). There is evidence that this rate of loss is diminishing (Friess et al., 2020; Campbell et al., 2022) and substantial gains to tidal wetland extent, in the order of 9,700 km^2, have been related to the success of restoration activities and natural expansion (Friess et al., 2019; Murray et al., 2022). Accordingly, the current distribution of BCEs indicates where current storage and additionality occurs but does not indicate storage that occurred prior to changes in land cover at millennia timescales or over the record of Earth observations. This has important implications for the future of blue carbon, and it is probable that the geographic distribution of BCEs will continue to change as sea level rises, coasts evolve, and humans living in the coastal zone adapt to a new configuration of the coast and BCE distribution.

To characterise the future of blue carbon as a natural climate solution, we apply concepts of uniformitarianism to consider how the contemporary distribution and behaviour of blue carbon can inform our understanding of the long-term evolution of coastal carbon storage. In this regard, we consider processes that influence blue carbon over the observational record (i.e. the present) are the same as those that have operated for millennia (i.e. the past), and, by extrapolation, consider blue carbon futures. We specifically consider the evidence preserved in stratigraphic records of the evolution of BCEs and present the case that blue carbon storage is related to coastal evolution and influenced by sediment supply and Holocene sea-level change. We also recognise that coastal evolution and the influence of humans on coastal landscapes means that the response of BCEs in the past is not a direct analogue for their future adaptation to anticipated sea-level rise and climate change (Woodroffe and Murray-Wallace, 2012). Nevertheless, present-day coastal landscapes are an archive of information that can be used to parameterise models projecting the response of BCEs to environmental change; thereby providing the critical information needed to inform coastal zone planning and decision-making, improve the resilience of BCEs and ensure their long-term application as a nature-based solution that contributes to climate mitigation efforts.

The PRESENT: Blue carbon in coastal landscapes

Mangroves and saltmarsh typically occupy the upper half of the intertidal zone, with mangrove forests dominating intertidal shorelines of the tropics and saltmarshes dominating intertidal shorelines of temperate zones (Figure 2). There is considerable overlap in the latitudinal distribution of mangroves and saltmarshes (Figure 1), with mangroves generally limited to ocean temperatures that exceed 20 °C during the coldest month (West, 1956; Quisthoudt et al., 2012; Osland et al., 2016), while saltmarsh distribution is influenced by substrate salinity (Bertness et al.,

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

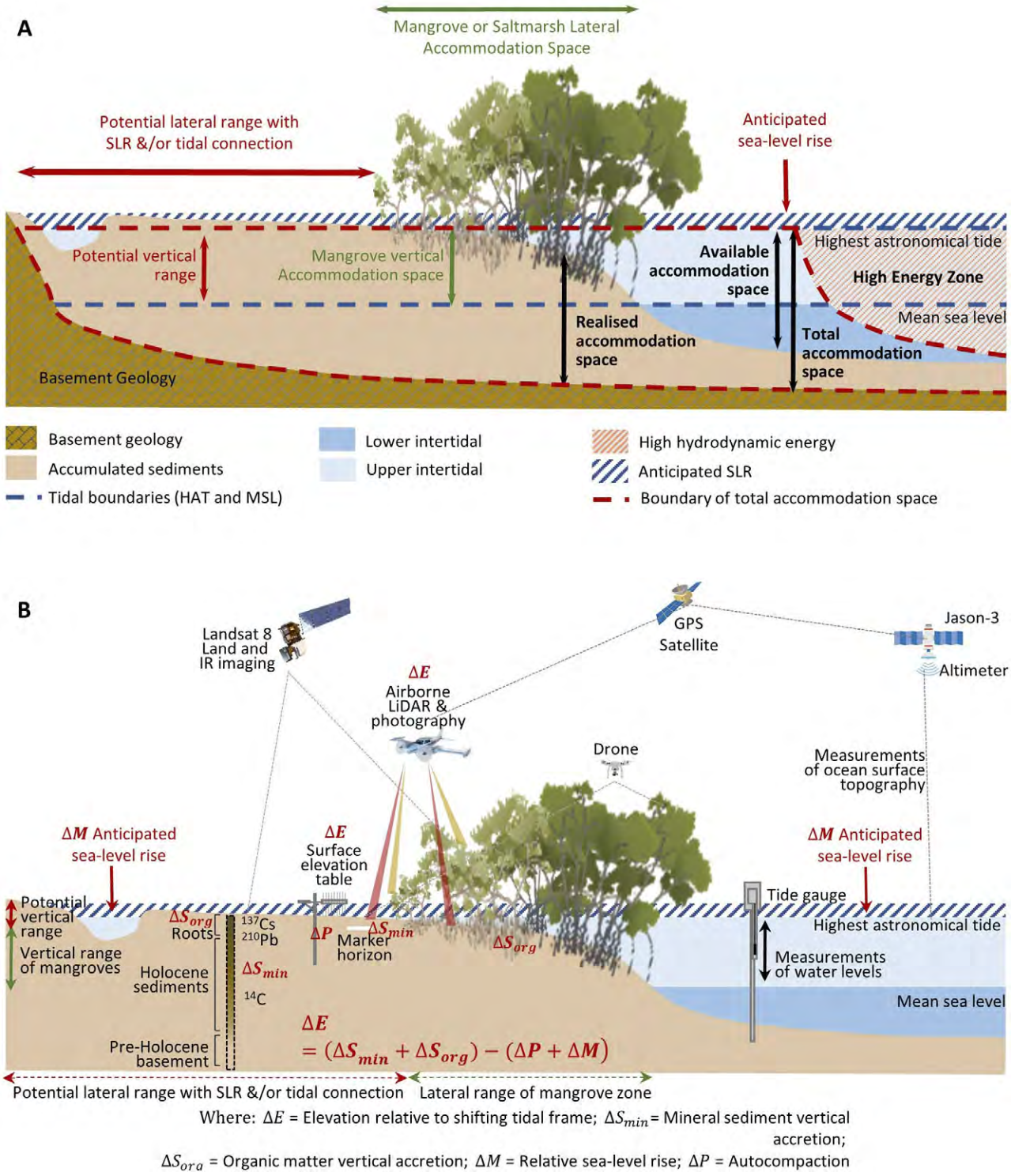


Figure 2. Profiles of BCE landscapes indicating (A) accommodation space, delimited by the highest astronomical tide, basement or bedrock geology, and hydrodynamic conditions favourable for mineral and organic matter accumulation (modified from Rogers (2021)); and (B) the range of techniques that can be used to observe and measure changes in substrate volume, mineral and organic matter accumulation, and position within the tidal frame, with specific focus on changing tidal position with sea-level rise, as per Allen (2000).

1992; Silvestri et al., 2005). Where salinity is very high and salts concentrate hypersaline flats/sandflats or sabkha predominate, often with cyanobacterial mats, and saltmarsh vegetation is sparse; in the tropics where rainfall is high, mangroves predominate in the upper half of the intertidal zone (Rogers and Woodroffe, 2014). Most seagrass species occupy fully inundated substrates (i.e. subtidal elevations) where water clarity is a significant control on productivity (Madsen et al., 2001). Where hydrodynamic conditions allow, a diversity of seagrass genera may also occupy the lower intertidal niche (i.e. below MSL) (Björk et al., 1999). Depth-constrained species of seagrass and macroalgae can accumulate organic material within substrates as they

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

adjust to changing water levels (e.g. *Zostera* spp., *Halophila* spp. and *Phyllospadix* spp.) (Koch, 2001; Madsen et al., 2001). While seagrass meadows may be an exceptional carbon source for sequestration elsewhere, their capacity for in situ blue carbon storage is largely limited to that stored within the living biomass and some detritus. Increased sequestration is therefore largely dependent upon an increase in the lateral extent of seagrass meadows (Greiner et al., 2013) and should be balanced against the additional CO_2 that is released by carbonate sediment production (Howard et al., 2018). While net ecosystem primary production may be high for macroalgae, with potential importance for the export of carbon to other environments, in situ burial of carbon is limited (Figure 1; Krause-Jensen and Duarte, 2016). For these reasons, this review focuses on mangrove and saltmarsh blue carbon futures.

Geomorphological settings occupied by BCEs are delimited to areas where low-energy intertidal substrates support the establishment and maintenance of salt-tolerant vegetation. Globally, deltas are hotspots for BCEs due to high rates of sediment supply promoting the development of broad intertidal environments where resource availability is high (Rovai et al., 2018; Worthington et al., 2020; Murray et al., 2022). Along tide-dominated coasts, favourable conditions may arise on the open coast where tidally borne sediments can accumulate, or within the intertidal zone of tide-dominated estuaries. Along wave-dominated coasts, barriers at estuary entrances dampen wave energy and terrigenous sediments supplied from catchments via distributaries contribute to intertidal development of fluvial deltas, and to a lesser extent marine sediment delivered by tides contribute to the development of flood-tide deltas that support BCEs. These fluvial and floodtide deltas associated with wave-dominated estuaries are also hotspots for blue carbon due to the development of low-gradient intertidal substrates (Kelleway et al., 2016a).

Global and continental scale analyses of above-ground biomass of mangroves and saltmarshes variably highlight the role of climatic factors that vary with latitude, proposing that optimal temperature and higher rainfall favours productivity and carbon addition to plants within BCEs (Kirwan and Mudd, 2012; Rovai et al., 2016; Sanders et al., 2016). For example, analyses of mangrove heights and biomass using the global shuttle radar topography mission altimetry dataset highlight the role of precipitation, temperature and cyclone frequency, explaining 74% of global trends in mangrove canopy height (Simard et al., 2019). Yet, these are also factors that modify substrate salinity and may promote decomposition of organic material (Chmura et al., 2003; Kirwan et al., 2014; Mueller et al., 2018). The outcome may be that once living standing stock reaches a threshold biomass, additions to the living biomass are offset by losses to the standing stock (Chmura et al., 2003).

Observations of mangrove above-ground biomass addition in forestry plots indicate that individual tree growth will asymptote at a threshold height and biomass addition is largely limited to small increments to woody components (i.e. thickening of trunks and stems) (Jin-Eong et al., 1995; Osland et al., 2020; Alongi, 2020b). It is this asymptotic nature of above-ground biomass addition over time that has led to many forestry-based carbon offsetting schemes having a minimum commitment period of at least 20 years before harvesting can occur (Galik et al., 2022) and this has translated into voluntary methods for blue carbon offsetting (Lovelock et al., 2022a). This aligns with the period over which biomass addition accelerates as plants establish and the rate of carbon sequestration is high. When mangrove forests and saltmarshes have reached their threshold capacity for standing above-ground biomass, then increases in the standing living stock are largely achieved by lateral increases in extent as increases in plant density in mature forests will be resource limited. Increases in below-ground biomass are presumed to be limited by vertical space within substrates for net biomass additionality and addition of biomass will increasingly be offset by decomposition of below-ground biomass as substrates asymptote towards higher elevations; that is unless relative sea-level rise creates more vertical space for below-ground storage. Critically, lateral increases in extent are constrained by the availability of land where conditions are favourable within the intertidal and supratidal zone. In addition, although intense cyclones and storms are reported to have a return interval of approximately 20 years (Elsner et al., 2006), aligning with the commitment period for restoration projects before harvesting can occur (Galik et al., 2022), the feasibility of restoration projects in regions with a propensity for cyclone activity may decrease should projected increases in the frequency and intensity of major storms eventuate (IPCC, 2021).

Partitioning of mangrove biomass between above-ground and below-ground differs from terrestrial forests in that a relatively high proportion is allocated to below-ground root systems (Saintilan, 1997; Lichacz et al., 2009), a possible adaptation to saline conditions (Ball, 1988). However, below-ground biomass is somewhat difficult to determine because decomposition is limited by saline and anaerobic conditions of tidally inundated substrates, and differentiating living and dead components of below-ground biomass is difficult (Adame et al., 2017). The proportion of mass allocated to above and below-ground components is influenced by environmental conditions, most notable is variation arising from soil water salinity, observed in both laboratory (Ball, 1988; Ball, 2002) and field studies (Saintilan, 1997), but also soil water nutrient conditions (Darby and Turner, 2008) and atmospheric CO_2 concentrations (Langley et al., 2009). Observations of below-ground root addition have been undertaken using root ingrowth bags and 'marsh organ' experiments, indicating rapid root development (Muhammad-Nor et al., 2019; Kihara et al., 2022), an observation supported by repeat measures of root biomass (Lamont et al., 2020).

While the addition of carbon to living biomass makes an important contribution to carbon drawdown from the atmosphere, the substrates of BCEs are typically the largest carbon pool within BCEs with soil organic carbon to a depth of 1 m estimated to comprise 77% of the total global mangrove stock and 95% of the total global saltmarsh stock (Alongi, 2020a). Constraining controls on global below-ground carbon storage has been more elusive, and variably related to edaphic conditions associated with climate and substrate salinity (Chmura et al., 2003; Kirwan and Mudd, 2012; Sanders et al., 2016; Rovai et al., 2018; Sanderman et al., 2018). It took some time for the role of sea-level rise to be linked to soil organic carbon accumulation (Wang et al., 2019; Rogers et al., 2019a); this is surprising given the geographic position of intertidal BCEs near mean sea level and the well-established influence of sea-level rise on coastal geomorphology. Increasing mangrove extent with relative sea-level rise and warmer temperatures over the past few decades has been observed and is particularly notable in Australia, Brazil, the Gulf and Atlantic US Coastline, Mexico, and South Africa where mangroves have expanded landward to higher elevations and/or to more poleward positions (Saintilan et al., 2014; Godoy and de Lacerda, 2015; Ximenes et al., 2016; Osland et al., 2017). Increases in soil organic carbon storage have occurred in consort (Kelleway et al., 2016b; Simpson et al., 2019), implying that links between soil organic carbon storage and sea level are partly mediated by vegetation change.

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

Increases in organic carbon accumulation have been measured in wetlands subject to increased rates of sea-level rise in southwest Florida (Breithaupt et al., 2020), and eastern Australia (Marx et al., 2020). Extreme rapid subsidence beneath a coastal wetland in Australia, in the order of 1 m, has served as a natural laboratory for observing the influence of relative sea-level rise on carbon storage and addition to mangrove and saltmarsh ecosystems (Rogers et al., 2019a). Here soil organic carbon addition accelerated following an increase in relative sea level. Following subsidence, conditions in the former higher elevation saltmarsh became favourable for mangroves, which rapidly established a deeper root network, supplementing the soil organic carbon pool. The submerged mangrove forest was inundated more frequently, providing more opportunities for carbon-rich tidally borne sediments to accumulate and increase the rate of carbon addition.

The great mangrove forests and saltmarsh plains prior to widespread human-driven change to the coastal zone have been reduced to remnants following decades of clearance for aquaculture, agriculture, coastal developments, and tidal obstructions (Gedan et al., 2009; Friess et al., 2019; Goldberg et al., 2020). This is compounded by conversion to open water arising from land subsidence following groundwater and hydrocarbon extraction and/or associated with diminishing sediment supply arising from damming and diversions. Losses in recent decades of mangrove forests (0.7–3.0% $yr.^{-1}$), saltmarshes (1.0–2.0% $yr.^{-1}$) and seagrass meadows (0.4–2.6% $yr.^{-1}$) have contributed an estimated 0.15–1.02 Pg of CO_2 emission per year (Pendleton et al., 2012) (by comparison, 3–19% of emissions from deforestation). These losses reverse decades of carbon sequestration within biomass and millennia of sequestration from substrates. In particular methane flux, a greenhouse gas with ~28 times higher global warming potential than carbon dioxide (Foster et al., 2021), is markedly higher following substrate disturbance. A global review of methane emissions arising from conversion of mangroves, saltmarshes, seagrasses and tidal flats for coastal aquaculture estimated a rise in methane emissions per area 7–430 times higher than emissions from non-converted coastal habitats (Rosentreter et al., 2021b). Fortunately, there is evidence that this trend of declining BCE extent is slowing (Pendleton et al., 2012; Friess et al., 2019; Friess et al., 2020), and losses are being offset by the creation of new wetlands (Murray et al., 2022).

Conceptualising blue carbon accommodation space

Accommodation is a term used to define the three-dimensional space available for mineral sediments and soil organic matter (Jervey, 1988) (Figure 2A). The maximum elevation of tidal inundation delimits both the landward extent that tidally borne mineral and organic matter can accumulate, and delimits the zone supporting living mangrove and saltmarsh vegetation and in situ soil organic matter contributions (Rogers, 2021). In situ contributions are also delimited at the seaward margin and along tidal creeks by the low-energy hydrodynamic conditions required for vegetation establishment and ongoing survival; in these locations, it is only detrital material that can accumulate within sediments. Initially, bedrock or basement geology delimits the zone in which sediments can accumulate, but as accommodation becomes increasingly infilled, or 'realised', via the accumulation of mineral and organic material, substrate elevations increase and become progressively terrestrialised and exposed to the oxidising conditions underpinning aerobic processes of soil organic matter decomposition. In these circumstances, an increase in available accommodation, either via autocompaction of sediments that have accumulated within the 'realised' accommodation, subsidence of the basement, or sea-level rise, is required to reinstate tidal inundation, preserve the niche of BCEs, minimise decomposition of organic material by processes of oxidation or methanogenesis and provide new space for additional soil organic matter.

Observations of mangrove and saltmarsh substrate elevation changes using techniques such as surface elevation tables, marker horizons and radiometric dating (Figure 2B) confirm that sedimentation and surface elevation gain are proportional to position in the tidal frame, reflecting the influence of accommodation on accumulation of mineral and organic material in substrates (Webb et al., 2013; Raw et al., 2020; Cahoon et al., 2021; Saintilan et al., 2022). The effect of sea-level rise on the position in the tidal frame of BCEs has been conceptualised by Allen (2000) to account for the addition of mineral and organic material, autocompaction and relative sea-level rise. Providing accommodation is available, below-ground biomass from established vegetation increases substrate volume and the mass of the soil organic carbon pool; above-ground biomass baffles tidal energy, improving hydrodynamic conditions for the deposition of suspended sediments. As substrate elevations increase, the space available for below-ground organic matter additions and mineral sediment addition diminishes, and organic matter decomposition may increase due to an associated reduction in inundation depth, duration and/or frequency (often termed hydroperiod). In combination, these factors generate a self-organising negative feedback that favours the stabilisation of substrate elevations. As a small increment in sea level increases accommodation, the associated increase in tidal inundation serves to enhance conditions favouring the accumulation of mineral and organic sediments, thereby offsetting the small increment in sea level, and maintaining the intertidal position of the substrate; addition of organic material is a vital component of this negative feedback. The coupling between inundation and organic matter addition that contributes to this negative feedback was initially conceptualised for marshes of the SE coast of the USA (Morris et al., 2002) and has formed the basis for models projecting the organic response of substrates to sea-level rise (Mudd et al., 2009; Mack et al., 2023). Field studies have also confirmed linkages between coastal wetland evolution, accommodation space and carbon concentrations in mangrove and saltmarsh substrates of SE Australia (Owers et al., 2022) (Figure 3).

The PAST: Sea-level rise, and blue carbon accommodation

For extended periods over Earth's history, when the coincidence of rising sea level, favourable coastal geomorphology and suitable tidal range has been conducive to extensive coastal wetland development, blue carbon has been an important and arguably dominant control on global trends in atmospheric CO_2. During the Oligo-Miocene, the combined influence of sea-level rise, high tidal range and a resultant extensive mangrove development in the South China Sea trapped up to 2000 Pg of organic carbon, equivalent to up to 60 p.p.m. of atmospheric CO_2 per Myr (Collins et al., 2017). The development of these forests could have been a major contributor to the reduction in atmospheric CO_2 concentrations from circa 800 to 300 p.p.m. since the Late Oligocene (34-0 Ma) (Collins et al., 2017).

At the peak of the last glacial maximum, sea level was 130–120 m lower than present; this low stand and the present high stand are indicative end points of global eustatic sea-level cycles (Murray-

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

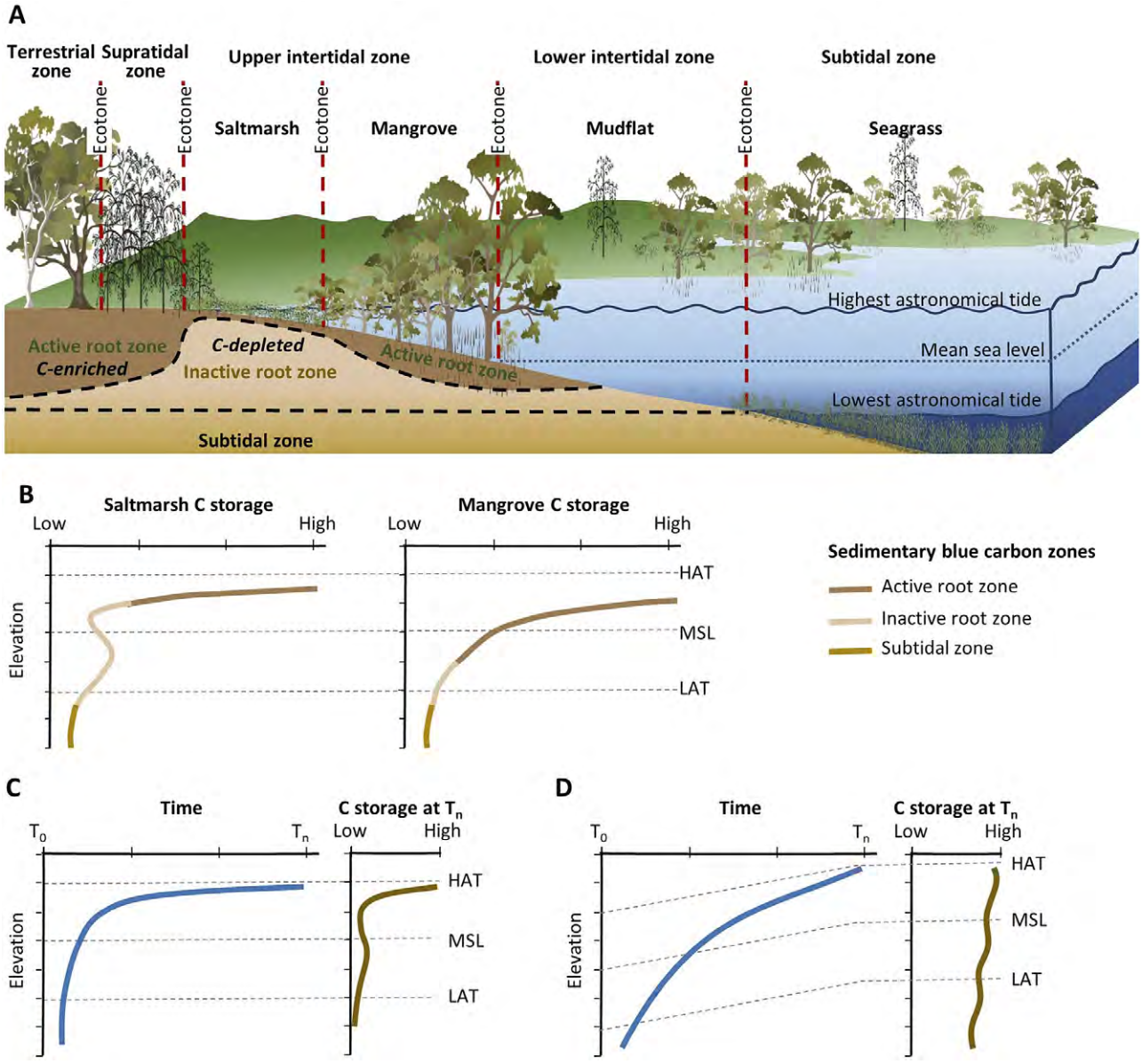


Figure 3. (A) Conceptual model of lateral zonation of BCEs of southeastern Australia with respect to tidal parameters, and varying distribution of soil organic carbon within the active root zone, inactive root zone and subtidal zone; and (B) associated generalised variation in carbon storage within BCEs (modified from Owers et al. (2022)). (C and D) Relationships between carbon storage and sea-level change (from T_0 to T_n) under conditions of (C) relatively stable sea level since the mid-Holocene and (D) rising sea level since the mid-Holocene (modified from Allen (2000)).

Wallace and Woodroffe, 2014). The response of mangrove forests and saltmarshes to sea-level rise since the last glacial maximum has been likened to the behaviour of coral reefs at the same period (Neumann and MacIntyre, 1985; Reed, 1990; Woodroffe and Davies, 2009), where, depending upon the rate of sediment supply relative to the rate of sea-level rise, mangrove forests and saltmarshes may be 'drowned', 'backstep', 'catch-up', 'keep-up', 'prograde' or 'emerge'. When rates of sea-level rise exceeded 1 m per century during the late-Pleistocene and early-Holocene, the capacity of mangrove forests to accumulate mineral and organic material appears to have been exhausted, and evidence of 'drowned' mangrove peats overtopped by marine transgressive sand sheets have been preserved on the Sahul Shelf (northwest Western Australia (Nicholas et al., 2014) and the Sunda Shelf (on the western rim of the South China Sea) at water depths of up to 100 m (Hanebuth et al., 2000). Extensive mangrove forest development at the time appears to have been terminated by Meltwater Pulse 1A, during which rates of relative sea-level rise increased to >20 mm $yr.^{-1}$ (Lambeck et al., 2014).

Deceleration in the rate of sea-level rise in the early-Holocene was broadly marked by mangrove development in the millennia prior to sea-level stabilisation near present levels. In settings of high sediment yield, including the Ganges-Brahmaputra delta, India (Hait and Behling, 2009) and the Queensland continental shelf, Australia (Grindrod et al., 1999), mangrove forests adjusted in situ to sea-level rise from the early-Holocene (~9,000 BP), but were subsequently 'drowned' and then 'backstepped'. By ~7,500 BP, relative sea-level rise had decelerated to less than 6–7 mm $yr.^{-1}$, and 'catch-up', or mangrove landward transgression, followed by 'progradation' occurred where sediment supply was high, resulting

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

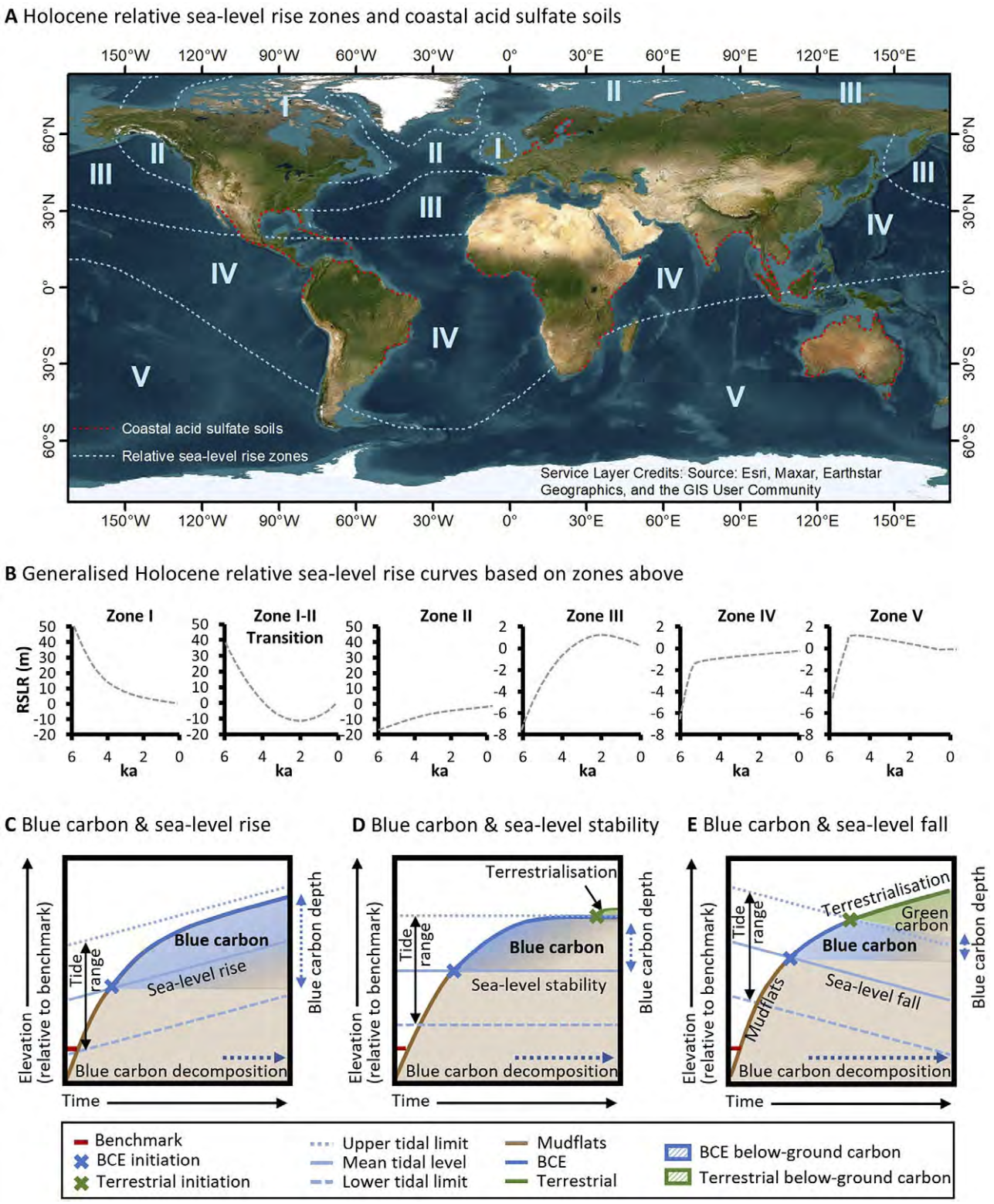


Figure 4. Relative sea-level change is a significant control on processes of carbon accumulation and decomposition, and varies globally according to the generalised Holocene relative sea-level zones (A) (Clark et al., 1978) and generalised Holocene relative sea-level curves across these zones (B). Note the distribution of coastal acid sulphate soils in (Michael, 2013) (A), which corresponds broadly with regions where sea-level conditions facilitated widescale mangrove and saltmarsh development throughout the late-Holocene. When sea levels are rising (C), sedimentary carbon continues to accumulate within available accommodation and pathways of decomposition are dampened under increasingly anaerobic conditions. Where sea level has been relatively stable (D), blue carbon additionality is limited by the upper limit of tidal inundation and substrates become increasingly mineral dominated and support terrestrial vegetation as accommodation diminishes. Under conditions of falling sea levels (E), substrates become increasingly terrestrialised (i.e. with terrestrial vegetation) and conditions favour aerobic decomposition and methanogenesis of blue carbon.

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

in extensive mangrove forests in tropical minerogenic settings. In many places, these forests were considerably greater in extent than contemporary mangrove forests, including Australia (Woodroffe et al., 1985), the Mekong and Red River deltas of Vietnam (Tran and Ngo, 2000; Li et al., 2012), and the Great Songkla Lakes, Thailand (Horton et al., 2005). High rates of organic matter accumulation in this globally synchronous phase of blue carbon development sequestered an estimated 20–60 Pg. C, contributing to a 5 p.p.m. decline in atmospheric CO_2 concentrations in the early Holocene (Saintilan et al., 2020). An early-mid Holocene decline in methane, primarily in the Southern Hemisphere, according to ice-core data (Beck et al., 2018), commenced over the same period, with reductions in Southern Hemisphere emissions estimates of ~19 Tg CH_4 $yr.^{-1}$ (Beck et al., 2018). The $\delta^{13}C$ signals in methane in the Southern Hemisphere for the period show a 1.5 p.p.t. depletion (Beck et al., 2018) consistent with a replacement of vegetation utilising the C_4 photosynthetic pathway (tropical grasslands and saltmarsh adapted to low atmospheric carbon dioxide) with mangroves utilising the C_3 pathway (Sowers, 2010).

By the mid-Holocene, eustatic sea level stabilised within approximately 2 m of its current elevation (Clark et al., 1978; Khan et al., 2015). However, the initiation of mangrove and saltmarsh transgressive phases was globally variable due to the influence of glacio-isostatic adjustment on varying rates of mid- to late-Holocene relative sea-level rise (Ribeiro et al., 2018), and the modulating effect of other climatic variables (e.g. droughts and/or frequent storms) on conditions conducive to intertidal vegetation expansion or decline (Sherrod and McMillan, 1985; Jones et al., 2019). Global scale variation in relative sea-level trends, largely arising from glacio-isostatic adjustment, had a profound influence on blue carbon accumulation throughout the mid- to late-Holocene and storage since this time (Rogers et al., 2019a; 2019b). Principally related to distance from regions of maximal ice sheet extent during the last glacial period, relative sea-level rise modifies the accommodation available for blue carbon. The delineation of zones across oceans globally where post-glacial sea-level trends are relatively similar (Figure 4A and 4B, Clark et al., 1978) therefore provides an indication of the accommodation available for blue carbon storage over the past few millennia. While more is known of post-glacial sea-level change since these zones were initially demarcated, their broad correspondence with what we now know of relative sea-level trends (Khan et al., 2015) provides some confidence in the geographic position of zones (noting that boundaries between zones are diffuse and not definite). Clark et al. (1978) delineated five zones across oceans globally (a sixth zone was associated with continental coastlines) that can be broadly grouped into three regions: (i) near-field locations are proximal to ice sheets of the last glacial maximum and typically exhibit continuous patterns of relative sea-level fall (i.e. Clark et al., 1978, zone I); (ii) intermediate locations exhibit complex sea-level trends; however, relative sea-level rise over the past few millennia is typical; and (iii) far-field locations are distal from ice sheets and eustatic sea-level trends dominate processes of glacio-isostatic adjustment. For brevity, we focus on end members: far-field locations (Zones IV and V) where the relative sea level has been relatively stable for millennia (or may have fallen); intermediate locations where relative sea level has been rising over the mid- to late-Holocene (Zones II and III); and near-field locations (Zone I) where relative sea level has been falling (Figure 4A).

Far-field locations (Zones IV and V), distal from regions of maximal ice sheet extent, exhibit patterns of mid-Holocene infill in mangrove (Woodroffe et al., 1993; Cohen et al., 2005; Hashimoto et al., 2006; Proske and Haberle, 2012; França et al., 2013; Boski et al., 2015; Punwong et al., 2018) and saltmarsh settings, with coastal barriers typically enclosing bays along the more southern wave-dominated coastlines (Compton, 2001; Vilanova et al., 2006; Fornari et al., 2012; Kennedy et al., 2021). Ongoing coastal and estuarine sedimentation, and a fall in sea level to present levels where a high stand occurred in the late Holocene, caused coastal floodplains to increasingly 'prograde' or become 'emergent', with accommodation being limited, and BCEs restricted to the fringes of estuarine shorelines (Woodroffe and Davies, 2009). BCEs were replaced by floodplain terrestrial forests and freshwater wetlands, a shift that may have contributed to gradual increases in atmospheric methane concentrations in the late-Holocene after declining in the early- to mid-Holocene (Beck et al., 2018). Preservation of soil organic carbon in far-field locations is limited by decomposition as coastal floodplains become increasingly terrestrialised and support grasses and sedges, else soil organic matter may be vulnerable to metabolisation and formation of pyrites when sulphate and sulphate reducing bacteria are present. This sets up the conditions for generation of acid sulphate soils when coastal floodplains are drained, and oxidisation occurs. The relationship between former distribution of saltmarshes and mangrove forests, relative sea-level stability and coastal acid sulphate soil development is well established (Pons et al., 1982; Van Breemen, 1982) and reflected in the greater extent of actual and potential coastal acid sulphate soils in SE Asia, Africa, Australia and South America (Michael, 2013) and their virtual absence from intermediate-field locations (see Figure 4A).

Intermediate field locations also exhibit broad agreement in geomorphological evolution over the Holocene (Woodroffe, 1981; Digerfeldt and Hendry, 1987; Parkinson, 1989; Parkinson et al., 1994; McKee, 2011). In Florida and the northern Gulf of Mexico, the early Holocene was marked by rates of relative sea-level rise that were too high for broadscale mangrove development (<~7,500 BP) (Sherrod and McMillan, 1985; Parkinson, 1989). Evident from interbedded peats and marls, the onset of the transgressive 'catch-up' phase occurred from about 3,500 BP (Scholl, 1964; Parkinson et al., 1994; Jones et al., 2019), although the occurrence of continuous vertical peat growth, typical of 'keep-up' behaviour, is modulated in some locations by other climatic factors, including a period of cooling, that may not have been conducive to widespread mangrove expansion and vertical growth (Sherrod and McMillan, 1985; Jones et al., 2019). Where conditions were favourable, vertical growth of mangrove peats is near continuous. In particular, the cenotes of the Yucatan Peninsula are reported to have among the highest mangrove carbon stocks globally, and their accumulation has been related to ongoing relative sea-level rise over the late-Holocene (Adame et al., 2021). The later onset of transgressive phases of mangrove development in intermediate field locations reflect stronger rates of relative sea-level rise throughout the mid-Holocene, ongoing sea-level rise in the late-Holocene, the influence of other climatic variables, as well as limited capacity for vertically adjustment to sea-level rise due to low rates of sediment supply in some carbonate dominated settings. Accordingly, ongoing sea-level rise and limited mineral sediment supply since the late-Holocene may explain the preservation of carbon-rich mangrove peats in this region (McKee, 2011). Similar preservation of saltmarsh peats and associated foraminifera is evident at intermediate-field sites with a history of increasing accommodation with sea-level rise throughout the mid- to late-Holocene (Redfield, 1972; Orson et al., 1998; Gehrels, 1999).

Saltmarshes at near-field locations (climate not suitable for mangroves throughout the Holocene), those proximal to regions

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

of maximum ice sheet extent at the last glacial maximum, exhibited a highly variable pattern of vertical growth and carbon accumulation dependent upon the influence of glacio-isostatic adjustment on relative sea-level rise (Khan et al., 2015). Analyses of radiocarbon dated saltmarsh sequences in the UK differentiated both transgressive sequences (i.e. 'catch-up'), representing increasing marine influence and regressive sequences (i.e. 'progradation' or 'emergent') indicating increasing terrestrialisation (Horton et al., 2018). The presence of these sequences aligned with Holocene sea-level history, with 'catch-up' transgressive sequences predominating in southern England where relative sea-level rise exhibited a pattern of deceleration, while regressive sequences were more prominent in Scotland, where relative sea level fell in both the early- and late-Holocene. Complex spatio-temporal patterns of postglacial relative sea-level change throughout the mid- to late-Holocene are also preserved in saltmarsh peats of near-field locations across the coastline of the North Atlantic (Vacchi et al., 2018; Cohen et al., 2022; Creel et al., 2022).

Patterns of relative sea-level change over the Holocene and its influence on the distribution of BCEs have provided important lines of evidence about the future of BCEs. Global analyses of soil organic carbon stocks in saltmarshes indicate that regions where sea level has a longer history of rising over the mid- to late-Holocene, that is intermediate and some near-field locations, exhibit higher soil organic carbon stocks and deeper soil organic carbon pools than far-field locations (Rogers et al., 2019a). This has been linked to the influence of relative sea-level rise on accommodation for blue carbon within substrates, the largest carbon pool within BCEs. Where sea level has been rising at a moderate rate for a few millennia, vertical space is created for storage of blue carbon within below-ground biomass and soils (Figure 4C). In contrast, where sea level has been relatively stable over the mid- to late-Holocene, that is across much of the Southern Hemisphere, carbon pools may be depleted and shallower (although the depth is dependent upon tidal range), and this has been related to the limitations placed on accommodation as substrates become increasingly dominated by mineral sediments (Figure 4D). Where sea level has been falling, substrates become increasingly terrestrialised with brackish to fresh substrate salinities that are aerobic and favour decomposition and methanogenesis (Figure 4E). These differences in organic matter content between far-, intermediate- and near-field locations are also reflected in the character of contemporary sediment accumulating in wetlands. Intermediate- and near-field locations have higher organic carbon accumulation above artificial marker horizons (Saintilan et al., 2020), reflecting both the comparatively higher contemporary rates sea-level rise, and possibly the more organic sub-tidal reservoirs of sediment contributing to marsh accretion (Hopkinson et al., 2018).

The FUTURE: The present and past as a guide to blue carbon futures

The spectre of climate change has focussed attention on reducing atmospheric carbon concentrations and limiting warming well below 2 °C, a commitment established in the Paris Agreement at COP21 (Iyer et al., 2015). Accordingly, the capacity of BCEs to draw carbon from the atmosphere is being leveraged as a climate mitigation strategy, and received considerable recognition in the latest IPCC report (Cooley et al., 2022). Conservation of BCEs aimed at minimising losses in extent through land use and land cover change (LULCC) and restoring condition through improved management will be important. The Reducing Emissions from Deforestation and Forest Degradation in Developing Countries (REDD+) program of the United Nations Framework Convention on Climate Change (UNFCCC) specifically targets the improved management of forests to minimise loss and release of greenhouse gases, and conservation efforts are increasing in developing countries (Ahmed and Glaser, 2016). Similar programs for non-forested ecosystems, such as saltmarshes, do not exist; however, there is a global peatland initiative that could be applied to saltmarshes. In many jurisdictions BCEs are already protected from loss because of the benefits they provide to society (Romañach et al., 2018). Despite these policies, loss of BCEs is ongoing (Gedan et al., 2009; Friess et al., 2019; Goldberg et al., 2020), and this increases the burden for carbon additionality by other mechanisms, such as restoration.

Restoring BCEs, achieved by planting vegetation, seeds or propagules, or managing barriers to tidal exchange that have been put in place to facilitate past LULCC, may enhance carbon sequestration as blue carbon vegetation re-establishes. Analyses suggest that restoration to recover BCE habitat that has been lost due to human activities in the coastal zone is potentially feasible for mangroves, less so for seagrasses and saltmarshes (Griscom et al., 2017; Macreadie et al., 2021). However, the capacity for large-scale restoration is constrained by socio-economic factors, particularly where the coastal zone is critical for maintaining livelihoods and food security (Herr et al., 2019). Efforts are in place globally to restore mangrove forests (Friess et al., 2019), but success is highly variable; often there is a lack of understanding of the geomorphological and hydrological controls on restoration success, and mangrove restoration efforts have been plagued with failure (Lee et al., 2019; Lovelock et al., 2022c). Saltmarsh restoration is also occurring, but receives considerably less scientific attention beyond North America; this likely reflects an efficient policy environment and sufficient financial capacity for restoration (Billah et al., 2022). Despite these challenges, restoration of BCEs is likely to accelerate, being buoyed by the United Nations declaration that 2021–2030 is the "United Nations Decade on Ecosystem Restoration" to help meet sustainable development goals (Billah et al., 2022).

Market mechanisms have been developed to incentivise BCE restoration, and currently there are two primary markets; the compliance and voluntary markets (Sapkota and White, 2020). Compliance markets are underpinned by regulations to offset greenhouse gas emissions and typically require offsets to be accounted for under existing standards and using approved methodologies, such as the Verified Carbon Standard (VCS) methodology for tidal wetlands (VM0033) (Emmer et al., 2015a; Emmer et al., 2015b). In some jurisdictions, the voluntary market is also highly regulated; for example, the Australian Government administers a voluntary market, the Emissions Reduction Fund, which provides tradeable credits (Australian Carbon Credit Units) for tidal restoration activities that increase blue carbon storage (Lovelock et al., 2022a; Lovelock et al., 2022b). The payment period for these programs is well-defined as the carbon benefits are likely to diminish in the above-ground carbon pool once vegetation has reached maturity, and in the below-ground pool when substrates are saturated with mineral and organic material (i.e. when accommodation is limited). The 25-year permanence time frame aligns with the period for which woody vegetation is anticipated to reach maturity and exhibit high rates of carbon addition to substrates (Osland et al., 2020), while the 100-year timeframe aligns with what is regarded to be permanently sequestered soil organic carbon (i.e. permanence) (Dynarski et al., 2020). Payments are dependent upon forward projections and ongoing verification.

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

Use of BCEs as a mechanism for carbon removal has received some criticism (Williamson and Gattuso, 2022) due to the high variability and errors in carbon burial rates, lateral carbon transport (Maher et al., 2018), methane and nitrous oxide fluxes (Rosentreter et al., 2021a; Malerba et al., 2022), carbonate formation and dissolution (Saderne et al., 2019; Van Dam et al., 2021), vulnerability to future climate change and non-climatic factors, and cost-effectiveness and scaleability (Macreadie et al., 2021). Confidence in forward projections is likely to be improved as data collection continues and knowledge gaps are addressed (Macreadie et al., 2019).

Permanence (i.e. beyond the 25-year and 100-year time frames) of blue carbon is fundamental to the success of BCEs as a natural climate solution. Critically, conservation and restoration activities will not occur in the absence of sea-level rise, warming and elevated atmospheric carbon dioxide concentrations, placing considerable uncertainty regarding permanence. The fate of sequestered carbon from BCEs once they succumb to sea-level rise is difficult to project, but likely to be highly variable. Palaeo-records provide the opportunity to validate projections of the response of BCEs to sea-level rise; however, do not fully indicate blue carbon futures as sea-level rise is now occurring on coastal landscapes that developed throughout the Holocene, have been highly modified and do not have a historic analogue (Woodroffe and Murray-Wallace, 2012). Projecting blue carbon futures therefore requires integration of information from the past and present behaviour.

Recent analyses have indicated that rising seas associated with ice melt following the last glacial maximum exceeded the capacity of tropical mangroves (Saintilan et al., 2020) and saltmarshes (Horton et al., 2018; Törnqvist et al., 2021) to remain in situ (i.e. 'keep-up') when sea level increased at rates exceeding ~5–7 mm $yr.^{-1}$. However, mangrove and saltmarsh sediments have been preserved since the Holocene (Hanebuth et al., 2000; McKee et al., 2007; Wang et al., 2009) following sea-level rise at rates higher than currently encountered (Redfield, 1972; McKee et al., 2007; Saintilan et al., 2020). Long-periods of sea-level stability across much of the Southern Hemisphere have contributed to the development of broad, mature coastal floodplains (i.e. considerable elevation capital) when conditions are conducive. These floodplains are not typically saturated with carbon (Rogers et al., 2019a), may be hot spots for potential and realised acid sulphate soils (Michael, 2013), and could become extensive BCEs, much like those of the mid-Holocene (Woodroffe et al., 1985). Many BCEs in the northern hemisphere have been adapting to sea-level rise for millennia and are likely to be lower-lying (i.e. less elevation capital) and have limited capacity to adapt to anticipated sea-level rise as the coastal zone is highly contested and coastal squeeze is likely.

The permanence of organic material exposed to drowning is an important consideration. Since it takes some time for mature trees and tidal marshes, that are high in the tidal frame to drown with incremental increases in sea level, it is feasible that submergence and death may occur beyond the minimum 25-year permanency time frame applied in managed blue carbon markets. Loss of standing biomass that is currently lower in the tidal frame or in the interior of saltmarshes may be high (Kearney et al., 1994), and depending on exposure to erosion, soil carbon may be variably preserved (Krauss et al., 2018; Rogers et al., 2019a) or reworked and transported elsewhere (DeLaune and White, 2012; Haywood et al., 2020). Increasing atmospheric carbon dioxide concentrations may enhance productivity of BCE vegetation, with enhanced root allocation contributing to sea-level rise adaptation and carbon sequestration via addition of carbon volume to substrates (Ball et al., 1997; Langley et al., 2009; McKee et al., 2012; Reef et al., 2017). Widespread mangrove dieback has been associated with short-term methane flux to the atmosphere (Jeffrey et al., 2019); this has potential implications on atmospheric carbon budgets in the event of broadscale mangrove mortality under high rates of sea-level rise, or short-term sea-level fluctuations. Figure 5 conceptualises the hypothesised carbon storage and greenhouse gas flux outcomes under scenarios of atmospheric carbon dioxide concentrations, warming and relative sea-level rise.

The degree to which climate change modifies BCEs is difficult to project as shoreline erosion is poorly preserved in the stratigraphy of depositional environments, limiting the capacity to parameterise models. In addition, multiple coastal processes contribute to shoreline change and observations indicate considerable local and regional variability in the operation of processes. Studies that project BCE dynamics with sea-level rise and infer carbon implications are therefore typically undertaken at the local scale, and at data-rich sites, and the outcomes can rarely be extrapolated to other locations. Otherwise, projections are dependent upon simplification of processes and apply reductive estimates of carbon concentrations (Lovelock and Reef, 2020; Wang et al., 2021), or explore future scenarios using simplified idealised models (Kirwan and Mudd, 2012). Spatial models typically require decisions regarding whether landward retreat of BCEs is parameterised, and, invariably, the projected outcomes are highly dependent upon model parameterisation. For example, recent projections estimated net gains in blue carbon in the order of 1.5 Pg to 2100 when coastal squeeze impacts are minimised and climate change impacts are high (i.e. RCP8.5 scenario), while net blue carbon gains are in the order of 0.8 Pg to the year 2100 when under moderate climate change scenario (i.e. RCP4.5 scenario) (Lovelock and Reef, 2020).

Models have consistently indicated the importance of minimising coastal squeeze to enhance climate adaptation and mitigation benefits from BCEs (Schuerch et al., 2018; Lovelock and Reef, 2020; Wang et al., 2021). Managing structures that modify tidal exchange and sediment supply will be crucial for maximising blue carbon benefits. Indeed, storm surge barriers are already managed to reduce coastal flooding impacts (Haigh et al., 2022) and engineering structures could be modified to meet design requirements anticipated with sea-level rise and to manage for blue carbon services (Sadat-Noori et al., 2021; Haigh et al., 2022). In many cases 'holding back the tide' will become challenging and costly, and it is likely that difficult land use decisions will be made to increase BCE extent and the provision of co-benefits (Rogers et al., 2022). Sea-level rise will reduce the viability of large tracts of low-lying coastal land for agriculture and grazing purposes, and the efficacy of existing structures to hold back tides, many of which were designed when rates of sea-level rise were negligible, will be tested. In these circumstances, the benefits of land cover conversion for BCEs should therefore be weighed against the costs associated with upgrading existing structures to meet future design requirements that account for the effects of sea-level rise and storm surges on tidal regimes. Momentum towards recognising BCE co-benefits for biodiversity, coastal fisheries and water quality is increasing (Rahman et al., 2021; Hagger et al., 2022), and efforts are underway to develop a 'blue chip' carbon markets that provide payments for blue carbon additionality and co-benefits (Macreadie et al., 2022). These blue-chip markets may sufficiently incentivise land managers to reconsider upgrades of tidal barriers and instead receive a blue carbon income as the land is restored to a BCE (Rogers et al., 2022).

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

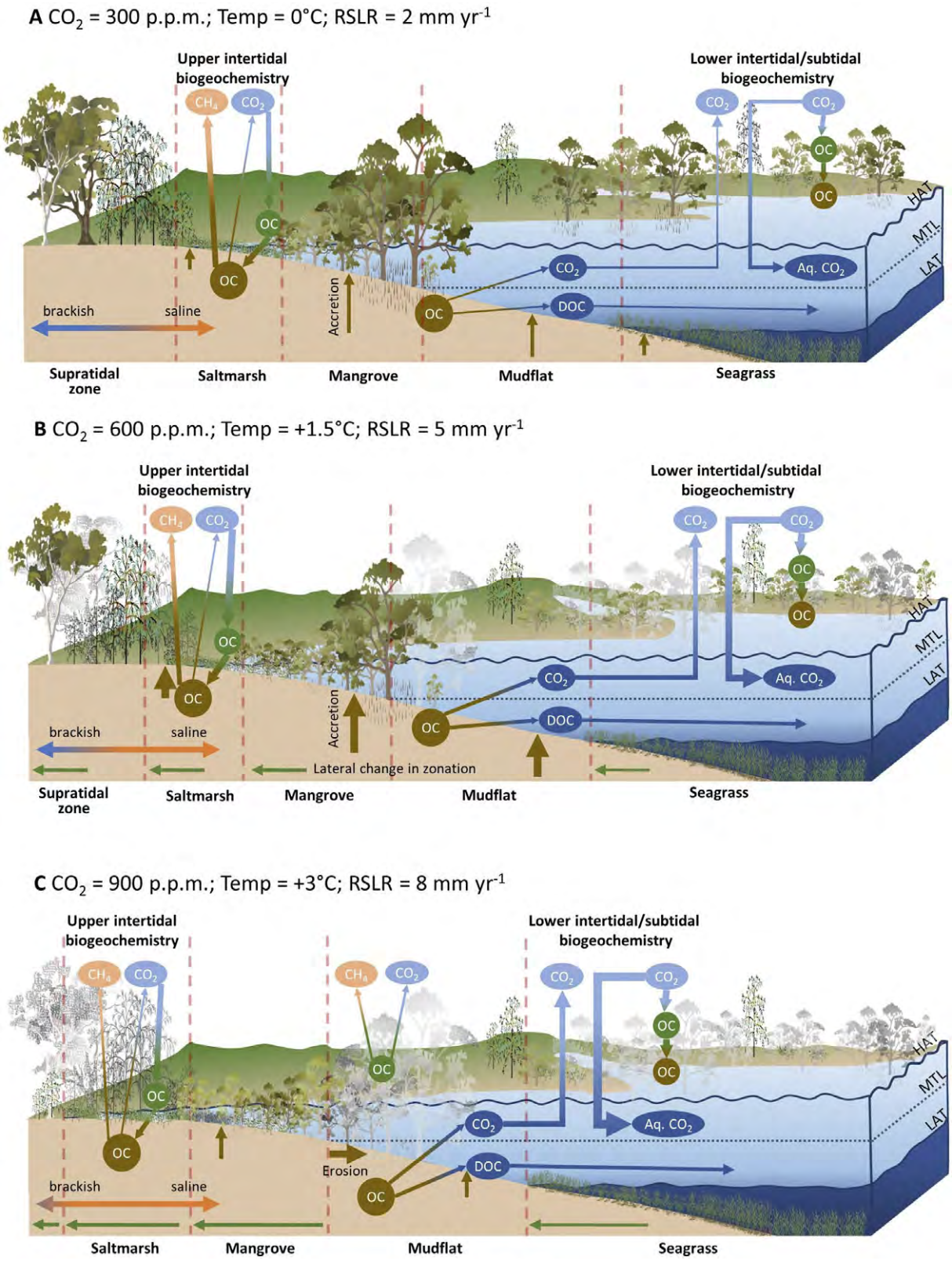


Figure 5. Conceptualisation of the interacting effects of atmospheric carbon dioxide, warming and relative sea-level rise on BCE projected to occur under a range of emissions scenarios. Under the baseline scenario (A) carbon is fixed by in situ vegetation and contributes to soil carbon accumulation and substrate volume via accretion. The landward margin under brackish conditions is a source of methane. Under the mid-range emissions scenario (B) the feedbacks between elevated atmospheric CO_2 and organic carbon sequestration and between relative sea-level rise (RSLR) and organic carbon production, preservation, and vertical accretion are strengthened. Saline intrusion reduces methane emissions in the landward fringe, although this may be counterbalanced by increased emissions resulting from increases in NPP induced by CO_2 and warming. Under the high-range emission scenario (C) a tipping point is reached where RSLR exceeds vertical accretion leading to mortality and shoreline retreat. Mortality of terrestrial vegetation contributes to elevated methane production in the short term. Note that the relative strength of interactions with greenhouse gases is indicated by the thickness of lines, and greyed-out vegetation is indicative of dieback or loss associated with the effects of rising sea levels.

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

Conclusion

In the short- to medium-term, climate change may increase the capacity of BCEs to capture and store atmospheric CO_2, largely due to processes that respond to elevated CO_2 and temperature, and influence carbon capture and storage. These processes include in situ responses such as CO_2 fixation, biomass storage, biogeochemical enhancement of burial efficiency, as well as the expansion of BCEs at local and global scales. The magnitude and duration of the negative feedback on climate may vary between hemispheres. Climate change is expected to squeeze mangrove and saltmarsh areas in the Northern Hemisphere between accelerating relative sea-level rise and hard barriers. In the Southern Hemisphere, opportunities for landward expansion of mangrove and saltmarsh may be available where late-Holocene sea-level history coupled with ongoing sediment supply and lower contemporary rates of relative sea-level rise has facilitated the development of broad coastal floodplains and where coastal squeeze effects are minimised. The long-term future for these negative feedbacks on radiative forcing is dependent upon decisions made in the coming decades. At the global scale, the rate of sea-level rise projected under high emissions scenarios will lead to degradation and loss of existing coastal wetlands. Sea-level rise of ~5–7 mm $yr.^{-1}$ is likely to be a critical tipping point at which the predominantly negative climate feedbacks driven by blue carbon sequestration become positive feedbacks driven by plant decomposition and remineralisation. This tipping point will be surpassed under high emissions scenarios within the next century.

The threat to in situ coastal wetlands makes local land-use and coastal protection the key determinant of long-term survival, driven by retreat of BCEs to higher elevations. Investment in coastal wetland conservation and restoration provides benefits not only for the preservation of ecosystem services such as coastal fisheries, but also a promising opportunity for nature-based mitigation. National governments are developing a broad spectrum of climate adaptation and mitigation responses with innovative approaches to financing these activities, including some focused specifically on blue carbon. Carbon markets are rapidly expanding as a tool for governments, private corporations, and individuals to reduce greenhouse gas emissions. While currently only a few blue carbon projects have reached the point of generating finance through carbon markets, projects are in development in Mexico, Kenya, Colombia, Madagascar and other locations, and blue carbon credits are in high demand due to the multitude of co-benefits provided. This suggests that carbon markets are promising to finance coastal restoration, climate adaptation, and livelihoods for coastal communities.

Critical knowledge gaps need to be overcome before the full benefit of blue carbon can be realised. Priorities include: establishing the full global extent of BCEs and developing ongoing monitoring at management-relevant resolutions; addressing the permanence and temporal continuity of blue carbon storage and sequestration subject to SLR, changing climatic conditions and their impact on the distribution of mangroves, tidal wetlands, seagrass and macroalgae at high latitudes; establishing the factors that determine the carbon storage and sequestration capacity at the site scale and how these might be managed to increase mitigation benefit; and establishing the carbon mitigation potential and pathways for other coastal and marine ecosystems such as macroalgae and tidal forests. Given the recent momentum in blue carbon research, scientists and policy makers are well placed to address these gaps, providing research is sufficiently supported. Crucial to the effectiveness of blue carbon research for policy and management application is actively focussing on the highly under-studied regions, particularly in the global south, where the distribution of mangrove forests is greatest.

Open peer review. To view the open peer review materials for this article, please visit http://doi.org/10.1017/cft.2023.17.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/cft.2023.17.

Data availability statement. Data were not generated to prepare this literature review.

Acknowledgements. The authors wish to acknowledge the traditional custodians of blue carbon estate globally and recognise their contribution to management and stewardship for millennia. We advocate for their leadership as blue carbon managers. Many collaborators have contributed to the research undertaken by the authors, and we appreciate their knowledge sharing.

Author contribution. Conception, writing and preparation of figures were principally undertaken by Rogers with substantial input for Kelleway and Saintilan. Figure 1 was prepared by Kelleway and Figures 4 and 5 by Rogers.

Financial support. We appreciate the financial support provided by respective institutions (University of Wollongong and Macquarie University), the Australian Research Council, and federal, state, and local governments who have supported the work of the authors.

References

Adame MF, Cherian S, Reef R and Stewart-Koster B (2017) Mangrove root biomass and the uncertainty of belowground carbon estimations. *Forest Ecology and Management* **403**, 52–60.

Adame M, Santini N, Torres-Talamante O and Rogers K (2021) Mangrove sinkholes (cenotes) of the Yucatan peninsula, a global hotspot of carbon sequestration. *Biology Letters* **17**(5), 20210037.

Ahmed N and Glaser M (2016) Coastal aquaculture, mangrove deforestation and blue carbon emissions: Is REDD+ a solution? *Marine Policy* **66**, 58–66.

Allen JRL (2000) Morphodynamics of Holocene salt marshes: A review sketch from the Atlantic and southern North Sea coasts of Europe. *Quaternary Science Reviews* **19**(12), 1155–1231.

Alongi DM (2012) Carbon sequestration in mangrove forests. *Carbon Management* **3**(3), 313–322.

Alongi DM (2020a) Carbon balance in salt marsh and mangrove ecosystems: A global synthesis. *Journal of Marine Science and Engineering* **8**(10), 767.

Alongi DM (2020b) Global significance of mangrove blue carbon in climate change mitigation. *Science* **2**(3), 67.

Atwood TB, Connolly RM, Almahasheer H, Carnell PE, Duarte CM, Ewers Lewis CJ, Irigoien X, Kelleway JJ, Lavery PS, Macreadie PI, Serrano O, Sanders CJ, Santos I, Steven ADL and Lovelock CE (2017) Global patterns in mangrove soil carbon stocks and losses. *Nature Climate Change* **7**(7), 523–528.

Ball MC (1988) Salinity tolerance in the mangroves *Aegiceras corniculatum* and *Avicennia marina*. I. Water use in relation to growth, carbon partitioning, and salt balance. *Functional Plant Biology* **15**(3), 447–464.

Ball MC (2002) Interactive effects of salinity and irradiance on growth: Implications for mangrove forest structure along salinity gradients. *Trees* **16**(2), 126–139.

Ball MC, Cochrane MJ and Rawson HM (1997) Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO_2. *Plant, Cell and Environment* **20**, 1158–1166.

Beck J, Bock M, Schmitt J, Seth B, Blunier T and Fischer H (2018) Bipolar carbon and hydrogen isotope constraints on the Holocene methane budget. *Biogeosciences* **15**(23), 7155–7175.

Bertness MD, Gough L and Shumway SW (1992) Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* **73**(5), 1842–1851.

Billah MM, **Bhuiyan MKA**, **Islam MA**, **Das J and Hoque ATMR** (2022) Salt marsh restoration: An overview of techniques and success indicators. *Environmental Science and Pollution Research* **29**(11), 15347–1563.

Bindoff NL, **Cheung WW**, **Kairo JG**, **Arístegui J**, **Guinder VA**, **Hallberg R**, et al. (2019) Changing ocean, marine ecosystems, and dependent communities. In Pörtner H-O, Roberts DC, Masson-Delmotte V, et al. (eds.), *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. Cambridge, UK and New York, NY, USA: Cambridge University Press, pp. 447–587.

Björk M, **Uku J**, **Weil A and Beer S** (1999) Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. *Marine Ecology Progress Series* **191**, 121–126.

Boski T, **Bezerra FH**, **de Fátima Pereira L**, **Souza AM**, **Maia RP and Lima-Filho FP** (2015) Sea-level rise since 8.2 ka recorded in the sediments of the Potengi–Jundiai Estuary, NE Brasil. *Marine Geology* **365**, 1–13.

Breithaupt JL, **Smoak JM**, **Bianchi TS**, **Vaughn DR**, **Sanders CJ**, **Radabaugh KR**, **Osland MJ**, **Feher LC**, **Lynch JC and Cahoon DR** (2020) Increasing rates of carbon burial in Southwest Florida coastal wetlands. *Journal of Geophysical Research: Biogeosciences* **125**(2), e2019JG005349.

Bunting P, **Rosenqvist A**, **Lucas R**, **Rebelo L-M**, **Hilarides L**, **Thomas N**, **Hardy A**, **Itoh T**, **Shimada M and Finlayson C** (2018) The global mangrove watch—A new 2010 global baseline of mangrove extent. *Remote Sensing* **10**(10), 1669.

Cahoon DR, **McKee KL and Morris JT** (2021) How plants influence resilience of salt marsh and mangrove wetlands to sea-level rise. *Estuaries and Coasts* **44** (4), 883–898.

Campbell AD, **Fatoyinbo L**, **Goldberg L and Lagomasino D** (2022) Global hotspots of salt marsh change and carbon emissions. *Nature* **612**, 701–706.

Canuel EA and Hardison AK (2016) Sources, ages, and alteration of organic matter in estuaries. *Annual Review of Marine Science* **8**, 409–434.

Chmura GL, **Anisfeld SC**, **Cahoon DR and Lynch JC** (2003) Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles* **17** (4), 1111.

Clark JA, **Farrell WE and Peltier WR** (1978) Global changes in postglacial sea level: A numerical calculation. *Quaternary Research* **9**(3), 265–287.

Cohen KM, **Cartelle V**, **Barnett R**, **Busschers FS and Barlow NL** (2022) Last Interglacial Sea-level data points from Northwest Europe. *Earth System Science Data* **14**(6), 2895–2937.

Cohen M, **Filho P**, **Lara R**, **Behling H and Angulo R** (2005) A model of Holocene mangrove development and Relative Sea-level changes on the Bragança Peninsula (Northern Brazil). *Wetlands Ecology and Management* **13**(4), 433–443.

Collins DS, **Avdis A**, **Allison PA**, **Johnson HD**, **Hill J**, **Piggott MD**, **Hassan MHA and Damit AR** (2017) Tidal dynamics and mangrove carbon sequestration during the Oligo–Miocene in the South China Sea. *Nature Communications* **8**(1), 1–12.

Compton JS (2001) Holocene Sea-level fluctuations inferred from the evolution of depositional environments of the southern Langebaan lagoon salt marsh, South Africa. *The Holocene* **11**(4), 395–405.

Cooley S, **Schoeman D**, **Bopp L**, **Boyd P**, **Donner S**, **Ghebrehiwet DY**, **Ito S-I**, **Kiessling W**, **Martinetto P**, **Ojea E**, **Racault M-F**, **Rost B**, **and Skern-Mauritzen M** (2022) Oceans and coastal ecosystems and their services. In Pörtner H-O, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A and Rama B (eds.), *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY, USA: Cambridge University Press, pp. 379–550. https://doi.org/10.1017/9781009325844.005

Creel RC, **Austermann J**, **Khan NS**, **D'Andrea WJ**, **Balascio N**, **Dyer B**, **Ashe E and Menke W** (2022) Postglacial relative sea level change in Norway. *Quaternary Science Reviews* **282**, 107422.

Darby FA and Turner RE (2008) Effects of eutrophication on salt marsh root and rhizome biomass accumulation. *Marine Ecology Progress Series* **363**, 63–70.

DeLaune R and White J (2012) Will coastal wetlands continue to sequester carbon in response to an increase in global sea level?: A case study of the rapidly subsiding Mississippi river deltaic plain. *Climatic Change* **110**(1), 297–314.

Digerfeldt G and Hendry M (1987) An 8000 year Holocene sea-level record from Jamaica: Implications for interpretation of Caribbean reef and coastal history. *Coral Reefs* **5**(4), 165–169.

Donato DC, **Kauffman JB**, **Murdiyarso D**, **Kurnianto S**, **Stidham M and Kanninen M** (2011) Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience* **4**(5), 293–297.

Duarte CM and Cebrian J (1996) The fate of marine autotrophic production. *Limnology and Oceanography* **41**(8), 1758–1766.

Duarte CM, **Losada IJ**, **Hendriks IE**, **Mazarrasa I and Marba N** (2013) The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change* **3**(11), 961–968.

Dynarski KA, **Bossio DA and Scow KM** (2020) Dynamic stability of soil carbon: Reassessing the "permanence" of soil carbon sequestration. *Frontiers in Environmental Science* **8**, 514701.

Elsner J, **Jagger T and Tsonis A** (2006) Estimated return periods for Hurricane Katrina. *Geophysical Research Letters* **33**(8), L08704. https://doi.org/10.1029/2005GL025452.

Emmer I, **Needelman B**, **Emmett-Mattox S**, **Crooks S**, **Megonigal P**, **Myers D**, **Oreska M**, **McGlathery K and Shoch DJVCS**, **Washington, DC** (2015a) VM0033 Methodology for Tidal Wetland and Seagrass Restoration, v1.0.

Emmer I, **von Unger M**, **Needelman B**, **Crooks S and Emmett-Mattox S** (2015b) *Coastal Blue Carbon in Practice: A Manual for Using the VCS Methodology for Tidal Wetland and Seagrass Restoration VM0033*. Arlington, Virginia: Restore America's Estuaries and Silvestrum.

Fornari M, **Giannini PCF and Junior DRN** (2012) Facies associations and controls on the evolution from a coastal bay to a lagoon system, Santa Catarina Coast, Brazil. *Marine Geology* **323**, 56–68.

Forster P, **Storelvmo T**, **Armour K**, **Collins W**, **Dufresne J-L**, **Frame D**, **Lunt DJ**, **Mauritsen T**, **Palmer MD**, **Watanabe M**, **Wild M and Zhang H** (2021) The earth's energy budget, climate feedbacks, and climate sensitivity. In Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekçi O, Yu R and Zhou B (eds.), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY, USA: Cambridge University Press, pp. 923–1054. https://doi.org/10.1017/9781009157896.009

França MC, **Cohen MC**, **Pessenda LC**, **Rossetti DF**, **Lorente FL**, **Junior AÁB**, **Guimarães JT**, **Friaes Y and Macario K** (2013) Mangrove vegetation changes on Holocene terraces of the Doce River, Southeastern Brazil. *Catena* **110**, 59–69.

Friess DA, **Rogers K**, **Lovelock CE**, **Krauss KW**, **Hamilton SE**, **Lee SY**, **Lucas R**, **Primavera J**, **Rajkaran A and Shi S** (2019) The state of the World's Mangrove Forests: Past, present, and future. *Annual Review of Environment and Resources* **44**(1), 89–115.

Friess DA, **Yando ES**, **Abuchahla GM**, **Adams JB**, **Cannicci S**, **Canty SW**, **Cavanaugh KC**, **Connolly RM**, **Cormier N and Dahdouh-Guebas F** (2020) Mangroves give cause for conservation optimism, for now. *Current Biology* **30**(4), R153–R154.

Galik C, **Baker JS**, **Daigneault A and Latta G** (2022) Crediting temporary forest carbon: Retrospective and empirical perspectives on accounting options. *Frontiers in Forests and Global Change Biology* **5**, 933020.

Gedan KB, **Silliman BR and Bertness MD** (2009) Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science* **1**(1), 117–141.

Gehrels WR (1999) Middle and late Holocene Sea-level changes in eastern Maine reconstructed from foraminiferal saltmarsh stratigraphy and AMS 14C dates on basal peat. *Quaternary Research* **52**(3), 350–359.

Godoy MD and de Lacerda LD (2015) Mangroves response to climate change: A review of recent findings on mangrove extension and distribution. *Anais da Academia Brasileira de Ciências* **87**, 651–667.

Goldberg L, **Lagomasino D**, **Thomas N and Fatoyinbo T** (2020) Global declines in human-driven mangrove loss. *Global Change Biology* **26**(10), 5844–5855.

Greiner JT, **McGlathery KJ**, **Gunnell J and McKee BA** (2013) Seagrass restoration enhances "blue carbon" sequestration in coastal waters. *PLoS One* **8**(8), e72469.

Grindrod J (2002) Late quaternary mangrove pollen records from continental shelf and ocean cores in the north Australian-Indonesian region. In Kershaw P,

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

David B, Tapper N, Penny D and Brown J (eds.), *Bridging Wallace's Line: The Environmental and Cultural History and Dynamics of the Australian-Southeast Asian Region*. Reiskirchen Germany: Catena-Verlag, pp. 119–146.

Grindrod J, **Moss P and Kaars SVD** (1999) Late quaternary cycles of mangrove development and decline on the north Australian continental shelf. *Journal of Quaternary Science* **14**(5), 465–470.

Griscom BW, **Adams J**, **Ellis PW**, **Houghton RA**, **Lomax G**, **Miteva DA**, **Schlesinger WH**, **Shoch D**, **Siikamäki JV**, **Smith P**, **Woodbury P**, **Zganjar C**, **Blackman A**, **Campari J**, **Conant RT**, **Delgado C**, **Elias P**, **Gopalakrishna T**, **Hamsik MR**, **Herrero M**, **Kiesecker J**, **Landis E**, **Laestadius L**, **Leavitt SM**, **Minnemeyer S**, **Polasky S**, **Potapov P**, **Putz FE**, **Sanderman J**, **Silvius M**, **Wollenberg E and Fargione J** (2017) Natural climate solutions. *Proceedings of the National Academy of Sciences* **114**(44), 11645.

Hagger V, **Waltham NJ and Lovelock CE** (2022) Opportunities for coastal wetland restoration for blue carbon with co-benefits for biodiversity, coastal fisheries, and water quality. *Ecosystem Services* **55**, 101423.

Haigh ID, **Dornbusch U**, **Brown J**, **Lyddon C**, **Nicholls RJ**, **Penning-Roswell E and Sayers P** (2022) Climate change impacts on coastal flooding relevant to the UK and Ireland. *MCCIP Science Review* **2022**, 1–18.

Hait AK and Behling H (2009) Holocene mangrove and coastal environmental changes in the Western Ganga–Brahmaputra Delta, India. *Vegetation History and Archaeobotany* **18**(2), 159–169.

Hanebuth T, **Stattegger K and Grootes PM** (2000) Rapid flooding of the Sunda Shelf: A late-glacial sea-level record. *Science* **288**(5468), 1033–1035.

Hashimoto TR, **Saintilan N and Haberle SG** (2006) Mid-Holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond River Estuary, New South Wales, Australia. *Geographical Research* **44**(1), 63–76.

Haywood BJ, **Hayes MP**, **White JR and Cook RL** (2020) Potential fate of wetland soil carbon in a deltaic coastal wetland subjected to high relative sea level rise. *Science of the Total Environment* **711**, 135185.

Herr D, **Blum J**, **Himes-Cornell A and Sutton-Grier A** (2019) An analysis of the potential positive and negative livelihood impacts of coastal carbon offset projects. *Journal of Environmental Management* **235**, 463–479.

Hopkinson CS, **Morris JT**, **Fagherazzi S**, **Wollheim WM and Raymond PA** (2018) Lateral marsh edge erosion as a source of sediments for vertical marsh accretion. *Journal of Geophysical Research: Biogeosciences* **123**(8), 2444–2465.

Horton BP, **Gibbard PL**, **Mine G**, **Morley R**, **Purintavaragul C and Stargardt JM** (2005) Holocene sea levels and palaeoenvironments, Malay-Thai Peninsula, Southeast Asia. *The Holcene* **15**(8), 1199–1213.

Horton BP, **Shennan I**, **Bradley SL**, **Cahill N**, **Kirwan M**, **Kopp RE and Shaw TA** (2018) Predicting marsh vulnerability to sea-level rise using Holocene relative sea-level data. *Nature Communications* **9**(1), 1–7.

Howard JL, **Creed JC**, **Aguiar MV and Fourqurean JW** (2018) CO_2 released by carbonate sediment production in some coastal areas may offset the benefits of seagrass "blue carbon" storage. *Limnology and Oceanography* **63**(1), 160–172.

Howard J, **Hoyt S**, **Isensee K**, **Pidgeon E and Telszewski M** (2014) *Coastal Blue Carbon: Methods for Assessing Carbon Stocks and Emissions Factors in Mangroves, Tidal Salt Marshes, and Seagrass Meadows*. Arlington, Virginia, USA: Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature.

IPCC (2021) Summary for policymakers. Climate change 2021: The physical science basis. In Masson-Delmotte V, Zhai P, Pirani A, et al. (eds), *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.

Iyer GC, **Edmonds JA**, **Fawcett AA**, **Hultman NE**, **Alsalam J**, **Asrar GR**, **Calvin KV**, **Clarke LE**, **Creason J and Jeong M** (2015) The contribution of Paris to limit global warming to 2°C. *Environmental Research Letters* **10**(12), 125002.

Jayathilake DRM and Costello MJ (2018) A modelled global distribution of the seagrass biome. *Biological Conservation* **226**, 120–126.

Jeffrey LC, **Reithmaier G**, **Sippo JZ**, **Johnston SG**, **Tait DR**, **Harada Y and Maher DT** (2019) Are methane emissions from mangrove stems a cryptic carbon loss pathway? Insights from a catastrophic forest mortality. *New Phytologist* **224**(1), 146–154.

Jervey M (1988) Quantitative geological modeling of siliciclastic rock sequences and their seismic expression. In Wilgus, CK, Hastings, BS, Posamentier, H, et al (eds.), *Sea Level Changes: An Integrated Approach: Society of Economic Paleontologists and Mineralogists Special Publication*, vol. 42. Tulsa, Oklahoma: SEPM (Society for Sedimentary Geology), pp. 47–69.

Jin-Eong O, **Khoon GW and Clough B** (1995) Structure and productivity of a 20-year-old stand of Rhizophora apiculata Bl. Mangrove forest. *Journal of Biogeography* **22**(2/3), 417–424.

Jones MC, **Wingard GL**, **Stackhouse B**, **Keller K**, **Willard D**, **Marot M**, **Landacre B and Bernhardt CE** (2019) Rapid inundation of southern Florida coastline despite low relative sea-level rise rates during the late-Holocene. *Nature Communications* **10**(1), 3231.

Kearney MS, **Stevenson JC and Ward LG** (1994) Spatial and temporal changes in marsh vertical accretion rates at Monie Bay: Implications for sea-level rise. *Journal of Coastal Research* **10**(4), 1010–1020.

Kelleway JJ, **Saintilan N**, **Macreadie PI and Ralph PJ** (2016a) Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes. *Ecosystems* **19**(5), 865–880.

Kelleway JJ, **Saintilan N**, **Macreadie PI**, **Skilbeck CG**, **Zawadzki A and Ralph PJ** (2016b) Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Global Change Biology* **22**(3), 1097–1109.

Kennedy D, **Wong V and Jacobsen G** (2021) Holocene infill of the Anglesea Estuary, Victoria: A keep-up estuary in a geologically constrained environment. *Australian Journal of Earth Sciences* **68**, 1–13.

Kerswell AP (2006) Global biodiversity patterns of benthic marine algae. *Ecology* **87**(10), 2479–2488.

Khan NS, **Ashe E**, **Shaw TA**, **Vacchi M**, **Walker J**, **Peltier W**, **Kopp RE and Horton BP** (2015) Holocene relative sea-level changes from near-, intermediate-, and far-field locations. *Current Climate Change Reports* **1**(4), 247–262.

Kihara Y, **Dannoura M and Ohashi M** (2022) Estimation of fine root production, mortality, and decomposition by using two core methods and litterbag experiments in a mangrove forest. *Ecological Research* **37**(1), 53–66.

Kirwan ML, **Guntenspergen GR and Langley J** (2014) Temperature sensitivity of organic-matter decay in tidal marshes. *Biogeosciences* **11**(17), 4801–4808.

Kirwan ML and Mudd SM (2012) Response of salt-marsh carbon accumulation to climate change. *Nature* **489**(7417), 550–553.

Koch EW (2001) Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* **24**(1), 1–17.

Komiyama A, **Ong JE and Poungparn S** (2008) Allometry, biomass, and productivity of mangrove forests: A review. *Aquatic Botany* **89**(2), 128–137.

Krause-Jensen D and Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. *Nature Geoscience* **9**(10), 737–742.

Krauss KW, **Demopoulos AW**, **Cormier N**, **From A**, **McClain-Counts JP and Lewis RR** (2018) Ghost forests of Marco Island: Mangrove mortality driven by belowground soil structural shifts during tidal hydrologic alteration. *Estuarine, Coastal and Shelf Science* **212**, 51–62.

Kroeger KD, **Crooks S**, **Moseman-Valtierra S and Tang J** (2017) Restoring tides to reduce methane emissions in impounded wetlands: A new and potent blue carbon climate change intervention. *Scientific Reports* **7**(1), 11914.

Lambeck K, **Rouby H**, **Purcell A**, **Sun Y and Sambridge M** (2014) Sea level and global ice volumes from the last glacial maximum to the Holocene. *Proceedings of the National Academy of Sciences* **111**(43), 15296–15303.

Lamont K, **Saintilan N**, **Kelleway JJ**, **Mazumder D and Zawadzki A** (2020) Thirty-year repeat measures of mangrove above-and below-ground biomass reveals unexpectedly high carbon sequestration. *Ecosystems* **23**(2), 370–382.

Langley JA, **McKee KL**, **Cahoon DR**, **Cherry JA and Megonigal JP** (2009) Elevated CO_2 stimulates marsh elevation gain, counterbalancing sea-level rise. *Proceedings of the National Academy of Sciences* **106**(15), 6182–6186.

Lee SY, **Hamilton S**, **Barbier EB**, **Primavera J and Lewis RR** (2019) Better restoration policies are needed to conserve mangrove ecosystems. *Nature Ecology and Evolution* **3**(6), 870–872.

Li Z, **Saito Y**, **Mao L**, **Tamura T**, **Song B**, **Zhang Y**, **Lu A**, **Sieng S and Li J** (2012) Mid-Holocene mangrove succession and its response to sea-level change in the upper Mekong River delta, Cambodia. *Quaternary Research* **78**(2), 386–399.

Lichacz W, **Hardiman S and Buckney R** (2009) Below-ground biomass in some intertidal wetlands in New South Wales. *Wetlands(Australia)* **4**(2), 56–62.

Lovelock CE, **Adame MF**, **Bradley J**, **Dittmann S**, **Hagger V**, **Hickey SM**, **Hutley LB**, **Jones A**, **Kelleway JJ and Lavery PS** (2022a) An Australian blue

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

carbon method to estimate climate change mitigation benefits of coastal wetland restoration. *Restoration Ecology*, e13739. https://doi.org/10.1111/rec.13739

Lovelock CE, Adame MF, Butler DW, Kelleway JJ, Dittmann S, Fest B, King KJ, Macreadie PI, Mitchell K and Newnham MJGEC (2022b) Modeled approaches to estimating blue carbon accumulation with mangrove restoration to support a blue carbon accounting method for Australia. *Limnology and Oceanography* **67**, S50–S60.

Lovelock CE, Barbier E and Duarte CM (2022c) Tackling the mangrove restoration challenge. *PLoS Biology* **20**(10), e3001836.

Lovelock CE and Duarte CM (2019) Dimensions of blue carbon and emerging perspectives. *Biology Letters* **15**(3), 20180781.

Lovelock CE and Reef R (2020) Variable impacts of climate change on blue carbon. *One Earth* **3**(2), 195–211.

Ma S, He F, Tian D, Zou D, Yan Z, Yang Y, Zhou T, Huang K, Shen H and Fang J (2018) Variations and determinants of carbon content in plants: A global synthesis. *Biogeosciences* **15**(3), 693–702.

Mack SK, Lane RR, Deng J, Morris JT and Bauer JJ (2023) Wetland carbon models: Applications for wetland carbon commercialization. *Ecological Modelling* **476**, 110228.

Macreadie PI, Anton A, Raven JA, Beaumont N, Connolly RM, Friess DA, Kelleway JJ, Kennedy H, Kuwae T, Lavery PS, Lovelock CE, Smale DA, Apostolaki ET, Atwood TB, Baldock J, Bianchi TS, Chmura GL, Eyre BD, Fourqurean JW, Hall-Spencer JM, Huxham M, Hendriks IE, Krause-Jensen D, Laffoley D, Luisetti T, Marbà N, Masque P, KJ MG, Megonigal JP, Murdiyarso D, Russell BD, Santos R, Serrano O, Silliman BR, Watanabe K and Duarte CM (2019) The future of blue carbon science. *Nature Communications* **10**(1), 3998.

Macreadie PI, Costa MD, Atwood TB, Friess DA, Kelleway JJ, Kennedy H, Lovelock CE, Serrano O and Duarte CM (2021) Blue carbon as a natural climate solution. *Nature Reviews Earth and Environment* **2**(12), 826–839.

Macreadie PI, Robertson AI, Spinks B, Adams MP, Atchison JM, Bell-James J, Bryan BA, Chu L, Filbee-Dexter K and Drake L (2022) Operationalizing marketable blue carbon. *One Earth* **5**(5), 485–492.

Madsen JD, Chambers PA, James WF, Koch EW and Westlake DF (2001) The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* **444**(1), 71–84.

Maher DT, Call M, Santos IR and Sanders CJ (2018) Beyond burial: Lateral exchange is a significant atmospheric carbon sink in mangrove forests. *Biology Letters* **14**(7), 20180200.

Malerba ME, Friess DA, Peacock M, Grinham A, Taillardat P, Rosentreter JA, Webb J, Iram N, Al-Haj AN and Macreadie PI (2022) Methane and nitrous oxide emissions complicate the climate benefits of teal and blue carbon wetlands. *One Earth* **5**(12), 1336–1341.

Marx SK, Knight JM, Dwyer PG, Child DP, Hotchkis MA and Zawadzki A (2020) Examining the response of an eastern Australian mangrove forest to changes in hydro-period over the last century. *Estuarine, Coastal and Shelf Science* **241**, 106813.

McKee KL (2011) Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuarine, Coastal and Shelf Science* **91**(4), 475–483.

McKee KL, Cahoon DR and Feller IC (2007) Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* **16**(5), 545–556.

McKee K, Rogers K and Saintilan N (2012) Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. In Middleton, BA (ed.), *Global Change and the Function and Distribution of Wetlands*, vol. 1. Netherlands: Springer, pp. 63–96.

McLeod E, Chmura GL, Bouillon S, Salm R, Björk M, Duarte CM, Lovelock CE, Schlesinger WH and Silliman BR (2011) A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment* **9**(10), 552–560.

Mcowen C, Weatherdon L, Bochove J-W, Sullivan E, Blyth S, Zockler C, Stanwell-Smith D, Kingston N, Martin C, Spalding M and Fletcher S (2017) A global map of saltmarshes. *Biodiversity Data Journal* **5**, e11764.

Michael PS (2013) Ecological impacts and management of acid sulphate soil: A review. *Asian Journal of Water, Environment and Pollution* **10**(4), 13–24.

Morris JT, Sundareshwar PV, Nietch CT, Kjerfve B and Cahoon DR (2002) Responses of coastal wetlands to rising sea-levels. *Ecology* **83**(10), 2869–2877.

Mudd SM, Howell SM and Morris JT (2009) Impact of dynamic feedbacks between sedimentation, sea-level rise, and biomass production on near-surface marsh stratigraphy and carbon accumulation. *Estuarine, Coastal and Shelf Science* **82**(3), 377–389.

Mueller P, Schile-Beers LM, Mozdzer TJ, Chmura GL, Dinter T, Kuzyakov Y, de Groot AV, Esselink P, Smit C and D'Alpaos A (2018) Global-change effects on early-stage decomposition processes in tidal wetlands–implications from a global survey using standardized litter. *Biogeosciences* **15**(10), 3189–3202.

Muhammad-Nor SM, Huxham M, Salmon Y, Duddy SJ, Mazars-Simon A, Mencuccini M, Meir P and Jackson G (2019) Exceptionally high mangrove root production rates in the Kelantan Delta, Malaysia; an experimental and comparative study. *Forest Ecology and Management* **444**, 214–224.

Murray NJ, Worthington TA, Bunting P, Duce S, Hagger V, Lovelock CE, Lucas R, Saunders MI, Sheaves M and Spalding MJS (2022) High-resolution mapping of losses and gains of Earth's tidal wetlands. *Science* **376**(6594), 744–749.

Murray-Wallace CV and Woodroffe CD (2014) *Quaternary Sea-Level Changes: A Global Perspective*. Cambridge: Cambridge University Press.

Neumann AC and Macintyre IG (1985) Reef response of sea level rise: Keep-up, catch-up or give-up. In Gabrie C, Toffart JL and Salvat B (eds.), *Proceedings of the Fifth International Coral Reef Congress, Tahiti, 27 May–1 June 1985: Volume 3, Symposia and Seminars (A)*, pp. 105–110.

Nicholas W, Nichol S, Howard F, Picard K, Dulfer H, Radke L, Carroll A, Tran M and Siwabessy P (2014) Pockmark development in the petrel sub-basin, Timor Sea, Northern Australia: Seabed habitat mapping in support of CO_2 storage assessments. *Continental Shelf Research* **83**, 129–142.

Orson RA, Warren RS and Niering WA (1998) Interpreting sea level rise and rates of vertical marsh accretion in a Southern New England tidal salt marsh. *Estuarine, Coastal and Shelf Science* **47**(4), 419–429.

Osland MJ, Enwright NM, Day RH, Gabler CA, Stagg CL and Grace JB (2016) Beyond just sea-level rise: Considering macroclimatic drivers within coastal wetland vulnerability assessments to climate change. *Global Change Biology* **22**(1), 1–11.

Osland MJ, Feher LC, Griffith KT, Cavanaugh KC, Enwright NM, Day RH, Stagg CL, Krauss KW, Howard RJ, Grace JB and Rogers K (2017) Climatic controls on the global distribution, abundance, and species richness of mangrove forests. *Ecological Monographs* **87**(2), 341–359.

Osland MJ, Feher LC, Spivak AC, Nestlerode JA, Almario AE, Cormier N, From AS, Krauss KW, Russell MJ and Alvarez F (2020) Rapid peat development beneath created, maturing mangrove forests: Ecosystem changes across a 25-yr chronosequence. *Ecological Applications* **30**(4), e02085.

Ouyang X and Lee S (2014) Updated estimates of carbon accumulation rates in coastal marsh sediments. *Biogeosciences* **11**(18), 5057–5071.

Owers CJ, Woodroffe CD, Mazumder D and Rogers K (2022) Carbon storage in coastal wetlands is related to elevation and how it changes over time. *Estuarine, Coastal and Shelf Science* **267**, 107775.

Parkinson RW (1989) Decelerating holocene sea-level rise and its influence on Southwest Florida coastal evolution; A transgressive/regressive stratigraphy. *Journal of Sedimentary Research* **59**(6), 960–972.

Parkinson RW, Ron DD and White JR (1994) Holocene sea-level rise and the fate of mangrove forests within the wider Caribbean Region. *Journal of Coastal Research* **10**(4), 1077–1086.

Pendleton L, Donato DC, Murray BC, Crooks S, Jenkins WA, Sifleet S, Craft C, Fourqurean JW, Kauffman JB and Marbà N (2012) Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS One* **7**(9), e43542.

Pham TD, Xia J, Ha NT, Bui DT, Le NN and Tekeuchi W (2019) A review of remote sensing approaches for monitoring blue carbon ecosystems: Mangroves, Seagrassesand salt marshes during 2010–2018. *Sensors* **19**(8), 1933.

Poffenbarger H, Needelman B and Megonigal J (2011) Salinity influence on methane emissions from tidal marshes. *Wetlands* **31**(5), 831–842.

Pons L, Van Breemen N and Driessen P (1982) Physiography of coastal sediments and development of potential soil acidity. *Acid Sulfate Weathering* **10**, 1–18.

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

Proske U and Haberle SG (2012) Island ecosystem and biodiversity dynamics in Northeastern Australia during the Holocene: Unravelling short-term impacts and long-term drivers. *The Holocene* **22**(10), 1097–1111.

Punwong P, Selby K and Marchant R (2018) Holocene mangrove dynamics and relative sea-level changes along the Tanzanian Coast, East Africa. *Estuarine, Coastal and Shelf Science* **212**, 105–117.

Quisthoudt K, Schmitz N, Randin C, Dahdouh-Guebas F, Robert ER and Koedam N (2012) Temperature variation among mangrove latitudinal range limits worldwide. *Trees* **26**(6), 1919–1931.

Radabaugh KR, Powell CE, Bociu I, Clark BC and Moyer RP (2017) Plant size metrics and organic carbon content of Florida salt marsh vegetation. *Wetlands Ecology and Management* **25**(4), 443–455.

Rahman MM, Zimmer M, Ahmed I, Donato D, Kanzaki M and Xu M (2021) Co-benefits of protecting mangroves for biodiversity conservation and carbon storage. *Nature Communications* **12**(1), 1–9.

Raven J (2018) Blue carbon: Past, present and future, with emphasis on macroalgae. *Biology Letters* **14**(10), 20180336.

Raw J, Riddin T, Wasserman J, Lehman T, Bornman T and Adams J (2020) Salt marsh elevation and responses to future sea-level rise in the Knysna Estuary, South Africa. *African Journal of Aquatic Science* **45**(1–2), 49–64.

Redfield AC (1972) Development of a New England salt marsh. *Ecological Monographs* **42**(2), 201–237.

Reed DJ (1990) The impact of sea-level rise on coastal salt marshes. *Progress in Physical Geography* **14**(4), 465–481.

Reef R, Spencer T, Möller I, Lovelock CE, Christie EK, McIvor AL, Evans BR and Tempest JA (2017) The effects of elevated CO_2 and eutrophication on surface elevation gain in a European salt marsh. *Global Change Biology* **23**(2), 881–890.

Ribeiro SR, Batista E.J.L, Cohen M.C.L, França MC, Pessenda LCR, Fontes NA, Alves ICC and Bendassolli JA (2018) Allogenic and autogenic effects on mangrove dynamics from the Ceará Mirim River, North-Eastern Brazil, during the middle and late Holocene. *Earth Surface Processes and Landforms* **43**(8), 1622–1635.

Rogers K (2021) Accommodation space as a framework for assessing the response of mangroves to relative sea-level rise. *Singapore Journal of Tropical Geography* **42**(2), 163–183.

Rogers K, Kelleway JJ, Saintilan N, Megonigal JP, Adams JB, Holmquist JR, Lu M, Schile-Beers L, Zawadzki A, Mazumder D and Woodroffe CD (2019a) Wetland carbon storage controlled by millennialscale variation in relative sea-level rise. *Nature* **567**, 91–95.

Rogers K, Lal KK, Asbridge EF and Dwyer PG (2022) *Coastal wetland rehabilitation first-pass prioritisation for blue carbon and associated co-benefits. Marine and Freshwater Research.* https://doi.org/10.1071/MF22014

Rogers K, Macreadie PI, Kelleway JJ and Saintilan N (2019b) Blue carbon in coastal landscapes: A spatial framework for assessment of stocks and additionality. *Sustainability Science* **14**(2), 453–467.

Rogers K and Woodroffe CD (2014) Tidal flats and salt marshes. In Masselink G and Gehrels R (eds.), *Coastal Environments and Global Change*. Oxford, UK: Wiley and Sons.

Romañach SS, DeAngelis DL, Koh HL, Li Y, Teh SY, Barizan RSR and Zhai L (2018) Conservation and restoration of mangroves: Global status, perspectives, and prognosis. *Ocean and Coastal Management* **154**, 72–82.

Rosentreter JA, Al-Haj AN, Fulweiler RW and Williamson P (2021a) Methane and nitrous oxide emissions complicate coastal blue carbon assessments. *Global Biogeochemical Cycles* **35**(2), e2020GB006858.

Rosentreter JA, Borges AV, Deemer BR, Holgerson MA, Liu S, Song C, Melack J, Raymond PA, Duarte CM and Allen GH (2021b) Half of global methane emissions come from highly variable aquatic ecosystem sources. *Nature Geoscience* **14**(4), 225–230.

Rosentreter JA, Maher DT, Erler DV, Murray RH and Eyre BD (2018) Methane emissions partially offset "blue carbon" burial in mangroves. *Science Advances* **4**(6), eaao4985.

Rovai A, Riul P, Twilley R, Castañeda-Moya E, Rivera-Monroy V, Williams A, Simard M, Cifuentes-Jara M, Lewis R and Crooks S (2016) Scaling mangrove aboveground biomass from site-level to continental-scale. *Global Ecology and Biogeography* **25**(3), 286–298.

Rovai AS, Twilley RR, Castañeda-Moya E, Riul P, Cifuentes-Jara M, Manrow-Villalobos M, Horta PA, Simonassi JC, Fonseca AL and Pagliosa PR (2018) Global controls on carbon storage in mangrove soils. *Nature Climate Change* **8**, 534–538.

Sadat-Noori M, Rankin C, Rayner D, Heimhuber V, Gaston T, Drummond C, Chalmers A, Khojasteh D and Glamore W (2021) Coastal wetlands can be saved from sea level rise by recreating past tidal regimes. *Scientific Reports* **11**(1), 1196.

Saderne V, Geraldi NR, Macreadie PI, Maher DT, Middelburg J, Serrano O, Almahasheer H, Arias-Ortiz A, Cusack M and BDJNc E (2019) Role of carbonate burial in Blue Carbon budgets. *Nature Communications* **10**(1), 1–9.

Saintilan N (1997) Above- and below-ground biomass of mangroves in a subtropical estuary. *Marine and Freshwater Research* **48**(7), 601–604.

Saintilan N, Khan N, Ashe E, Kelleway J, Rogers K, Woodroffe CD and Horton B (2020) Thresholds of mangrove survival under rapid sea level rise. *Science* **368**(6495), 1118–1121.

Saintilan N, Kovalenko KE, Guntenspergen G, Rogers K, Lynch JC, Cahoon DR, Lovelock CE, Friess DA, Ashe E and Krauss KW (2022) Constraints on the adjustment of tidal marshes to accelerating sea level rise. *Science* **377** (6605), 523–527.

Saintilan N, Rogers K, Mazumder D and Woodroffe C (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in Southeastern Australian coastal wetlands. *Estuarine, Coastal and Shelf Science* **128**, 84–92.

Saintilan N, Wilson NC, Rogers K, Rajkaran A and Krauss KW (2014) Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology* **20**, 147–157.

Sanderman J, Hengl T, Fiske G, Solvik K, Adame MF, Benson L, Bukoski JJ, Carnell P, Cifuentes-Jara M and Donato D (2018) A global map of mangrove forest soil carbon at 30 m spatial resolution. *Environmental Research Letters* **13**(5), 055002.

Sanders CJ, Maher DT, Tait DR, Williams D, Holloway C, Sippo JZ and Santos IR (2016) Are global mangrove carbon stocks driven by rainfall? *Journal of Geophysical Research: Biogeosciences* **121**(10), 2600–2609.

Sani DA, Hashim M and Hossain MS (2019) Recent advancement on estimation of blue carbon biomass using satellite-based approach. *International Journal of Remote Sensing* **40**(20), 7679–7715.

Sapkota Y and White JR (2020) Carbon offset market methodologies applicable for coastal wetland restoration and conservation in the United States: A review. *Science of the Total Environment* **701**, 134497.

Scholl DW (1964) Recent sedimentary record in mangrove swamps and rise in sea level over the Southwestern Coast of Florida: Part 1. *Marine Geology* **1**(4), 344–366.

Schuerch M, Spencer T, Temmerman S, Kirwan ML, Wolff C, Lincke D, McOwen CJ, Pickering MD, Reef R, Vafeidis AT, Hinkel J, Nicholls RJ and Brown S (2018) Future response of global coastal wetlands to sea-level rise. *Nature* **561**(7722), 231–234.

Sefton JP, Woodroffe SA and Ascough P (2021) Radiocarbon dating of mangrove sediments. In Friess DA and Sidik F (eds) *Dynamic Sedimentary Environments of Mangrove Coasts*. Amsterdam: Elsevier, pp. 199–210.

Sherrod CL and McMillan C (1985) The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contributions in Marine Science* **28**, 129–140

Silvestri S, Defina A and Marani M (2005) Tidal regime, salinity and salt marsh plant zonation. *Estuarine, Coastal and Shelf Science* **62**(1–2), 119–130.

Simard M, Fatoyinbo L, Smetanka C, Rivera-Monroy VH, Castañeda-Moya E, Thomas N and Van der Stocken T (2019) Mangrove canopy height globally related to precipitation, temperature and cyclone frequency. *Nature Geoscience* **12**(1), 40.

Simpson L, Stein C, Osborne T and Feller I (2019) Mangroves dramatically increase carbon storage after 3 years of encroachment. *Hydrobiologia* **834**(1), 13–26.

Sowers T (2010) Atmospheric methane isotope records covering the Holocene period. *Quaternary Science Reviews* **29**(1–2), 213–221.

Spivak AC, Sanderman J, Bowen JL, Canuel EA and Hopkinson CS (2019) Global-change controls on soil-carbon accumulation and loss in coastal vegetated ecosystems. *Nature Geoscience* **12**(9), 685–692.

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

Thursby G, **Chintala M**, **Stetson D**, **Wigand C and Champlin D** (2002) A rapid, non-destructive method for estimating aboveground biomass of salt marsh grasses. *Wetlands* **22**(3), 626–630.

Törnqvist TE, **Cahoon DR**, **Morris JT and Day JW** (2021) Coastal wetland resilience, accelerated sea-level rise, and the importance of timescale. *Advances* **2**(1), e2020AV000334.

Tran N and Ngo QT (2000) Development history of deposits in the Quaternary of Vietnam. In: Nguyen TV (ed.), *The Weathering Crust and Quaternary Sediments in Vietnam. Department of Geology and Minerals of Vietnam, Hanoi*, pp. 177–192.

Vacchi M, **Engelhart SE**, **Nikitina D**, **Ashe EL**, **Peltier WR**, **Roy K**, **Kopp RE and Horton BP** (2018) Postglacial relative sea-level histories along the eastern Canadian coastline. *Quaternary Science Reviews* **201**, 124–146.

Van Breemen N (1982) Genesis, morphology, and classification of acid sulfate soils in coastal plains. *Acid Sulfate Weathering* **10**, 95–108.

Van Dam BR, **Zeller MA**, **Lopes C**, **Smyth AR**, **Böttcher ME**, **Osburn CL**, **Zimmerman T**, **Pröfrock D**, **Fourqurean JW and Thomas H** (2021) Calcification-driven CO_2 emissions exceed "blue carbon" sequestration in a carbonate seagrass meadow. *Science Advances* **7**(51), eabj1372.

Van de Broek M, **Vandendriessche C**, **Poppelmonde D**, **Merckx R**, **Temmerman S and Govers G** (2018) Long-term organic carbon sequestration in tidal marsh sediments is dominated by old-aged allochthonous inputs in a macrotidal estuary. *Global Change Biology* **24**(6), 2498–2512.

Vilanova I, **Prieto AR and Espinosa M** (2006) Palaeoenvironmental evolution and sea-level fluctuations along the southeastern Pampa grasslands coast of Argentina during the Holocene. *Journal of Quaternary Science: Published for the Quaternary Research Association* **21**(3), 227–242.

Wang F, **Lu X**, **Sanders CJ and Tang J** (2019) Tidal wetland resilience to sea level rise increases their carbon sequestration capacity in United States. *Nature Communications* **10**(1), 1–11.

Wang F, **Sanders CJ**, **Santos IR**, **Tang J**, **Schuerch M**, **Kirwan ML**, **Kopp RE**, **Zhu K**, **Li X and Yuan J** (2021) Global blue carbon accumulation in tidal wetlands increases with climate change. *National Science Review* **8**(9), nwaa296.

Wang X, **Sun X**, **Wang P and Stattegger K** (2009) Vegetation on the Sunda shelf, South China Sea, during the last glacial maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **278**(1–4), 88–97.

Webb EL, **Friess DA**, **Krauss KW**, **Cahoon DR**, **Guntenspergen GR and Phelps J** (2013) A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. *Nature Climate Change* **3**(5), 458–465.

West RC (1956) Mangrove swamps of the Pacific Coast of Colombia. *Annals of the Association of American Geographers* **46**(1), 98–121.

Williamson P and Gattuso J-P (2022) Carbon removal using coastal blue carbon ecosystems is uncertain and unreliable, with questionable climatic cost-effectiveness. *Frontiers in Climate* **4**, 853666.

Woodroffe CD (1981) Mangrove swamp stratigraphy and Holocene transgression, grand Cayman Island, West Indies. *Marine Geology* **41**(3), 271–294.

Woodroffe CD and Davies G (2009) The morphology and development of tropical coastal wetlands. In Perillo G, Wolanski E, Cahoon D and Brinson M (eds.), *Coastal Wetlands: An Integrated Ecosystem Approach*. Amsterdam, The Netherlands and Oxford, United Kindgdom: Elsevier, pp. 65–88.

Woodroffe CD, **Mulrennan ME and Chappell J** (1993) Estuarine infill and coastal progradation, Southern van Diemen Gulf, Northern Australia. *Sedimentary Geology* **83**(3–4), 257–275.

Woodroffe CD and Murray-Wallace CV (2012) Sea-level rise and coastal change: The past as a guide to the future. *Quaternary Science Reviews* **54**, 4–11.

Woodroffe CD, **Thom BG and Chappell J** (1985) Development of widespread mangrove swamps in mid-Holocene times in Northern Australia. *Nature* **317**, 711–713.

Worthington TA, **Zu Ermgassen PS**, **Friess DA**, **Krauss KW**, **Lovelock CE**, **Thorley J**, **Tingey R**, **Woodroffe CD**, **Bunting P and Cormier N** (2020) A global biophysical typology of mangroves and its relevance for ecosystem structure and deforestation. *Scientific Reports* **10**(1), 1–11.

Ximenes A, **Maeda E**, **Arcoverde G and Dahdouh-Guebas F** (2016) Spatial assessment of the bioclimatic and environmental factors driving mangrove tree species' distribution along the Brazilian coastline. *Remote Sensing* **8**(6), 451.

Xiong Y, **Liao B and Wang F** (2018) Mangrove vegetation enhances soil carbon storage primarily through in situ inputs rather than increasing allochthonous sediments. *Marine Pollution Bulletin* **131**, 378–385.

https://doi.org/10.1017/cft.2023.17 Published online by Cambridge University Press

CSIRO PUBLISHING

SPECIAL ISSUE

Marine and Freshwater Research, 2022, **73**, 1255–1262
https://doi.org/10.1071/MF21233

Perspective

Australian forested wetlands under climate change: collapse or proliferation?

Neil Saintilan[A,J], *Emma Asbridge*[B,C], *Richard Lucas*[D], *Kerrylee Rogers*[B,C], *Li Wen*[E], *Megan Powell*[A,E], *Matthew J. Colloff*[F], *Jose F. Rodriguez*[G,H], *Patricia M. Saco*[G,H], *Steven Sandi*[G,H], *Tien Dat Pham*[A] and *Leo Lymburner*[I]

[A]Department of Earth and Environmental Sciences, Macquarie University, Sydney, NSW, Australia.
[B]School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW, Australia.
[C]GeoQuEST Research Centre, University of Wollongong, Wollongong, NSW, Australia.
[D]Aberystwyth University, Aberystwyth, Wales, UK.
[E]Science, Economics and Insights Division, NSW Department of Planning, Industry and Environment, Sydney, NSW, Australia.
[F]Fenner School of Environment and Society, Australian National University, Canberra, ACT, Australia.
[G]Centre for Water Security and Environmental Sustainability, University of Newcastle, Newcastle, NSW, Australia.
[H]School of Engineering, University of Newcastle, Newcastle, NSW, Australia.
[I]Geoscience Australia, Canberra, ACT, Australia.
[J]Corresponding author. Email: neil.saintilan@mq.edu.au

Abstract. Climatically driven perturbations (e.g. intense drought, fire, sea surface temperature rise) can bring ecosystems that are already stressed by long-term climate change and other anthropogenic impacts to a point of collapse. Recent reviews of the responses of Australian ecosystems to climate change and associated stressors have suggested widespread ecosystem collapse is occurring across multiple biomes. Two commonly cited case studies concern forested wetland ecosystems: mangrove forest dieback in northern Australia (2015–16) and riverine forest dieback in the south-east of the continent (2002–09). We present an alternative interpretation that emphasises the dominant signal of climate change effects, rather than the interdecadal signal of climate variability that drives wetland forest dynamics. For both the south-east Australian riverine forests and mangroves of northern Australia, aerial extent remains greater after dieback than in the early 1990s. We interpret dieback and defoliation in both systems as a dry phase response and provide evidence of a current and near-future climate change trajectory of increased areal extent and cover (i.e. tree colonisation and range infilling). In both case studies, climate change-driven increases in tree cover and extent are occurring at the expense of wetland grasslands and the important ecosystem functions they support.

Received 11 August 2021, accepted 18 October 2021, published online 9 November 2021

Concerns raised over Australian forested wetlands

The effect of a warming climate on patterns of tree recruitment, growth and mortality is a topic of considerable debate (Allen *et al.* 2015; Hartmann *et al.* 2015). Observations of woody vegetation growth at regional and continental scales suggest an overarching pattern of biomass increase in the absence of local deforestation, an outcome of CO_2 fertilisation, increased water use efficiency, a warmer atmosphere and locally enhanced atmospheric water content (Sittaro *et al.* 2017; Song *et al.* 2018; Wang *et al.* 2018). The expansion of woody vegetation into grasslands has been described from North America (Van Auken 2009), semi-arid and tropical Australia (Fensham *et al.* 2005), Europe (Maestre *et al.* 2009), India (Misra 1983) and China (Peng *et al.* 2013), contributing to an increase in tree canopy cover across the globe (Song *et al.* 2018). However, the combination of elevated temperatures and severe drought appear to be increasing tree mortality in several biomes, including tropical and boreal forests (Sitch *et al.* 2015; Birch *et al.* 2019; Locosselli *et al.* 2020). The increasing coincidence of drought and higher temperatures ('hotter droughts') is likely to increase the

Journal compilation © CSIRO 2022 Open Access CC BY-NC-ND

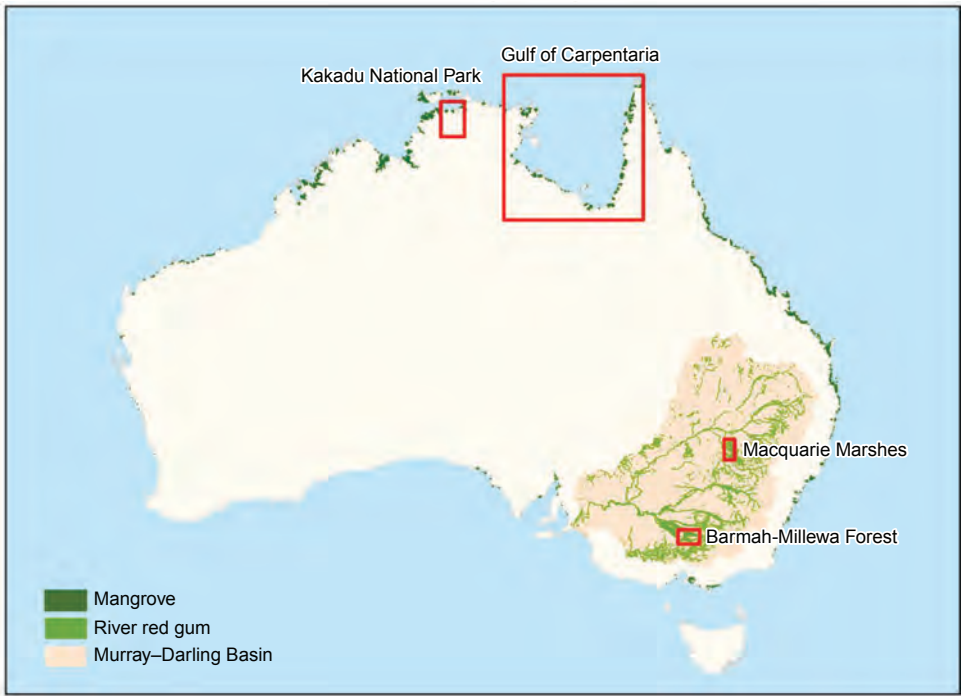


Fig. 1. Spatial distribution of forested wetlands of concern: river red gum forests in the Murray–Darling Basin, and mangrove distribution, showing the locations of Kakadu National Park and the Gulf of Carpentaria.

prevalence and speed of tree mortality under climate change (Allen *et al.* 2015; McDowell *et al.* 2020), increasing the vulnerability of forests already exposed to increased fire risk (Kirchmeier-Young *et al.* 2019) and insect predation (Pureswaran *et al.* 2018).

Short-term extreme climate events, superimposed on the background stress of climate change and other anthropogenic stressors, have been proposed to explain recent widespread changes in Australian ecosystems in recent reviews (Harris *et al.* 2018; Australian Academy of Science 2021; Bergstrom *et al.* 2021). Of these ecosystems of concern, two may be categorised as forested wetlands: mangrove forests of northern Australia and riverine (river red gum) forests of the south-east of the continent (Fig 1). Across the north of Australia, extreme low rainfall corresponding to a negative phase of the El Niño–Southern Oscillation and a positive phase of the Indian Ocean Dipole, coincided with a low sea level anomaly and record high air temperatures contributing to conditions of extreme water stress (Asbridge *et al.* 2016; Bergstrom *et al.* 2021), reducing mangrove cover by ~6% in the Gulf of Carpentaria in 2015 (Duke *et al.* 2017). River red gum forests, the most widespread wetland forests in the south-east of the continent, have been reduced from their pre-European extent due to forestry, land clearing and changes to flood regimes due to irrigation development, with an estimated 60% of the pre-European extent of floodplain forest retained in Victoria and 68% in New South Wales (Mac Nally *et al.* 2011). Widespread declines in the condition of riverine forests occurred throughout the Murray–Darling Basin during the Millennium Drought (Mac Nally *et al.* 2011), a period of prolonged below-average rainfall extending from 1997 to 2010 (van Dijk *et al.* 2013).

Here, we consider trends in mangrove and river red gum forest cover, reviewing the most extensive available mapping (Bowen *et al.* 2017; Lymburner *et al.* 2020; Saintilan *et al.* 2021), applying common mapping protocols to assess changes in spatial distribution and canopy cover through time. Although phases of drought clearly affect canopy condition and mortality rates in both forest types, we provide evidence of an overarching pattern of long-term expansion in forest cover, a likely outcome of global climate drivers. This expansion is associated with a concerning trend of a loss in the extent of wetland grasslands, a vegetation community that makes unique contributions to wetland biodiversity.

Observations of forested wetland resilience and expansion

In common with many *Eucalyptus* species, the river red gum *Eucalyptus camaldulensis* sheds its leaves to reduce transpiration as an adaptation to drought and water stress, but recovers its canopy rapidly by epicormic growth following improvement in soil moisture conditions (Cunningham *et al.* 2007; Doody *et al.* 2015; Souter 2019), as evident during and following the Millennium Drought (Colloff and Baldwin 2010; Wen *et al.* 2012; Wen and Saintilan 2015; Curtis *et al.* 2019). The species can survive decadal-long periods between inundation (Colloff 2014; Doody *et al.* 2015; Shaeri Karimi *et al.* 2021), although with greatly reduced canopy cover. Long-term mapping of some of the most extensive *E. camaldulensis* forests (the Barmah–Millewa Forest and the Macquarie Marshes) using historical aerial photography suggests a substantial increase in extent at the expense of wetland grassland communities over recent decades. For example, in the Barmah–Millewa Forest (35°50′S, 145°00′E), the largest stand of *E. camaldulensis* in Australia,

forest extent has expanded since the 1940s (Bren 1992; Colloff *et al.* 2014; Saintilan *et al.* 2021), primarily into areas previously occupied by flood-dependent Moira grass *Pseudoraphis spinescens*. Under natural recruitment regimes, *E. camaldulensis* stands in the forest were at higher densities and higher canopy cover following the Millennium Drought compared with the historical, pre-logging era in the previous century (McGregor *et al.* 2016). In the Macquarie Marshes (30°43′S, 147°32′E), *E. camaldulensis* forest extent increased between 1991 and 2013 (Bino *et al.* 2015; Bowen *et al.* 2017; Saintilan *et al.* 2021). Although mortality has been reported during and after the Millennium Drought (Catelotti *et al.* 2015), dead trees were clustered primarily in areas that were already identified as stressed (Table 1) during a benchmark survey in 1993 (Bacon 1996).

In the case of the mangroves in northern Australia, the same trend of long-term expansion applies. Progressive landward and seaward extension over the period 1987–2015 was identified using a time-series of Earth observation datasets in Kakadu National Park in the Northern Territory (NT; Asbridge and Lucas 2016) and the Gulf of Carpentaria (Queensland and NT; Asbridge *et al.* 2016). The landward extension was attributed to sea-level fluctuation consistent with trends across the continent (Saintilan *et al.* 2014), facilitating the incursion of salt water (particularly through networks of tidal creeks), leading to greater propagule dispersal, allowing mangroves to establish and, in some cases, rapidly colonise low-lying flood plains (Lucas *et al.* 2018; Asbridge *et al.* 2019).

Landsat-based satellite observations of annual mangrove cover at the continental scale between 1988 and 2017 show an expansion in mangrove extent and a thickening of mangrove canopy cover, particularly since the early 1990s and along low-lying coastal plains (Lymburner *et al.* 2020). Maximum mangrove extent in the Gulf of Carpentaria was attained *c.* 2011 (Fig. 2), with subsequent decline, most obvious in 2015, reversing gains made in the previous two decades (Fig. 2) and affecting mangroves recruited in that period (Asbridge and Lucas 2016; Asbridge *et al.* 2016, 2019; Lymburner *et al.* 2020). The expansion and contraction in mangrove cover in the Gulf of Carpentaria is suggestive of a response to modes of climate and sea level variability (the El Niño–Southern Oscillation and the Indian Ocean Dipole) superimposed on a longer-term trend of increasing extent and canopy cover (Fig 2).

Detailed space- and air-borne observations from the West Alligator River, Kakadu National Park, also show that the extent of mangroves following the 2015 defoliation and dieback was greater than the 1991 reference point due to the longer-term pattern of landward encroachment and on-going seaward expansion in some areas associated with estuary infill and sediment redistributions (Asbridge *et al.* 2019). Phases of contraction and subsequent expansion in extent and canopy cover have occurred previously in relation to El Niño events, associated with reductions in sea levels and an increase in pore water salinity (Lovelock *et al.* 2017).

Consistency with global patterns of change and climate drivers

Tree cover expansion in large wetland complexes in Australia is consistent with trends in wetlands across the globe, covering a wide range of climatic, biogeographical and geomorphological settings. Tree cover expansion has been documented as replacing wetland grasslands in many of the world's most iconic wetlands, including the Pantanal (Barbosa da Silva *et al.* 2016; Arieira *et al.* 2018), the Florida Everglades (Martin *et al.* 2009) and the Okavango Delta, where 27% of open grassland has been replaced by mixed woodland (Hamandawana and Chanda 2010). High-latitude and alpine sedgeland bogs and fens have also been subject to woody encroachment (Elmendorf *et al.* 2012), including on the Qinghai–Tibet plateau (Brandt *et al.* 2013) and in Alaska (Berg *et al.* 2009), Canada (Favreau *et al.* 2019), the US (Stine *et al.* 2011), Europe (Middleton *et al.* 2006) and Tasmania, Australia (Bowman *et al.* 2008).

The drivers of woody encroachment into wetland grasslands, whether inland or coastal, may vary between settings depending on the biophysical characteristics of the landscape and the degree of anthropogenic influences (Saintilan and Rogers 2015). Many changes have been driven primarily by climate, particularly changes in temperature and atmospheric carbon dioxide (CO_2). Increased temperatures have led to changes in the frequency and intensity of wildfires. This has provided opportunities for tree recruitment in dryland savannas (Van Auken 2000; Kgope *et al.* 2010), although a return to historical fire regimes has, in some cases, been insufficient to reverse the trend of woody encroachment (Wigley *et al.* 2010). Warmer temperatures have also allowed altitudinal and latitudinal expansion of tree ranges, and decreased frost frequency has been associated with mangrove proliferation at high latitudes in the US (Cavanaugh *et al.* 2014; Osland *et al.* 2017).

In dryland grasslands at the arid limits of tree growth, elevated atmospheric CO_2 may facilitate woody plant survival by conferring higher water use efficiency (Idso 1992; Polley

Table 1. Branch condition scores in the 1993 survey of Bacon (1996) and in the 2011 survey of Catelotti *et al.* (2015), separating plots identified as stressed and healthy in the Bacon (1996) survey

Branches were scored from 1 (main branch dead) to 5 (no dead branches). Differences in condition are non-significant for healthy plots. Data show the mean ± s.d. The stressed plots *P*-values are based on paired *t*-tests

	1993	2011	*P*-value
Stressed plots			
17	2.81 ± 0.66	3.25 ± 0.43	0.140
15	1.40 ± 0.49	0.0 ± 0.0	0.003
6	2.55 ± 0.48	0.0 ± 0.0	<0.001
2	2.95 ± 0.52	1.48 ± 1.56	<0.001
4	2.14 ± 1.03	2.43 ± 0.82	0.418
8	2.67 ± 0.59	0.42 ± 1.11	<0.001
10	2.91 ± 0.67	0.0 ± 0.0	<0.001
13	2.68 ± 0.67	1.9 ± 1.6	0.093
Healthy plots			
16	3.64 ± 0.55	2.86 ± 1.06	0.024
14	3.46 ± 0.72	2.77 ± 1.37	0.125
5	3.55 ± 0.35	2.43 ± 0.82	0.002
1	3.15 ± 0.71	2.80 ± 1.33	0.308
3	3.27 ± 0.51	2.20 ± 1.47	0.016
7	3.56 ± 0.63	2.50 ± 1.58	0.111
9	3.08 ± 0.67	0.15 ± 0.53	<0.001
11	2.67 ± 0.47	3.00 ± 0.00	0.348
12	2.50 ± 0.00	1.33 ± 0.94	0.164

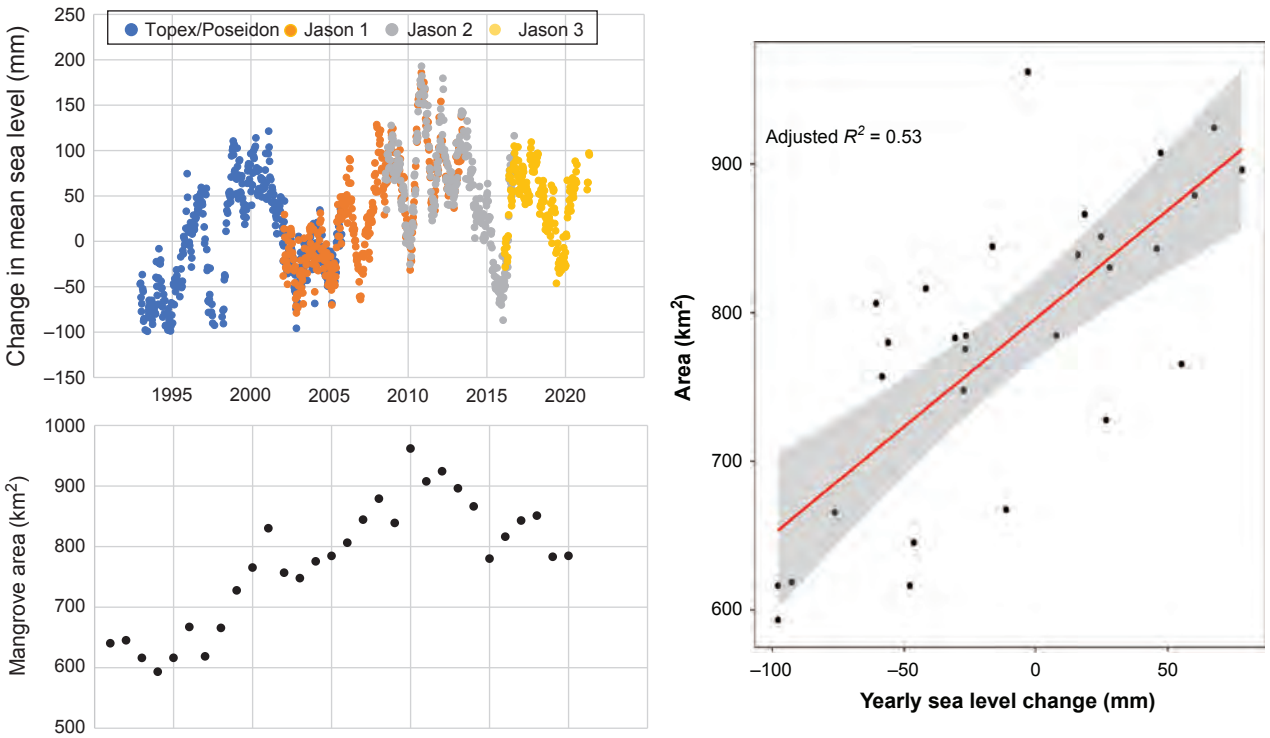


Fig. 2. Mangrove area in the Gulf of Carpentaria and mean regional sea level. Sea level data are derived from satellite altimeters (NOAA/NESDIS/STAR Laboratory for Satellite Altimetry; https://www.star.nesdis.noaa.gov/socd/lsa/SeaLevelRise/LSA_SLR_timeseries_global.php). Mangrove area data and methods are from Lymburner *et al.* (2020). Linear regression analysis of mangrove area indicated by the dotted line ($R^2 = 0.52$; $P < 0.0001$).

et al. 1997). By contrast, many wetland grassland communities gain little benefit from this increase and are being replaced by woody encroachment. These communities include *Sporobolus virginicus* saltmarsh and freshwater grasslands of *P. spinescens* (Moira grass) and *Paspalum distichum* (water couch), which use the C_4 photosynthetic pathway. However, rushes and sedges that use the C_3 pathway, including *Juncus kraussii* in the saltmarsh and *Typha* spp. (cumbungi) in freshwater systems, seem more resistant to colonisation by woody vegetation during and following drought (Saintilan *et al.* 2014, 2021; Sandi *et al.* 2019), although differences in growth habit and location may also confer resilience to larger, thicker rushes and reeds. Atmospheric CO_2 fertilisation may be an important factor contributing to *Eucalyptus* survival on the outer flood plains of Australian semi-arid rivers where water diversions for irrigation have resulted in decreases in the inundation extent and frequency of flood events (Sims *et al.* 2012; Saintilan and Rogers 2015). Elevated CO_2 concentrations may also facilitate mangrove colonisation of 'physiologically dry' environments, such as hypersaline upper intertidal saltmarsh, reinforcing the benefit of increased inundation frequency associated with sea level rise (McKee and Rooth 2008).

Implications for wetland grasses and trees

The fate of Australian forested wetlands in a +3°C warmer world may differ from trends observed under current warming (Australian Academy of Science 2021). While we argue that a continuation of mangrove expansion into northern Australian coastal flood plains is likely during coming decades, there is little evidence to suggest that large mangrove forests can persist *in situ* for long periods under rates of sea level rise projected by the end of the present century under high or even mid-range climate change projections (Saintilan *et al.* 2020; Breda *et al.* 2021). The benefits to tree growth conferred by the CO_2 fertilisation effect may diminish under hotter drought conditions. Such droughts are projected to become more frequent and severe, given the increased prevalence of the dry phase of two key Australian climate drivers in recent decades, namely the Indian Ocean Dipole (Abram *et al.* 2020) and the Southern Annular Mode (Dätwyler *et al.* 2018). An increase in the frequency of short-term mortality events may tip the balance towards river red gum and mangrove forest decline in some settings. These declines may be exacerbated by successive climate events and processes that affect ecosystems in different ways and progressively compromise the ability of ecosystems to recover (Asbridge *et al.* 2018).

On current observations, we expect the immediate effect of climate change will be a continued expansion in the extent of mangrove and river red gum during coming decades. Based on patterns of recent mangrove expansion (Asbridge *et al.* 2016; Lymburner *et al.* 2020) and projections of landward retreat with sea level rise, the trend of mangrove expansion into broad coastal and estuarine flood plains of northern Australia will likely continue (Lovelock *et al.* 2015; Schuerch *et al.* 2018; Asbridge *et al.* 2019), furthering the contraction of coastal

floodplain freshwater wetlands in the region (Bowman *et al.* 2010; Saintilan *et al.* 2019).

The capacity for river red gum to survive extended drought by accessing a range of water sources (lateral seepage from rivers, saline groundwater, rainfall and palaeo-channel reservoirs) and reducing water uptake by shedding its canopy (Mensforth *et al.* 1994; Doody *et al.* 2015) makes it unlikely that drought-mediated declines will be widespread or persistent. This is particularly because river red gum is the most broadly distributed *Eucalyptus* species throughout arid Australia and is widespread across a range of climatic and biogeographical settings (Colloff 2014). Reductions in flooding frequency also promote the invasion of reed beds and freshwater grasslands by river red gum (Bren 1992; Colloff 2014; Bowen *et al.* 2017). Although spike-rush (*Eleocharis* spp.) swamps have shown some post-drought recovery (Wassens *et al.* 2017), this has not been observed for the wetland grasslands dominated by *P. spinescens* and *P. distichum*, which may have suffered permanent losses at several locations, often to river red gum (Vivian *et al.* 2015; Wassens *et al.* 2017; Saintilan *et al.* 2021).

The decline of wetland grasslands has important implications for maintaining or enhancing biodiversity, including through conservation and land management and ecosystem restoration. The wetland grasslands of the Murray–Darling Basin are preferred feeding habitat for a diverse range of species, including herbivorous waterbirds (Braithwaite and Frith 1969; Colloff 2014) and mammals (e.g. kangaroos; Iles *et al.* 2010). Temperate coastal saltmarshes that overlap in range with temperate mangrove distribution are used as feeding habitat by migratory shorebirds and endemic grassland birds, many of which are endangered, including the orange-bellied parrot *Neophema chrysogaster*, the yellow chat *Epthianura crocea macgregori* and the slender-billed thornbill *Acanthiza iredalei rosinae* (Spencer *et al.* 2006; Kelleway *et al.* 2017). Three species of threatened microbats, namely *Chalinolobus dwyeri*, *Mormopterus norfolkensis* and *Saccolaimus flaviventris*, were found to feed exclusively in saltmarsh habitats (Gonsalves *et al.* 2012).

Conclusions

The defoliation response of forest wetland trees to drought is easily monitored at broad spatial scales. On the Australian continent, where phases of the El Niño–Southern Oscillation and the Indian Ocean Dipole have driven sharp downturns in canopy extent, these changes have been widely reported. Case studies of forest decline, specifically the mangroves of northern Australia and the river red gum forests of the Murray–Darling Basin, have been posited as exemplars of ecosystem collapse under climate change in recent reviews (Harris *et al.* 2018; Bergstrom *et al.* 2021; and references therein). We have argued that detailed mapping both cases demonstrates an overarching trend of wetland tree proliferation at the expense of wetland grasslands.

Fortunately, from a conservation perspective, the vulnerability of temperate and subtropical coastal saltmarsh to climate change has been recognised, including through their listing as a vulnerable or threatened ecological community under state and commonwealth legislation (Rogers *et al.* 2016). The potential of 'blue carbon' benefits also provides a further incentive for restoration under national emissions reduction initiatives (Kelleway *et al.* 2020). Conservation outcomes for freshwater wetland grasslands have received less attention, despite concerns raised by reserve managers of a trend towards tree monocultures in freshwater floodplain wetlands (Fazey *et al.* 2006). Hence, there is an urgent requirement to consider the future changes in these ecosystems, particularly given further impacts of climate change on water availability and ongoing discussions on environmental water policy, management and allocation (Chen *et al.* 2021; Kirsch *et al.* 2021). This is becoming paramount given that changes in the flooding frequency and depth favour ongoing eucalypt expansion into core grassland habitat.

Data availability

The data used in generating Fig. 1 are available at https://www.star.nesdis.noaa.gov/socd/lsa/SeaLevelRise/LSA_SLR_timeseries_global.php and http://dea-public-data.s3-website-ap-southeast-2.amazonaws.com/?prefix=mangrove_cover/v2.0.2/

Declaration of funding

This research did not receive any specific funding.

Conflicts of interest

Kerrylee Rogers is an Associate Editor for *Marine and Freshwater Research* but did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this Journal. *Marine and Freshwater Research* encourages its editors to publish in the Journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

References

Abram, N. J., Hargreaves, J. A., Wright, N. M., Thirumalai, K., Ummenhofer, C. C., and England, M. H. (2020). Palaeoclimate perspectives on the Indian Ocean dipole. *Quaternary Science Reviews* **237**, 106302. doi:10.1016/J.QUASCIREV.2020.106302

Allen, C. D., Breshears, D. D., and McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**(8), art129. doi:10.1890/ES15-00203.1

Arieira, J., Padovani, C. R., Schuchmann, K. L., Landeiro, V. L., and Santos, S. A. (2018). Modeling climatic and hydrological suitability for an encroaching tree species in a Neotropical flooded savanna. *Forest Ecology and Management* **429**, 244–255. doi:10.1016/J.FORECO.2018.07.019

Asbridge, E., and Lucas, R. (2016). Mangrove response to environmental change in Kakadu National Park. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* **9**(12), 5612–5620. doi:10.1109/JSTARS.2016.2616449

Asbridge, E., Lucas, R., Ticehurst, C., and Bunting, P. (2016). Mangrove response to environmental change in Australia's Gulf of Carpentaria. *Ecology and Evolution* **6**(11), 3523–3539. doi:10.1002/ECE3.2140

Asbridge, E., Lucas, R., Rogers, K., and Accad, A. (2018). The extent of mangrove change and potential for recovery following severe Tropical Cyclone Yasi, Hinchinbrook Island, Queensland, Australia *Ecology and Evolution* **8**, 10416–10434. doi:10.1002/ECE3.4485

Asbridge, E. F., Bartolo, R., Finlayson, C. M., Lucas, R. M., Rogers, K., and Woodroffe, C. D. (2019). Assessing the distribution and drivers of mangrove dieback in Kakadu National Park, northern Australia.

Estuarine, Coastal and Shelf Science **228**, 106353. doi:10.1016/J.ECSS.2019.106353

Australian Academy of Science (2021). The risks to Australia of a 3°C warmer world. (AAS.) Available at https://www.science.org.au/supporting-science/science-policy-and-analysis/reports-and-publications/risks-australia-three-degrees-c-warmer-world

Bacon, P. (1996) Relationships between water supply, water quality and the performance of *Eucalyptus camaldulensis* in the Macquarie Marshes of NSW. Department of Land and Water Conservation, Dubbo, NSW, Australia.

Barbosa da Silva, F. H., Arieira, J., Parolin, P., Nunes da Cunha, C., and Junk, W. J. (2016). Shrub encroachment influences herbaceous communities in flooded grasslands of a neotropical savanna wetland. *Applied Vegetation Science* **19**, 391–400. doi:10.1111/AVSC.12230

Berg, E. E., Hillman, K. M., Dial, R., and DeRuwe, A. (2009). Recent woody invasion of wetlands on the Kenai Peninsula Lowlands, south-central Alaska: a major regime shift after 18 000 years of wet *Sphagnum*–sedge peat recruitment. *Canadian Journal of Forest Research* **39**, 2033–2046. doi:10.1139/X09-121

Bergstrom, D. M., Wienecke, B. C., van den Hoff, J., Hughes, L., Lindenmayer, D. B., Ainsworth, T. D., Baker, C. M., Bland, L., Bowman, D. M. J. S., Brooks, S. T., Canadell, J. G., Constable, A. J., Dafforn, K. A., Depledge, M. H., Dickson, C. R., Duke, N. C., Helmstedt, K. J., Holz, A., Johnson, C. R., McGeoch, M. A., Melbourne-Thomas, J., Morgain, E., Nicholson, E., Prober, S. M., Raymond, B., Ritchie, E. G., Robinson, S. A., Ruthrof, K. X., Setterfield, S., Sgrò, C. M., Stark, J. S., Travers, T., Trebilco, R., Ward, D. F. L., Wardle, G. M., Williams, K. J., Zylstra, P. J., and Shaw, J. D. (2021). Combating ecosystem collapse from the tropics to the Antarctic. *Global Change Biology* **27**, 1692–1703. doi:10.1111/gcb.15539

Bino, G., Sisson, S. A., Kingsford, R. T., Thomas, R. F., and Bowen, S. (2015). Developing state and transition models of floodplain vegetation dynamics as a tool for conservation decision-making: a case study of the Macquarie Marshes Ramsar wetland. *Journal of Applied Ecology* **52**, 654–664. doi:10.1111/1365-2664.12410

Birch, J. D., Lutz, J. A., Hogg, E. H., Simard, S. W., Pelletier, R., LaRoi, G. H., and Karst, J. (2019). Decline of an ecotone forest: 50 years of demography in the southern boreal forest. *Ecosphere* **10**(4), e02698. doi:10.1002/ECS2.2698

Bowen, S., Simpson, S. L., Hosking, T., and Shelly, D. S. (2017). Changes in the extent and condition of the vegetation of the Macquarie Marshes and floodplain 1991–2008–2013. NSW Office of Environmental and Heritage, Sydney, NSW, Australia.

Bowman, D. M. J. S., Riley, J. E., Boggs, G. S., Lehmann, C. E. R., and Prior, L. D. (2008). Do feral buffalo (*Bubalus bubalis*) explain the increase of woody cover in savannas of Kakadu National Park, Australia? *Journal of Biogeography* **35**, 1976–1988. doi:10.1111/J.1365-2699.2008.01934.X

Bowman, D. M. J. S., Prior, L. D., and De Little, S. C. (2010). Retreating *Melaleuca* swamp forests in Kakadu National Park: evidence of synergistic effects of climate change and past feral buffalo impacts. *Austral Ecology* **35**(8), 898–905. doi:10.1111/J.1442-9993.2009.02096.X

Braithwaite, L. W., and Frith, H. J. (1969). Waterfowl in an inland swamp in New South Wales. 1. Habitat. *CSIRO Wildlife Research* **14**, 1–16. doi:10.1071/CWR9690001

Brandt, J. S., Haynes, M. A., Kuemmerle, T., Waller, D. M., and Radeloff, V. C. (2013). Regime shift on the roof of the world: Alpine meadows converting to shrublands in the southern Himalayas. *Biological Conservation* **158**, 116–127. doi:10.1016/J.BIOCON.2012.07.026

Breda, A., Saco, P. M., Sandi, S. G., Saintilan, N., Riccardi, G., and Rodríguez, J. F. (2021). Accretion, retreat and transgression of coastal wetlands experiencing sea-level rise. *Hydrology and Earth System Sciences* **25**, 769–786. doi:10.5194/HESS-25-769-2021

Bren, L. J. (1992). Tree invasion of an intermittent wetland in relation to changes in flooding frequency of the River Murray, Australia. *Australian Journal of Ecology* **17**, 395–408. doi:10.1111/J.1442-9993.1992.TB00822.X

Catelotti, K., Kingsford, R. T., Bino, G., and Bacon, P. (2015). Inundation requirements for persistence and recovery of river red gums (*Eucalyptus camaldulensis*) in semi-arid Australia. *Biological Conservation* **184**, 346–356. doi:10.1016/J.BIOCON.2015.02.014

Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., and Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences of the United States of America* **111**(2), 723–727. doi:10.1073/PNAS.1315800111

Chen, Y., Colloff, M. J., Lukasiewicz, A., and Pittock, J. (2021). A trickle, not a flood: environmental watering in the Murray-Darling Basin, Australia. *Marine and Freshwater Research* **72**, 601–619. doi:10.1071/MF20172

Colloff, M. J. (2014). 'Flooded Forest and Desert Creek: Ecology and History of the River Red Gum.' (CSIRO Publishing: Melbourne, Vic., Australia.)

Colloff, M. J., and Baldwin, D. S. (2010). Resilience of floodplain ecosystems in a semi-arid environment. *The Rangeland Journal* **32**(3), 305–314. doi:10.1071/RJ10015

Colloff, M. J., Ward, K. A., and Roberts, J. (2014). Ecology and conservation of grassy wetlands dominated by spiny mud grass *Pseudoraphis spinescens* in the southern Murray–Darling Basin, Australia. *Aquatic Conservation* **24**(2), 238–255. doi:10.1002/AQC.2390

Cunningham, S. C., Read, J., Baker, P. J., and Mac Nally, R. (2007). Quantitative assessment of stand condition and its relationship to physiological stress in stands of *Eucalyptus camaldulensis* (Myrtaceae). *Australian Journal of Botany* **55**, 692–699. doi:10.1071/BT07031

Curtis, E. J., Gorrod, E. J., Ellis, M. V., and Chisholm, L. A. (2019). A spatio-temporal analysis of canopy dynamics and intra-stand competition in a riparian forest, south-eastern Australia. *Forest Ecology and Management* **432**, 189–199. doi:10.1016/J.FORECO.2018.08.044

Dätwyler, C., Neukom, R., Abram, N. J., Gallant, A. J., Grosjean, M., Jacques-Coper, M., Karoly, D. J., and Villalba, R. (2018). Teleconnection stationarity, variability and trends of the Southern Annular Mode (SAM) during the last millennium. *Climate Dynamics* **51**(5–6), 2321–2339. doi:10.1007/S00382-017-4015-0

Doody, T. M., Colloff, M. J., Davies, M., Koul, V., Benyon, R. G., and Nagler, P. L. (2015). Quantifying water requirements of riparian river red gum (*Eucalyptus camaldulensis*) in the Murray-Darling Basin, Australia – implications for environmental water allocations. *Ecohydrology* **8**, 1471–1487. doi:10.1002/ECO.1598

Duke, N. C., Kovacs, J. M., Griffiths, A. D., Preece, L., Hill, D. J., van Oosterzee, P., Mackenzie, J., Morning, H. S., and Burrows, D. (2017). Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. *Marine and Freshwater Research* **68**(10), 1816–1829. doi:10.1071/MF16322

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H., Day, T. A., and Fosaa, A. M. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* **15**(2), 164–175. doi:10.1111/J.1461-0248.2011.01716.X

Favreau, M., Pellerin, S., and Poulin, M. (2019). Tree encroachment induces biotic differentiation in *Sphagnum*-dominated bogs. *Wetlands* **39**(4), 841–852. doi:10.1007/S13157-018-1122-6

Fazey, I., Proust, K., Newell, B., Johnson, B., and Fazey, J. A. (2006). Eliciting the implicit knowledge and perceptions of on-ground conservation managers of the Macquarie Marshes. *Ecology and Society* **11**(1), art25. doi:10.5751/ES-01665-110125

Fensham, R. J., Fairfax, R. J., and Archer, S. R. (2005). Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* **93**, 596–606. doi:10.1111/J.1365-2745.2005.00998.X

Gonsalves, L., Law, B., Webb, C., and Monamy, V. (2012). Are vegetation interfaces important to foraging insectivorous bats in endangered coastal saltmarsh on the Central Coast of New South Wales? *Pacific Conservation Biology* **18**(4), 282–292. doi:10.1071/PC120282

Hamandawana, H., and Chanda, R. (2010). Natural and human dimensions of environmental change in the proximal reaches of Botswana's Okavango Delta. *The Geographical Journal* **176**, 58–76. doi:10.1111/J.1475-4959.2009.00339.X

Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. B., Fletcher, M. S., Keatley, M. R., Woodward, C. A., Williamson, G., Duke, N. C., and Bowman, D. M. J. S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change* **8**(7), 579–587. doi:10.1038/S41558-018-0187-9

Hartmann, H., Adams, H. D., Anderegg, W. R., Jansen, S., and Zeppel, M. J. (2015). Research frontiers in drought-induced tree mortality: crossing scales and disciplines. *New Phytologist* **205**, 965–969. doi:10.1111/NPH.13246

Idso, S. (1992). Shrubland expansion in the American Southwest. *Climatic Change* **22**, 85–86. doi:10.1007/BF00143345

Iles, J., Kelleway, J., Kobayashi, T., Mazumder, D., Knowles, L., Priddel, D., and Saintilan, N. (2010). Grazing kangaroos act as local recyclers of energy on semiarid floodplains. *Australian Journal of Zoology* **58**, 145–149. doi:10.1071/ZO10020

Kelleway, J. J., Cavanaugh, K., Rogers, K., Feller, I. C., Ens, E., Doughty, C., and Saintilan, N. (2017). Review of the ecosystem service implications of mangrove encroachment into salt marshes. *Global Change Biology* **23**(10), 3967–3983. doi:10.1111/GCB.13727

Kelleway, J. J., Serrano, O., Baldock, J. A., Burgess, R., Cannard, T., Lavery, P. S., Lovelock, C. E., Macreadie, P. J., Masqué, P., Newnham, M., Saintilan, N., and Steven, A. D. L. (2020). A national approach to greenhouse gas abatement through blue carbon management. *Global Environmental Change* **63**, 102083. doi:10.1016/J.GLOENVCHA.2020.102083

Kgope, B. S., Bond, W. J., and Midgley, G. F. (2010). Growth responses of African savanna trees implicate atmospheric [CO_2] as a driver of past and current changes in savanna tree cover. *Austral Ecology* **35**(4), 451–463. doi:10.1111/J.1442-9993.2009.02046.X

Kirchmeier-Young, M. C., Gillett, N. P., Zwiers, F. W., Cannon, A. J., and Anslow, F. S. (2019). Attribution of the influence of human-induced climate change on an extreme fire season. *Earth's Future* **7**(1), 2–10. doi:10.1029/2018EF001050

Kirsch, E., Colloff, M. J., and Pittock, J. (2021). Lacking character? A policy analysis of environmental watering of Ramsar wetlands in the Murray–Darling Basin, Australia. *Marine and Freshwater Research*. [Published online early 31 May 2021]. doi:10.1071/MF21036

Locosselli, G. M., Brienen, R. J., de Souza Leite, M., Gloor, M., Krottenthaler, S., de Oliveira, A. A., Barichevich, J., Anhuf, D., Ceccantini, G., Schöngart, J., and Buckeridge, M. (2020). Global tree-ring analysis reveals rapid decrease in tropical tree longevity with temperature. *Proceedings of the National Academy of Sciences of the United States of America* **117**(52), 33358–33364. doi:10.1073/PNAS.2003873117

Lovelock, C. E., Cahoon, D. R., Friess, D. A., Guntenspergen, G. R., Krauss, K. W., Reef, R., Rogers, K., Saunders, M. L., Sidik, F., Swales, A., Saintilan, N., Tuyen, L. X., and Triet, T. (2015). The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* **526**(7574), 559–563. doi:10.1038/NATURE15538

Lovelock, C. E., Feller, I. C., Reef, R., Hickey, S., and Ball, M. C. (2017). Mangrove dieback during fluctuating sea levels. *Scientific Reports* **7**(1), 1680. doi:10.1038/S41598-017-01927-6

Lucas, R., Finlayson, C. M., Bartolo, R., Rogers, K., Mitchell, A., Woodroffe, C. D., Asbridge, E., and Ens, E. (2018). Historical perspectives on the mangroves of Kakadu National Park. *Marine and Freshwater Research* **69**(7), 1047–1063. doi:10.1071/MF17065

Lymburner, L., Bunting, P., Lucas, R., Scarth, P., Alam, I., Phillips, C., Ticehurst, C., and Held, A. (2020). Mapping the multi-decadal mangrove dynamics of the Australian coastline. *Remote Sensing of Environment* **238**, 111185. doi:10.1016/J.RSE.2019.05.004

Mac Nally, R., Cunningham, S. C., Baker, P. J., Horner, G. J., and Thomson, J. R. (2011). Dynamics of Murray-Darling floodplain forests under multiple stressors: the past, present, and future of an Australian icon. *Water Resources Research* **47**(12), W00G05. doi:10.1029/2011WR010383

Maestre, F. T., Bowker, M. A., Puche, M. D., Hinojosa, B. B., Martinez, I., Garcia-Palacios, P., Castillo, A. P., Soliveres, S., Luzuriaga, A. L., Carreira, J. A., Gallardo, A., and Escudero, A. (2009). Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters* **12**, 930–941. doi:10.1111/J.1461-0248.2009.01352.X

Martin, M. R., Tipping, P. W., and Sickman, J. O. (2009). Invasion by an exotic tree alters above and belowground ecosystem components. *Biological Invasions* **11**, 1883–1894. doi:10.1007/S10530-008-9366-3

McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clarke, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., Turner, M. G., Uriate, M., Walker, A. P., and Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world. *Science* **368**(6494), eaaz9463. doi:10.1126/SCIENCE.AAZ9463

McGregor, H. W., Colloff, M. J., and Lunt, I. D. (2016). Did early logging or changes in disturbance regimes promote high tree densities in river red gum forests? *Australian Journal of Botany* **64**(6), 530–538. doi:10.1071/BT16025

McKee, K. L., and Rooth, J. E. (2008). Where temperate meets tropical: multi-factorial effects of elevated CO_2, nitrogen enrichment, and competition on a mangrove-salt marsh community. *Global Change Biology* **14**(5), 971–984. doi:10.1111/J.1365-2486.2008.01547.X

Mensforth, L., Thorburn, P., Tyerman, S., and Walker, G. (1994). Sources of water used by riparian *Eucalyptus camaldulensis* overlying highly saline groundwater. *Oecologia* **100**, 21–28. doi:10.1007/BF00317126

Middleton, B. A., Holsten, B., and van Diggelen, R. (2006). Biodiversity management of fens and fen meadows by grazing, cutting and burning. *Applied Vegetation Science* **9**, 307–316. doi:10.1111/J.1654-109X.2006.TB00680.X

Misra, R. (1983). Indian savannas. In 'Ecosystems of the World' (Ed. F. Bourliere.) pp. 151–166. (Elsevier: New York, NY, USA.)

Osland, M. J., Day, R. H., Hall, C. T., Brumfield, M. D., Dugas, J. L., and Jones, W. R. (2017). Mangrove expansion and contraction at a poleward range limit: climate extremes and land-ocean temperature gradients. *Ecology* **98**(1), 125–137. doi:10.1002/ECY.1625

Peng, H. Y., Li, X. Y., Li, G. Y., Zhang, Z. H., Zhang, S. Y., Li, L., Chao, G. Q., Jiang, Z. Y., and Ma, Y. J. (2013). Shrub encroachment with increasing anthropogenic disturbance in the semiarid Inner Mongolian grasslands of China. *Catena* **109**, 39–48. doi:10.1016/J.CATENA.2013.05.008

Polley, H. W., Mayeux, H. S., Johnson, H. B., and Tischler, C. R. (1997). Viewpoint: atmospheric CO_2, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management* **50**, 278–284. doi:10.2307/4003730

Pureswaran, D. S., Roques, A., and Battisti, A. (2018). Forest insects and climate change. *Current Forestry Reports* **4**(2), 35–50. doi:10.1007/S40725-018-0075-6

Rogers, K., Boon, P. I., Branigan, S., Duke, N. C., Field, C. D., Fitzsimons, J. A., Kirkman, H., Mackenzie, J. R., and Saintilan, N. (2016). The state of legislation and policy protecting Australia's mangrove and salt marsh

and their ecosystem services. *Marine Policy* **72**, 139–155. doi:10.1016/J.MARPOL.2016.06.025

Saintilan, N., and Rogers, K. (2015). Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. *New Phytologist* **205**, 1062–1070. doi:10.1111/NPH.13147

Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., and Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology* **20**(1), 147–157. doi:10.1111/GCB.12341

Saintilan, N., Rogers, K., Kelleway, J. J., Ens, E., and Sloane, D. R. (2019). Climate change impacts on the coastal wetlands of Australia. *Wetlands* **39**(6), 1145–1154. doi:10.1007/S13157-018-1016-7

Saintilan, N., Khan, N. S., Ashe, E., Kelleway, J. J., Rogers, K., Woodroffe, C. D., and Horton, B. P. (2020). Thresholds of mangrove survival under rapid sea level rise. *Science* **368**(6495), 1118–1121. doi:10.1126/SCIENCE.ABA2656

Saintilan, N., Bowen, S., Maguire, O., Shaeri Karimi, S., Wen, L., Powell, M., Colloff, M. J., Sandi, S. G., Saco, P., and Rodriguez, J. (2021). Resilience of trees and the vulnerability of grasslands to climate change in temperate Australian wetlands. *Landscape Ecology* **36**(3), 803–814. doi:10.1007/S10980-020-01176-5

Sandi, S. G., Saco, P. M., Saintilan, N., Wen, L., Riccardi, G., Kuczera, G., Willgoose, G., and Rodríguez, J. F. (2019). Detecting inundation thresholds for dryland wetland vulnerability. *Advances in Water Resources* **128**, 168–182. doi:10.1016/J.ADVWATRES.2019.04.016

Schuerch, M., Spencer, T., Temmerman, S., Kirwan, M. L., Wolff, C., Lincke, D., McOwen, C. J., Pickering, M. D., Reef, R., Vafeidis, A., Hinkel, J., Nicholls, R. J., and Brown, S. (2018). Future response of global coastal wetlands to sea-level rise. *Nature* **561**(7722), 231–234. doi:10.1038/S41586-018-0476-5

Shaeri Karimi, S., Saintilan, N., Wen, L., Cox, J., and Valavi, R. (2021). Influence of inundation characteristics on the distribution of dryland floodplain vegetation communities. *Ecological Indicators* **124**, 107429. doi:10.1016/J.ECOLIND.2021.107429

Sims, N. C., Chariton, A., Jin, H., and Colloff, M. J. (2012). A classification of floodplain ecosystems in the Murray-Darling Basin based on changes in flows following water resource development. *Wetlands* **32**, 239–248. doi:10.1007/S13157-011-0231-2

Sitch, S., Friedlingstein, P., Gruber, N., Jones, S. D., Murray-Tortarolo, G., Ahlström, A., Doney, S. C., Graven, H., Heinze, C., and Huntingford, C. (2015). Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences* **12**, 653–679. doi:10.5194/BG-12-653-2015

Sittaro, F., Paquette, A., Messier, C., and Nock, C. A. (2017). Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Global Change Biology* **23**(8), 3292–3301. doi:10.1111/GCB.13622

Song, X. P., Hansen, M. C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E. F., and Townshend, J. R. (2018). Global land change from 1982 to 2016. *Nature* **560**, 639–643. doi:10.1038/S41586-018-0411-9

Souter, N. J. (2019). The red gum condition index: a multi-variable tree condition index for visually assessed river red gum (*Eucalyptus camaldulensis*) trees. *Transactions of the Royal Society of South Australia* **143**(1), 67–85. doi:10.1080/03721426.2018.1557994

Spencer, S., Monamy, V., and Breitfuss, M. (2006). Saltmarsh as habitat for birds and other vertebrates. In 'Australian Saltmarsh Ecology'. (Ed. N. Saintilan.) pp 149–165. (CSIRO Publishing: Melbourne, Vic., Australia.)

Stine, M. B., Resler, L. M., and Campbell, J. B. (2011). Ecotone characteristics of a southern Appalachian Mountain wetland. *Catena* **86**, 57–65. doi:10.1016/J.CATENA.2011.02.006

Van Auken, O. W. (2000). Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* **31**(1), 197–215. doi:10.1146/ANNUREV.ECOLSYS.31.1.197

Van Auken, O. W. (2009). Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* **90**, 2931–2942. doi:10.1016/J.JENVMAN.2009.04.023

van Dijk, A. I. J. M., Beck, H. E., Crosbie, R. S., de Jeu, R. A., Liu, Y. Y., Podger, G. M., Timbal, B., and Viney, N. R. (2013). The Millennium Drought in southeast Australia (2001–2009): natural and human causes and implications for water resources, ecosystems, economy, and society. *Water Resources Research* **49**, 1040–1057. doi:10.1002/WRCR.20123

Vivian, L., Ward, K., Marshall, D. J., and Godfree, R. C. (2015). *Pseudoraphis spinescens* (Poaceae) grasslands at Barmah Forest, Victoria, Australia: current distribution and implications for floodplain conservation. *Australian Journal of Botany* **63**, 526–540. doi:10.1071/BT15090

Wang, L., Tian, F., Wang, Y., Wu, Z., Schurgers, G., and Fensholt, R. (2018). Acceleration of global vegetation greenup from combined effects of climate change and human land management. *Global Change Biology* **24**(11), 5484–5499. doi:10.1111/GCB.14369

Wassens, S., Ning, N., Hardwick, L., Bino, G., and Maguire, J. (2017). Long-term changes in freshwater aquatic plant communities following extreme drought. *Hydrobiologia* **799**(1), 233–247. doi:10.1007/S10750-017-3219-Y

Wen, L., and Saintilan, N. (2015). Climate phase drives canopy condition in a large semi-arid floodplain forest. *Journal of Environmental Management* **159**, 279–287. doi:10.1016/J.JENVMAN.2015.05.027

Wen, L., Yang, X., and Saintilan, N. (2012). Local climate determines the NDVI-based primary productivity and flooding creates heterogeneity in semi-arid floodplain ecosystem. *Ecological Modelling* **242**, 116–126. doi:10.1016/J.ECOLMODEL.2012.05.018

Wigley, B. J., Bond, W. J., and Hoffman, M. T. (2010). Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Global Change Biology* **16**(3), 964–976. doi:10.1111/J.1365-2486.2009.02030.X

Handling Editor: Max Finlayson

ENVIRONMENTAL STUDIES

The lunar nodal cycle controls mangrove canopy cover on the Australian continent

Neil Saintilan[1]*, Leo Lymburner[2], Li Wen[3], Ivan D. Haigh[4], Emma Ai[2], Jeffrey J. Kelleway[5], Kerrylee Rogers[5], Tien Dat Pham[1], Richard Lucas[6]

Copyright © 2022 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).

Long-phase (interannual) tidal cycles have been shown to influence coastal flooding and sedimentation, but their role in shaping the extent and condition of tidal wetlands has received little attention. Here, we show that the 18.61-year lunar nodal cycle, popularly termed the "lunar wobble," is a dominant control over the expansion and contraction of mangrove canopy cover over much of the Australian continent. Furthermore, the contrasting phasing of the 18.61-year lunar nodal cycle between diurnal and semidiurnal tidal settings has mediated the severity of drought impacts in northern bioregions. Long-phase tidal cycles regulate maximum tide heights, are an important control over mangrove canopy cover, and may influence mangrove ecosystem services including forest productivity and carbon sequestration at regional scales.

INTRODUCTION

Over interannual time scales, precessions in the orbit of the moon drive variability in tidal range principally over two time scales: the 18.61-year lunar nodal cycle and the 8.85-year cycle of lunar perigee, which influences high tide levels over a 4.4-year cycle (the lunar perigean subharmonic) (*1*). Interannual tidal cycles have previously been demonstrated to influence hydrodynamic energy, altering patterns of sedimentation (*2*, *3*), and coastal erosion (*4*), water level, and coastal flooding risk (*5*). To date, little, if any, consideration has been given to the influence of multiyear and decadal tidal cycles on the structure and function of tidal wetland ecosystems. Vegetated tidal wetlands (such as mangroves and tidal marsh) occur between mean sea level and mean high water spring tides (*6*), a position in the tidal frame likely to be strongly influenced by long period alterations in tidal range.

The influence of long-phase tidal harmonics on mangrove growth may be important over much of the Australian continent (Fig. 1). The influence of the 18.61-year nodal cycle on tidal amplitude is ~10 to 20 cm across much of the northern coastline, while a similar magnitude is evident for the 4.4-year perigean subharmonic on the Kimberly and Dampier coastlines in the West and the northern Great Barrier Reef coastline in the east (Fig. 1 and Materials and Methods) (*1*, *7*). In the Gulf of Carpentaria, the combined influence of the 18.61-year nodal cycle and the 4.4-year perigean subharmonic on the maximum tide height is ~30 to 40 cm, among the highest in the world (*1*). This variability in tidal amplitude is potentially higher than other influences on water level in upper intertidal environments, with the effect temporally clustered such that the influence is sustained over successive extremes of tidal amplitude minima and maxima (*5*).

Previous observations from northern Australia suggest the possible influence of long-phase tidal harmonics on coastal processes. Multidecadal phases of mangrove creek extension have been previously noted for the Kakadu region (*8*), the period of each wave of extension being ~two decades (*9*, *10*). The authors could not point to a hydrological driver of this change, noting that sea level trends for the period showed a slightly falling trend of 0.4 mm year^{-1} (*10*). The largest mangrove dieback event recorded globally, involving more than 1000 km of mangrove shoreline in the Gulf of Carpentaria (*11*) in 2015/2016, has been linked to a weakening of the monsoon wet season, lower than average rainfall, and a temporary decrease in mean sea level (*10*). These conditions were driven by an extreme negative phase of the El Niño Southern Oscillation (ENSO) coincident with a positive phase of the Indian Ocean Dipole (IOD) (*11*, *12*). However, dieback in the adjacent Arnhem and Great Barrier Reef bioregions was far less severe, despite the similar imposition of the ENSO and IOD events on sea level and climate.

Here, we test whether the 18.61-year nodal tidal cycle and the 4.4-year perigean subharmonic influence mangrove canopy expansion and contraction in Australia. Mangroves are pan-continental in distribution, reaching their greatest diversity and extent in the tropical north (*13*). They are absent from Tasmania and scarce in the arid southwest of the continent. Mangrove extent and cover for every year between 1987 and 2020 were quantified for the entire Australian continent using Landsat sensor data at 25-m resolution, nominally at a 16-day frequency (Materials and Methods) (*14*). The percentage of the Planimetric Canopy Cover (PCC%) was calculated for each calendar year, and the extent of canopy classes of closed forest (>80% cover), open forest (50 to 80% cover), and woodland (20 to 50% cover) was collated at the scale of coastal bioregions. Bioregions were grouped into those for which the 18.61-year tidal modulation was predicted to be important (Table 1), whether diurnal (the Gulf of Carpentaria; subdivided into three regions: group 1) or semidiurnal (Arnhem and Carnarvon bioregions: group 2) (Fig. 1). We also included four bioregions within which the 4.4-year modulation was predicted to influence maximum tidal variation (the Northern Great Barrier Reef, Bonaparte, Kimberley Coast, and Dampier Coast: group 3) and bioregions for which neither the 18.61-year nodal cycle nor the 4.4-year perigean subharmonic was modeled to be important [combined influence of less than ~6 cm; South East (SE) Queensland and SE Coast and Temperate Southern Coast: group 4], regions in which rainfall has previously been proposed as a control on mangrove extent and canopy cover (Table 1) (*15*–*17*).

We compared changes in the extent of mangrove cover and the proportion of closed forest canopy (an indicator of dieback if negative

[1]School of Natural Sciences, Macquarie University. [2]Department of Planning and Environment. [3]Department of Planning, Industry and Environment, Parramatta, NSW, Australia. [4]National Oceanography Centre, University of Southampton, Southampton, UK. [5]School of Earth, Atmospheric, and Life Sciences, University of Wollongong, Wollongong, NSW, Australia. [6]Aberystwyth University, Wales, UK. *Corresponding author. Email: neil.saintilan@mq.edu.au

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

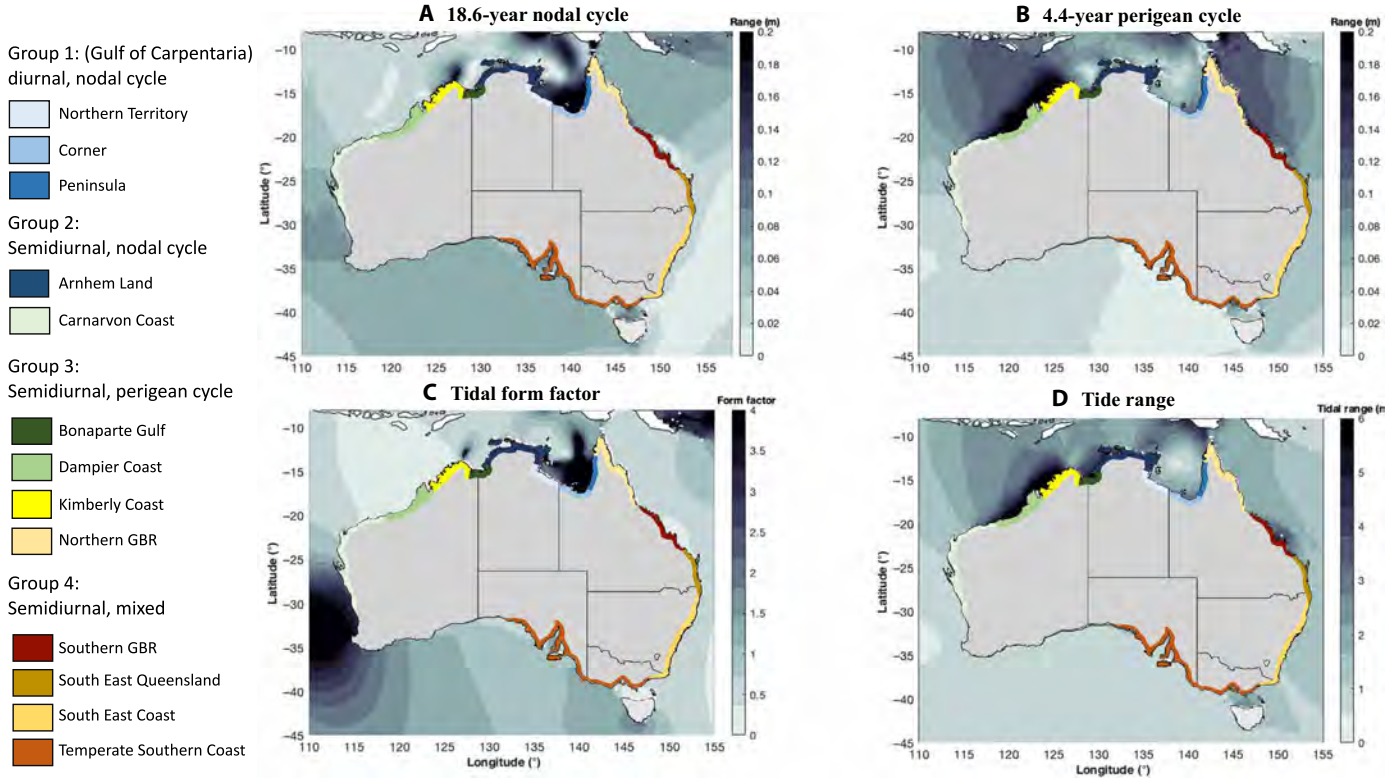


Fig. 1. Long-phase tidal cycles influencing Australian coastal bioregions. The modeled influence of the 18.6-year nodal cycle (**A**) and the 4.4-year perigean cycle (**B**) on tidal amplitude (Materials and Methods). Tidal form factor (**C**) ranges from semidiurnal (<0.25) to diurnal (>3), which influences the phasing of the nodal tidal cycle. Tidal range (**D**) varies markedly between bioregions.

Table 1. Tidal properties, rates of relative sea level rise, and mangrove area. Overall linear trend in monthly mean and maximum water level (mm year^{-1}) and the linear rate before and following the nodal diurnal tide maxima in 2006 (Gulf: Milner Bay; Kakadu: Darwin; Dampier, Kimberly, and Carnarvon: Broome; Northern Great Barrier Reef (Nth GBR): Cape Ferguson; Southern Great Barrier Reef (Sth GBR): Rosslyn Bay; Southern Queensland (Qld): Rosslyn Bay; Southeast (SE) Coast: Port Kembla; and Temperate Southern Coast: Portland) (Materials and Methods). Mangrove area in 2020 (woodland, open forest, and closed forest combined). SL, sea level.

Bioregion (group)	Tidal character (range, form, cycle)	Mean SL (1993–2020) (mm year^{-1})	Max SL (1993–2020) (mm year^{-1})	Max SL (1993–2006) (mm year^{-1})	Max SL (2007–2020) (mm year^{-1})	Mangrove (2020) (km^2)
Gulf (1)	Mesotidal, diurnal, 18.6 years	3.43	3.47	6.97	−25.29	646
Arnhem (2)	Mesotidal, semidiurnal, 18.6 years	4.71	5.00	−14.13	−0.02	3274
Carnarvon (2)	Mesotidal, semidiurnal*, 18.6 years	5.37	2.19	−14.12	6.17	378
Bonaparte (3)	Mesotidal, semidiurnal, 4.4 years	4.71	5.00	−14.13	−0.02	610
Kimberly (3)	Macrotidal, semidiurnal, 4.4 years	5.37	2.19	−14.12	6.17	1086
Dampier (3)	Macrotidal, semidiurnal, 4.4 years	5.37	2.19	−14.12	6.17	317
Nth GBR (3)	Mesotidal, semidiurnal, 4.4 years	4.53	5.84	0.11	−2.23	1620
Sth GBR (4)	Macrotidal, semidiurnal	4.78	6.75	−1.02	0.89	1013
SE Qld (4)	Mesotidal, semidiurnal	4.78	6.75	−1.02	0.89	418
SE Coast (4)	Mesotidal, semidiurnal	3.69	3.94	7.010	2.15	85.7
Temperate (4)	Mesotidal, semidiurnal	2.85	2.41	7.34	−9.86	207

*The diurnal component of the Carnarvon bioregion contains <2 km^2 mangrove.

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

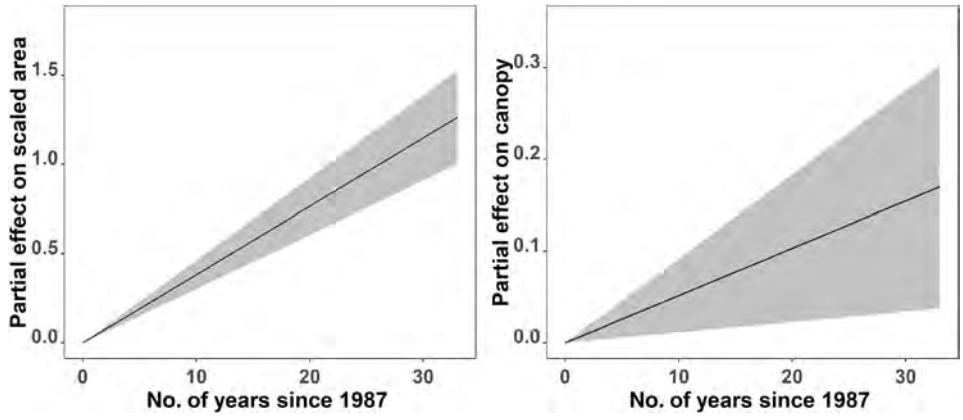


Fig. 2. Fitted overall trends of mangrove area and canopy condition (proportion of closed forest) Black lines are the estimate, and gray shaded areas are 95% confident intervals. Across the coastal bioregions, both the extent and canopy condition of mangrove increased significantly ($P < 0.001$ for both canopy condition model and area model; table S1). The partial effect is the effect of "year" on the dependent variable when the other independent variables are kept constant.

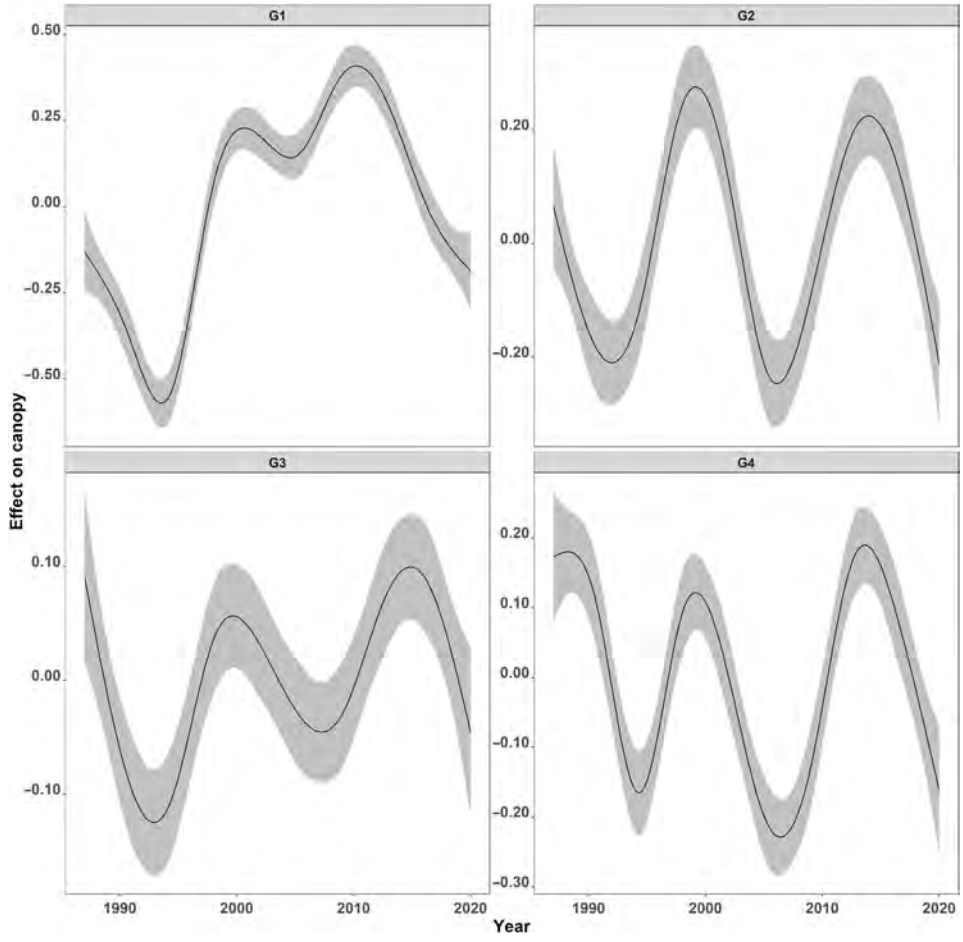


Fig. 3. Fitted long-term trends of mangrove canopy cover (proportion of closed forest to total mangrove area) at each bioregion after removing the overarching increasing trend. Black lines are the estimate, and gray shaded areas are 95% confident intervals. Note the differences in the *y*-axis scale. G1, Gulf; G2, Arnhem/Carnarvon; G3, Bonaparte/Kimberly/Dampier/Northern Great Barrier Reef; G4, Southern Great Barrier Reef/SE Queensland/SE Coast/Temperate as in Fig. 1 and Table 1.

and vegetative thickening if positive) with the lowest monthly maximum water levels, which occur during the dry season (August to November) due to prevailing easterly trade winds (*18*). We related interannual patterns in the lowest monthly maximum water level to the modeled influence of the 18.61-year lunar nodal cycle and the 4.4-year perigean subharmonic (Materials and Methods). Our hypothesis was that inundation high in the tidal frame (and consequently the duration of mangrove inundation within this period)

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

would be reduced under the low amplitude phase of the 18.61- and 4.4-year tidal cycles, leading to a reduction in hydroperiod, elevated water stress, and lower mangrove canopy cover.

These changes are expected to occur in the context of an overarching signal of climate change, associated with rising sea levels, higher air temperatures, and elevated atmospheric CO_2, all factors associated with mangrove expansion, increasing productivity, and canopy thickening (*6*). Statistical modeling was undertaken to decompose time series mangrove extent and proportion of closed canopy data within coastal bioregions into components describing the length of record trend and short-term fluctuations. Models were also developed for each coastal bioregion to investigate the response of mangroves to tidal and climatic variables.

RESULTS

Across all coastal bioregions, an overarching trend of increasing mangrove extent and canopy cover over time was established ($P < 0.0001$; Figs. 2 and 3 and table S1). Mangrove canopy cover was strongly related to the mean sea level, lowest maximum water level each year, and annual rainfall (bioregional group model r^2 ranging from 0.62 to 0.97; Fig. 4 and table S2), the relative importance of these factors varying between bioregion groupings as predicted by the strength of the nodal tidal cycle.

In the semidiurnal coastlines of the Carnarvon and Arnhem bioregions, patterns of closed canopy expansion and open forest and woodland contraction were synchronized (Figs. 5 and 6). In addition, phases of high canopy cover corresponded to high tidal amplitude phases of the 18.61-year lunar nodal cycle (Figs. 5 and 6). This pattern held over the two phases of the 18.61-year cycle since 1990. The transition from open mangrove woodland and open forest to closed mangrove forest occurred across one-quarter (~500 km^2) of the maximum closed forest area (~1900 km^2). In the Arnhem bioregion, the 2015–2016 El Niño was timed at the tidal amplitude maximum within the 18.61-year cycle, the period of the nodal tidal cycle during which mangrove forests are expected to be least prone to canopy

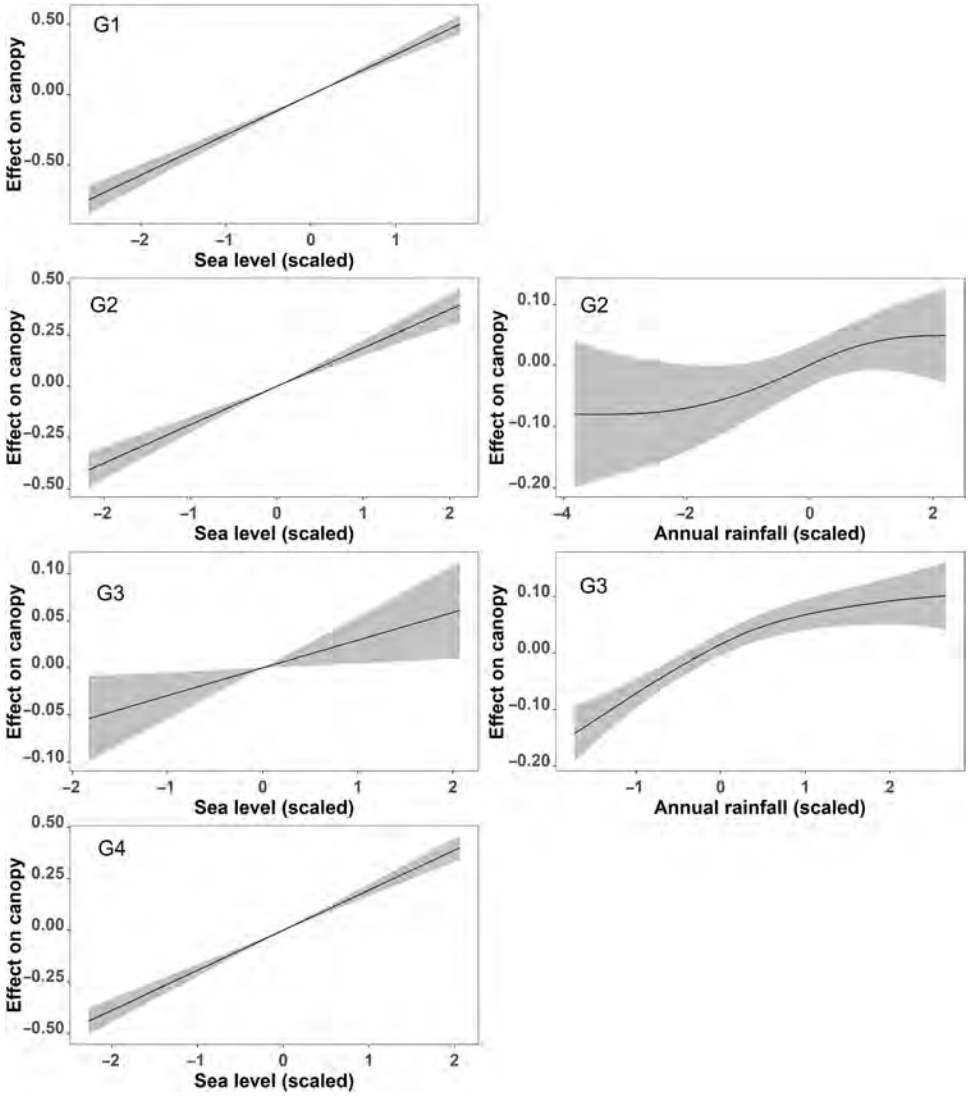


Fig. 4. The response of mangrove canopy cover to lowest maximum monthly sea level and rainfall in the four bioregion groupings. Note that rainfall was not included in the final model for G1 and G4 (table S1).

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

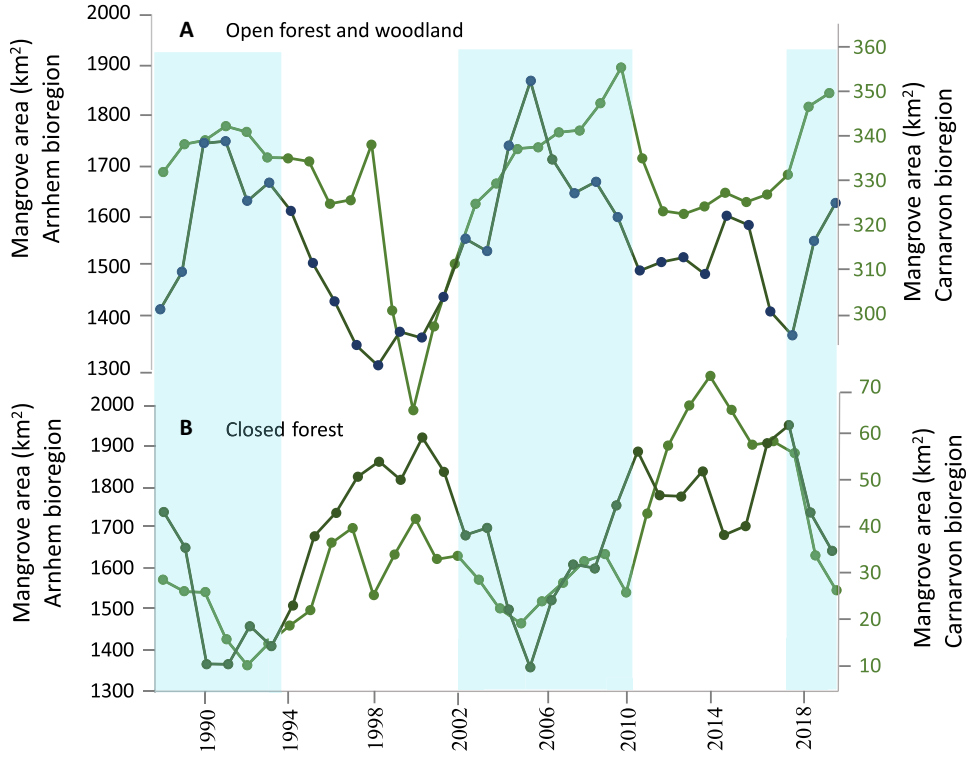


Fig. 5. Canopy tracking the nodal cycle in the G2 (semidiurnal/nodal cycle) bioregions. The area of open forest and woodland (**A**) and closed forest (**B**) in the Arnhem bioregion (dark green) and Carnarvon bioregion (light green) (two-year running means). The trend follows two phases of the 18.61-year nodal cycle (see also Fig. 4), with alternating phases of closed and open canopy associated with a positive anomaly (no shading) or negative anomaly (blue shading), in tide range respectively.

dieback. While the trend toward higher closed forest cover is reversed in 2015–2016, this was quickly restored, suggesting resilient responses of mangroves in this bioregion and limited mortality (Fig. 5).

Within the Gulf of Carpentaria, the maximum sea level exerts the strongest control over mangrove canopy of all bioregions ($P < 0.001$) (Fig. 4), and inclusion of monthly tidal SD (an indicator of the nodal tidal cycle) explains 90% of variation in mangrove canopy cover (table S2). Here, tides are diurnal, with the result that the phase of the 18.61-year nodal tidal cycle is the inverse of the neighboring Arnhem bioregion (Figs. 2 adn 6D). The minimum amplitude of the 18.61-year nodal tidal cycle occurred in 2015, coincident with the minimum amplitude of the 4.4-year perigean harmonic (Fig. 6, C and D), a combination with a return period of ~40 years. The resulting extreme moderation of tidal amplitude in that year (~0.45 m lower than the maxima; Fig. 6C) explains most of the observed decline in maximum tide level over the period 2007–2015. The coincident strong El Niño lowered mean water level and extended the dry season, which normally occurs between May and October, into November (*11*). A phase of canopy dieback that had commenced in the Gulf of Carpentaria in 2012 (Fig. 6) was exacerbated by drought, resulting in more extensive mangrove mortality and sustained canopy loss than occurred in the adjacent Arnhem bioregion, where we propose that the impact of the El Niño was tempered by the high amplitude phase of the nodal tidal cycle.

We hypothesized that mangrove canopy cover would be influenced by changes in maximum tidal range at the 4.4-year perigean cycle in the northern Great Barrier Reef, Kimberly, Bonaparte, and Dampier bioregions, where this cycle predominates (Fig. 1). Spring tides are lowest in the late dry season (August to October), at the time of lowest rainfall and maximum water stress. Years in which these tides are particularly low are phased with the 4.4-year subharmonic and are associated with lower closed forest cover ($P = 0.636$, $P = 0.682$, $P = 0.274$, and $P = 0.686$ for the Dampier, the northern Great Barrier Reef, Bonaparte, and Kimberly bioregions, respectively; Fig. 7 and Materials and Methods). However, annual rainfall had a stronger predictive influence on canopy cover in these bioregions than maximum dry season tide level, with the additive term of rainfall explaining 96.5% of the deviance with adjusted $r^2 = 0.96$ (table S2). Rainfall also dominated the interannual variability in group 4, the southeastern bioregions of Southern Queensland, South East Coast, and Temperate Southern Coast, a finding consistent with previous assessments (*15*, *16*), and the relatively low amplitude of long phase tidal harmonics in the region (4 to 6 cm).

Patterns of mangrove loss and expansion in the Norman River in the eastern corner and the Roper River in the western corner of the Gulf of Carpentaria (Fig. 8) illustrate the importance of geomorphic context in the expansion and contraction of mangrove canopy cover. In both estuaries, mangrove expansion continues at the tidal head in 2014–2016, while dieback is concentrated in geomorphic settings subject to the full tidal range (mudflats fringing coastlines and river channels) (*19*).

DISCUSSION

The trend of mangrove proliferation and thickening has been noted for mangrove poleward limits globally (*20*) and, in Australia, is

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

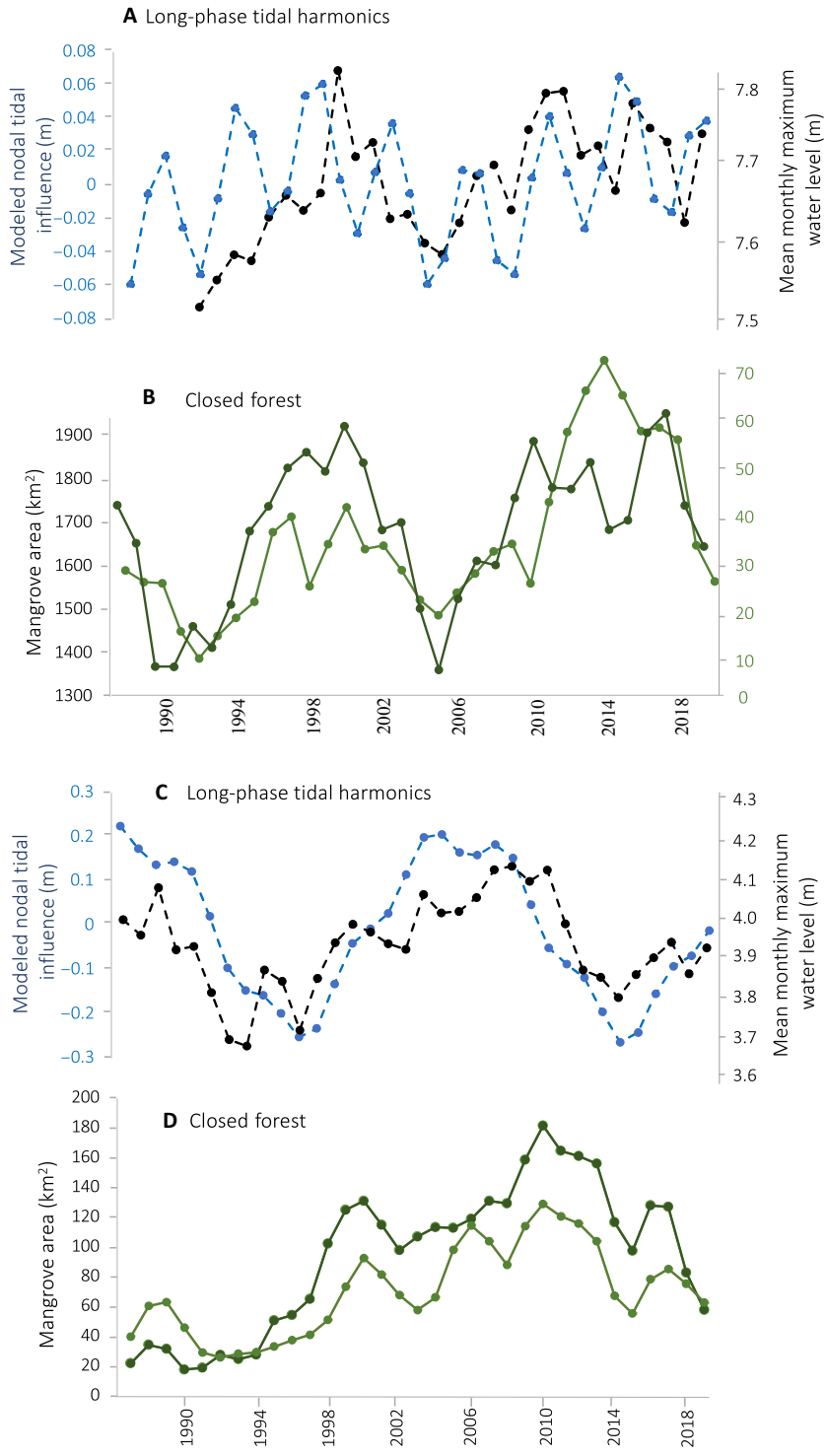


Fig. 6. The 18.6-year lunar nodal cycle in relation to mangrove canopy cover. Modeled combined influence of the 18.6 nodal tidal cycle and 4.4-year perigean subharmonic on the 99.5 percentile tide (combined; blue dashed lines) and observed average monthly maximum water level (black dashed lines) in Milner Bay, Arnhem Bioregion (**A**), and Karumba in the corner subregion of the Gulf of Carpentaria (**C**), illustrating the 180° shift in phasing of the 18.61-year cycle. The 2-year running mean area of mangrove closed forest (**B**) within the Arnhem bioregion (dark green) and the Carnarvon bioregion (light green) and the 2-year running mean area of mangrove closed forest (**D**) within the northern territory (dark green) and the corner (light green) subregions of the Gulf of Carpentaria (locations in Fig. 1). An intense El Niño in 2015–2016 is coincident with the maxima of tidal amplitude in Arnhem Land and the minima of tidal amplitude in the Gulf of Carpentaria.

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

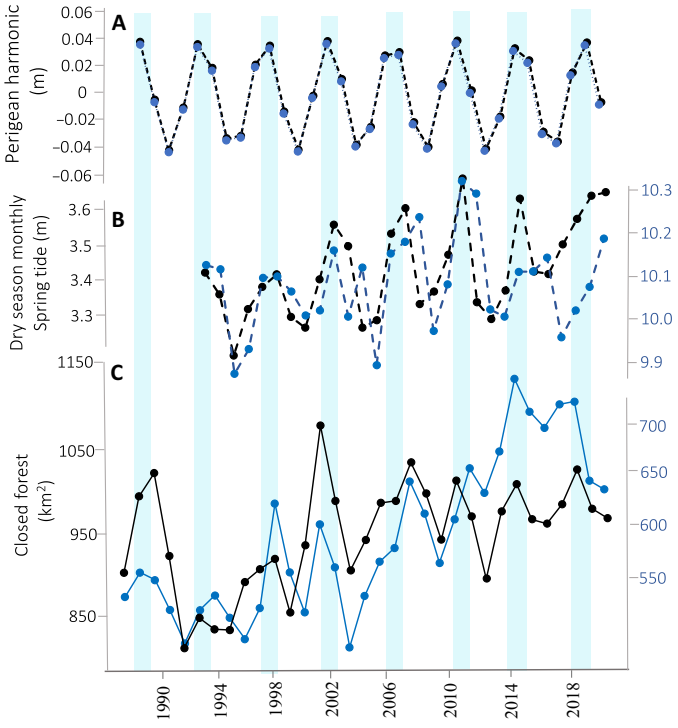


Fig. 7. The perigean subharmonic in relation to spring tidal level and mangrove canopy on opposite sides of the northern Australian continent. The modeled influence of the Perigean subharmonic (**A**) at Broome, Western Australia (black dashed line) and Cape Fergusson, Queensland (blue dashed line); mean monthly maximum water level for the late dry season (August to October) (**B**) at Broome tidal gauge, Western Australia (black dashed line) and Cape Ferguson, Queensland (blue dashed line). Area of closed canopy mangrove forest (2-year running means) in the Kimberly and Dampier bioregions (combined; black solid line) and the northern Great Barrier Reef (blue solid line) (**C**). The eight periods' positive anomaly/high tidal amplitude (blue shading) aligns with phases of higher mangrove canopy cover, but rainfall is a stronger predictor of interannual variability.

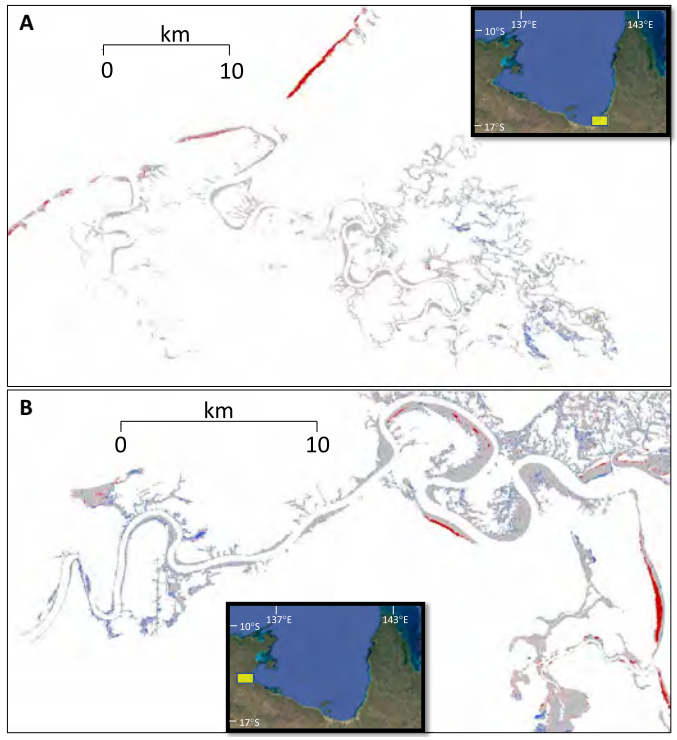


Fig. 8. Geomorphic context of mangrove dieback in the Gulf of Carpentaria. Patterns of mangrove expansion (blue) and dieback (red), no change (gray) between 2014 and 2016 in the Norman River at Karumba (17°28′S; 140°48′E) (**A**) and the Roper River (14°42′S; 135°17′E) (**B**), Gulf of Carpentaria. Dieback is concentrated in areas of full tidal range, while expansion continues at the tidal head, where tidal range is dampened.

ubiquitous across latitudes and bioregions in this study. Mangrove expansion is consistent with moderate rates of sea level rise (Table 1) and other global drivers favoring mangrove growth, including elevated atmospheric CO_2 and, in higher latitudes, temperature (*20*, *21*). We propose that long-phase tidal modulation is an important control over mangrove canopy condition in Australia. While the long-phase tidal components modify tidal amplitude by about 3% (*3*), in macrotidal regions, this component can translate into 20 to 50 cm of interannual variability in high water levels (*7*). Because mangroves occupy gently sloping upper intertidal mudflats, the 18.61- and 4.4-year modulations have influenced interannual variation in controlling mangrove canopy cover hydroperiod and mangrove growth.

We provide three lines of evidence supporting a role for the lunar nodal cycle. First, the alternation between open and closed canopy in semidiurnal coastlines follows the negative and positive phasing of the 18.6-year nodal cycle, a phasing discernible across all bioregions (Fig. 3) and particularly dominant in regions where the nodal cycle influence is pronounced (the Arnhem, Carnarvon, and Gulf of Carpentaria bioregions; Fig. 4). Observations from the 2015 dieback event suggest that the gray mangrove *Avicennia marina* is particularly susceptible to canopy decline under reduced inundation (*11*). *A. marina* is the most widely distributed species in Australia, dominating subtropical and temperate mangroves, and this may explain the consistency of the nodal cycle influence on mangrove canopy cover across the continent.

Second, the alternate phasing of the nodal cycle in the diurnal coastline of the Gulf of Carpentaria is associated with a corresponding shift in the phasing of canopy cover, with the maintenance of high canopy cover with the 2006 optima and stronger declines associated with the 2015 minima. While there is little doubt that the strong El Niño event contributed to mangrove mortality, we propose that the coincidence of the El Niño with the minimum tidal amplitude phase of the nodal cycle in the Gulf of Carpentaria was the reason for much higher mortality in this bioregion than in adjacent semidiurnal bioregions where the El Niño coincided with the high amplitude phase.

Third, the pattern of dieback within estuaries during the 2015–2016 event in the Gulf of Carpentaria suggests declines to be concentrated in areas subject to full tidal amplitude (and therefore tidal range dampening during the nodal cycle minima). Within the Roper and Norman Rivers, mangrove expansion continues through the El Niño drought of 2015–2016, where tidal range and the influence of the tidal modulation are limited, but the effects of sea level rise remain. This expansion occurs despite these environments consisting of newly recruited trees subject to the full effect of low rainfall, reduced freshwater inflow, and higher temperature observed at the time (*11*).

The impact on mangrove ecosystem processes associated with these nodal cycle events is likely to be profound. In the Arnhem bioregion, the 18.61-year nodal cycle drove the transition between

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

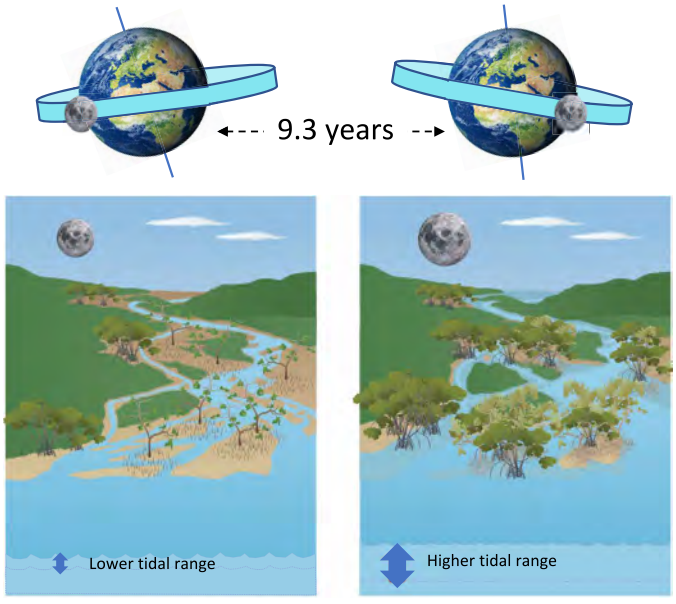


Fig. 9. Conceptual model of the influence of the nodal cycle on mangrove canopy cover. The precession of the lunar nodes has an influence on tidal amplitude, and this influence on inundation high in the tidal frame may be relatively large over the 18.61-year cycle compared to climatic drivers. The vigor of mangrove growth may reflect this periodicity, thereby influencing canopy cover, litterfall, and carbon burial rates.

open and closed canopy cover for 25% of the mangrove forest areal extent, some 500 km^2 of forest. In the Gulf of Carpentaria, where the coincident minima of the 18.61- and 4.4-year modulations in 2015 occurred during intense El Niño event, the proportion of closed mangrove canopy subject to dieback was ~50%. The coincidence between recent intense El Niño and troughs of the 18.61-year cycle (1997–1998 and 2014–2015) has been previously noted (*22*, *23*), and on these occasions, mangroves in diurnal settings subject to full tidal range are particularly vulnerable to loss (*24*).

Tide gauge analyses suggest that an influence of the 18.61-year nodal cycle comparable to that observed in our study (>10-cm range) is evident in Central America, Vietnam, Thailand, the Philippines, and Indonesia (*7*). Together with Australia, these regions contain 55% of the world's remaining mangroves (*25*). Given the disproportionately important role tropical mangroves play as a natural carbon sink (*26*), variability in canopy cover at regional and global scales would influence the rate of atmospheric carbon drawdown over decadal time scales. Canopy extent maxima might be expected in ~2024 in Indochina, Borneo, and the Philippines and in ~2033 in Indonesia and Central America, on the basis of phases in nodal modulation (*7*).

MATERIALS AND METHODS

Conceptual model and analytical approach

The position within the tidal frame suitable for mangrove colonization may vary with hydrological, geomorphological, and edaphic conditions, but in general, Australian mangroves are situated between mean high water and mean high water spring tidal levels, with the extent of cover of mangrove at upper intertidal positions dependent on aridity conditions (*27*, *28*). Mangroves are therefore more likely influenced by alterations to the periodicity of high water levels than mean or low water levels within the tidal frame. Changes to the frequency and duration of high-tide inundation caused by lunar precession is likely to be expressed in alterations to soil water content and soil water salinity. We hypothesize that these effects will be most pronounced during the dry season in tropical climates, when spring tide inundation is lower than at other times due to prevailing easterly trade winds (*18*), and mangroves most susceptible to water stress. The immediate response to water stress is expected to be canopy thinning (Fig. 9). While mangrove extent may also be influenced by changes to hydroperiod in the upper intertidal, the timing and observation of these changes are likely to be lagged in relation to this driver and more influenced by changes to mean sea level at the tidal head. We therefore focused on the response of mangrove canopy cover to maximum water level changes driven by long-period tidal cycles, along with other putative drivers such as rainfall.

Our approach was to use a prior classification of Australian coastal bioregions (*29*) as a framework for comparing the influence of tidal cycles on mangrove canopy cover at a continental scale (Fig. 1). We matched bioregions with the modeled influence of the 18.61-year nodal cycle and the 4.4-year perigean subharmonic, which vary predictably across the continent in relation to coastal morphology, tidal range, and tidal form factor (the extent of diurnal versus semidiurnal tidal form). The timing of the 18.61-year lunar nodal cycle varies between diurnal and semidiurnal settings (*1*), with the maximum amplitude in semidiurnal settings corresponding to the minimum amplitude in diurnal settings. This allowed for testing of the influence of the nodal cycle along coastlines subject to common climatic influence but contrasting tidal form. Because the Gulf of Carpentaria was the only region with a diurnal tide subject to the 18.6-year nodal cycle, the region was subdivided to improve replication (Northern Territory and Corner and Peninsula subregions; Fig. 1).

Mangrove extent and canopy cover

Mangrove extent and canopy cover was defined using methods described by Lymburner *et al.* (*14*). Limits of mangrove extent used to constrain the analysis were defined using the global trend and extent maps generated by the Global Mangrove Watch, which used both Landsat time series and Advanced Land Observation Satellite (ALOS) Phase Array L-band Synthetic Aperture Radar data from a baseline year of 2010, with subsequent annual change away from this baseline from 1996 to 2016 (*30*). Available Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper Plus, and Landsat 8 Operational Land Imager observations have been geometrically corrected, converted to surface reflectance, adjusted for solar illumination and viewing angles, restructured to remove cloud and cloud shadow, and archived within the National Computational Infrastructure Facility at the Australian National University from 1987 onward. For each year between 1987 and 2020, the 10th percentile green photosynthetic fraction (GV_{10}) was calculated, identifying vegetated areas persistently green throughout the year (mangroves as opposed to sympatric herbaceous and woody vegetation). PCC% was determined at selected locations using light detection and ranging–derived canopy height models with a resolution of ~≤1 m. GV_{10} was subsequently related to PCC% using 50% of the PCC% dataset, while the remaining PCC% dataset was used for validation. Following validation, GV_{10} was calibrated against PCC% for each year to indicate spatial and temporal changes in mangrove canopy cover (*14*).

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

Environmental variables

Monthly maximum, mean, and minimum water levels were accessed using tide gauge records from the Australian Baseline Sea Level Monitoring Project, managed by the Australian Bureau of Meteorology (www.bom.gov.au/oceanography/projects/abslmp/abslmp.shtml). Stations within this network provide reasonable coverage of the marine and coastal bioregions, as follows: Gulf of Carpentaria: Milner Bay/Groote Eylandt tide gauge (13.8600°S, 136.4158°E), Karumba storm tide gauge (17.50°S, 140.8333°E), and Weipa tide gauge (12.6666°S, 141.8666°E); Kakadu: Darwin Harbour tide gauge (12.4719°S, 130.8458°E); Dampier and Kimberly bioregions: Broome tide gauge (18.0008°S, 122.2183°E); Carnarvon bioregion: Hillarys tide gauge (31.8256°S, 115.7286°E); Northern Great Barrier Reef bioregion: Cape Ferguson tide gauge (19.2774S, 147.0586°E); Southern Great Barrier Reef: Rosslyn Bay tide gauge (23.1610°S, 150.7901°E); Southeast Coast: Port Kembla tide gauge (34.4734°S, 150.9118°E); and Temperate Southern Coast: Portland tide gauge (38.3439°S, 141.6136°E). Data gaps were filled by spline interpolation if the number of consecutive missing data points is less than 4. However, if more data are missing, then regression with records from nearby stations was used. In addition, the monthly Southern Oscillation Index (SOI) for the study period was downloaded from National Oceanic and Atmospheric Administration (NOAA)'s Climate Prediction Center (www.cpc.ncep.noaa.gov/data/indices/soi).

Monthly rainfall aggregate and mean maximum temperature were accessed from the Australian Bureau of Meteorology, Climate Data Online (www.bom.gov.au/climate/data). Stations were chosen for continuity of record over the analysis period: Gulf of Carpentaria (Centre Island, Karumba, and Weipa), the Carnarvon Bioregion (Exmouth), Northern Great Barrier Reef (Cairns), Southern Great Barrier Reef (Mackay), SE Queensland (Hervey Bay), South East Coast (Williamstown air base), Arnhem bioregion (Darwin), Bonaparte bioregion (Darwin), Kimberley bioregion (Broome). Dampier bioregion (Broome), and Temperate Southern Coast (Melbourne).

Modeling of long-phase tidal cycle influence

To extract the magnitude and phase of the 18.61-year lunar nodal tidal cycle and the 8.85-year cycle of lunar perigee at sites around the coastline of Australia, we followed (*1*). We used tidal constituents from the TPXO7.2 global tidal model from Oregon State University. Using these constituents (which have a one-quarter degree resolution), we predicted multidecadal time series of astronomical tides at different sites around the coast of Australia using the Tidal Model Driver (TMD) MATLAB toolbox created by scientists at Earth & Space Research. TMD includes standard satellite modulation corrections based on equilibrium tide expectations. From the time series of predicted tidal series, we extracted annual time series of the 99th percentile. The amplitude and phase of the tidal modulations and their subharmonics were estimated from the annual percentile time series using harmonic analysis fitted to 18.61-, 9.305-, 8.85-, and 4.4-year sinusoidal signals. The amplitudes of the 9.305- and 8.85-year cycles were typically more than an order of magnitude smaller than that of the 18.61- and 4.4-year cycles, respectively, and, hence, were not considered further.

To test the influence of the nodal cycle and perigean subharmonic on mangrove canopy cover, we first assessed the relationship between modeled maximum tide and observed maximum tide for representative tide stations (listed above) and, second, the relationship between observed lowest maximum tide (the dry season maximum tides in the tropics) and mangrove canopy cover (as described below).

Statistical modeling of mangrove extent and canopy cover

A two-step modeling approach was used to explore the dynamics of mangrove extent (i.e., total mangrove area in a coast bioregion) and canopy conditions (i.e., the proportion of closed forest). Generalized additive mixed models (*31*) were used to decompose the time series of mangrove area and condition into (i) a global length-of-record trend component and (ii) a component for short-term fluctuations within coastal bioregions (*32*, *33*). GAMM is a semiparametric extension of generalized linear models, which can account for the nonlinear relationships between dependent variables and covariates (*34*, *35*). A GAMM was applied to each coastal bioregion to investigate the response of mangroves to tidal and climatic variables described above. First, we used GAMM (*34*) to decompose the time series of mangrove area and canopy cover into a global long-term trend component and a component for short-term fluctuations within each coast bioregion (*32*, *33*). Second, we investigated the response of mangrove to environmental variations (i.e., sea level and rainfall) by fitting individual GAMM for every coastal bioregion. To make it easier to interpret the estimated coefficients, all environmental variables for a site were standardized before model building such that each observation was subtracted from the mean and divided by the SD. The resulting scaled data had a mean of 0 and an SD of 1, providing internal consistency and facilitating comparison between environmental variables and among bioregions. The total mangrove area was also standardized within each bioregion to allow the comparisons between sites so that observed changes were analyzed at the same scale. We followed (*36*) for variable selection by adding an additional penalty term in the smoothness selection procedure, thereby removing redundant covariates.

As the variable of mangrove canopy condition is a proportion (calculated as the ratio of the closed forest and the total mangrove area, and ranging from 0 to 1 may not be normally distributed), we tested three error distribution families—Beta, Gamma, and Gaussian—for model fitting, with the result that Beta was chosen as the link function for GAMM. We also checked the autocorrelation in model residuals using the Durbin-Watson test (*37*).

To explore how sea level influences mangrove dynamics, we considered three sea level variables: mean meanly sea level, the lowest maximum monthly sea level, and the SD of monthly sea level. To examine the possible lagged mangrove response to environmental forcing, we considered lags of up to 3 years but all lagged environmental variables statistically insignificant ($p < 0.05$). Each model was fitted with annual total rainfall, mean SOI, and one of the sea level variables. Variable selection was based on the chi-square test (*35*). However, in cases of nonsignificant chi-square test ($P > 0.05$), the model with the lowest Akaike information criterion was selected and reported on. In all cases, SOI was not selected, suggesting that this index lacked explanatory power at the bioregional level of study.

The time series of area of closed mangrove forest displayed a monotonic increasing trend in all regions except South East Queensland ($P = 0.65$) and Temperate Southern Coast ($P = 0.21$) based on the Mann-Kendall test (*38*). We tested whether the dynamics of closed forest area were synchronous with the variation in spring high tides using a nonparametric test suitable for testing synchronism of trends in multiple time series (*39*). The modeling procedures were carried out with the "mgcv" package (*35*). Package "funtimes" (*39*) was used for the trend tests. All statistical analyses were carried out using the R v4.1.0 statistical software (*40*).

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

Elevation of mangroves in the Roper River and Norman River

We illustrate the pattern of mangrove decline and advance within estuaries in the Gulf of Carpentaria in the period 2014–2016 using two representative case studies: the Roper River in the SE corner of the Gulf and the Norman River in the SW corner (Fig. 9). We used the ALOS Global Digital Surface Model, namely, the ALOS World 3D at 30-m spatial resolution (AW3D30) (www.eorc.jaxa.jp/ALOS/en/dataset/aw3d30/aw3d30_e.htm), to generate the elevations of the mangrove dieback (red color; Fig. 3) zone and the mangrove expansion (blue color; Fig. 8) zone in the Norman and the Roper Rivers. First, we downloaded the AW3D30 covering the two rivers and extracted the elevation values for all pixel classes computed from the raster datasets archived in Digital Earth Australia between 2014 and 2016 using Landsat time series data (https://maps.dea.ga.gov.au/#share=s-t59vXkV2NWTL9Hvf2hSB0uqLcAb). We compared the elevations of the mangrove dieback and the mangrove expansion zones to establish whether there was a significant difference in elevation between each zone in each river. The *t* test was used to test the significant difference in elevation between the two zones in each river.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.abo6602

REFERENCES AND NOTES

1. I. D. Haigh, M. Eliot, C. Pattiaratchi, Global influences of the 18.61 year nodal cycle and 8.85 year cycle of lunar perigee on high tidal levels. *J. Geophys. Res. Oceans* **116**, C06025 (2011).
2. A. Oost, H. De Haas, F. Ijnsen, J. M. Van den Boogert, P. L. De Boer, The 18.6 yr nodal cycle and its impact on tidal sedimentation. *Sediment. Geol.* **87**, 1–11 (1993).
3. N. Gratiot, E. J. Anthony, A. Gardel, C. Gaucherel, C. Proisy, J. T. Wells, Significant contribution of the 18.6 year tidal cycle to regional coastal changes. *Nat. Geosci.* **1**, 169–172 (2008).
4. A. Smith, L. Guastella, S. Bundy, A. Mather, Combined marine storm and Saros spring high tide erosion events along the KwaZulu-Natal coast in March 2007: News & views. *S. Afr. J. Sci.* **103**, 274–276 (2007).
5. P. R. Thompson, M. J. Widlansky, B. D. Hamlington, M. A. Merrifield, J. J. Marra, G. T. Mitchum, W. Sweet, Rapid increases and extreme months in projections of United States high-tide flooding. *Nat. Clim. Chang.* **11**, 584–590 (2021).
6. K. McKee, K. Rogers, N. Saintilan, Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate and sea level, in *Global Change and the Function and Distribution of Wetlands* (Springer, 2012), pp. 63–96.
7. D. Peng, E. M. Hill, A. J. Meltzner, A. D. Switzer, Tide gauge records show that the 18.61-year nodal tidal cycle can change high water levels by up to 30 cm. *J. Geophys. Res. Oceans* **124**, 736–749 (2019).
8. A. D. Knighton, C. D. Woodroffe, K. Mills, The evolution of tidal creek networks, Mary river, northern Australia. *Earth Surf. Process. Landf.* **17**, 167–190 (1992).
9. C. Woodroffe, J. Chappell, B. Thom, *Geomorphological Dynamics and Evolution of the South Alligator Tidal River and Plains, Northern Territory* (The Australian National University, North Australia Research Unit, 1986).
10. M. E. Mulrennan, C. Woodroffe, Saltwater intrusion into the coastal plains of the Lower Mary River, Northern Territory, Australia. *J. Environ. Manage.* **54**, 169–188 (1998).
11. N. C. Duke, J. M. Kovacs, A. D. Griffiths, L. Preece, D. J. E. Hill, P. van Oosterzee, J. Mackenzie, H. S. Morning, D. Burrows, Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: A severe ecosystem response, coincidental with an unusually extreme weather event. *Mar. Freshw. Res.* **68**, 1816–1829 (2017).
12. K. J. Allen, D. C. Verdon-Kidd, J. Z. Sippo, P. J. Baker, Compound climate extremes driving recent sub-continental tree mortality in northern Australia have no precedent in recent centuries. *Sci. Rep.* **11**, 18337 (2021).
13. N. Duke, M. Ball, J. Ellison, Factors influencing biodiversity and distributional gradients in mangroves. *Glob. Ecol. Biogeogr. Lett.* **7**, 27–47 (1998).
14. L. Lymburner, P. Bunting, R. Lucas, P. Scarth, I. Alam, C. Phillips, C. Ticehurst, A. Held, Mapping the multi-decadal mangrove dynamics of the Australian coastline. *Remote Sens. Environ.* **238**, 111185 (2020).
15. L. Eslami-Andargoli, P. Dale, N. Sipe, J. Chaseling, Mangrove expansion and rainfall patterns in Moreton Bay, southeast Queensland, Australia. *Estuar. Coast. Shelf Sci.* **85**, 292–298 (2009).
16. A. A. Whitt, R. Coleman, C. E. Lovelock, C. Gillies, D. Ierodiaconou, M. Liyanapathirana, P. I. Macreadie, March of the mangroves: Drivers of encroachment into southern temperate saltmarsh. *Estuar. Coast. Shelf Sci.* **240**, 106776 (2020).
17. L. Eslami-Andargoli, P. Dale, N. Sipe, Does spatial scale affect the pattern of mangrove change under different rainfall regimes? An example in southeast Queensland, Australia. *Austral Ecol.* **38**, 208–218 (2013).
18. A. Forbes, J. Church, Circulation in the Gulf of Carpentaria. II. Residual currents and mean sea level. *Mar. Freshw. Res.* **34**, 11–22 (1983).
19. E. Asbridge, R. Bartolo, C. M. Finlayson, R. M. Lucas, K. Rogers, C. D. Woodroffe, Assessing the distribution and drivers of mangrove dieback in Kakadu National Park, northern Australia. *Estuar. Coast. Shelf Sci.* **228**, 106353 (2019).
20. N. Saintilan, N. C. Wilson, K. Rogers, A. Rajkaran, K. W. Krauss, Mangrove expansion and salt marsh decline at mangrove poleward limits. *Glob. Chang. Biol.* **20**, 147–157 (2014).
21. K. C. Cavanaugh, E. M. Dangremond, C. L. Doughty, A. P. Williams, J. D. Parker, M. A. Hayes, W. Rodriguez, I. C. Feller, Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. *Proc. Natl. Acad. Sci.* **116**, 21602–21608 (2019).
22. I. Yasuda, Impact of the astronomical lunar 18.6-yr tidal cycle on El-Niño and Southern Oscillation. *Sci. Rep.* **8**, 15206 (2018).
23. R. S. Cerveny, J. A. Shaffer, The moon and El Niño. *Geophys. Res. Lett.* **28**, 25–28 (2001).
24. S. Abhik, P. Hope, H. H. Hendon, L. B. Hutley, S. Johnson, W. Drosdowsky, J. R. Brown, N. C. Duke, Influence of the 2015–2016 El Niño on the record-breaking mangrove dieback along northern Australia coast. *Sci. Rep.* **11**, 20411 (2021).
25. D. A. Friess, K. Rogers, C. E. Lovelock, K. W. Krauss, S. E. Hamilton, S. Y. Lee, R. Lucas, J. Primavera, A. Rajkaran, S. Shi, The state of the world's mangrove forests: Past, present, and future. *Annu. Rev. Env. Resour.* **44**, 89–115 (2019).
26. T. B. Atwood, R. M. Connolly, H. Almahasheer, P. E. Carnell, C. M. Duarte, C. J. Ewers Lewis, X. Irigoien, J. J. Kelleway, P. S. Lavery, P. I. Macreadie, O. Serrano, C. J. Sanders, I. Santos, A. D. L. Steven, C. E. Lovelock, Global patterns in mangrove soil carbon stocks and losses. *Nat. Clim. Chang.* **7**, 523–528 (2017).
27. B. G. Thom, L. Wright, J. M. Coleman, Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf-ord river, western Australia. *J. Ecol.* , 203–232 (1975).
28. E. Gilman, J. Ellison, R. Coleman, Assessment of mangrove response to projected relative sea-level rise and recent historical reconstruction of shoreline position. *Environ. Monit. Assess.* **124**, 105–130 (2007).
29. R. Thackway, I. D. Cresswell, A bioregional framework for planning the national system of protected areas in Australia. *Nat. Areas J.* **17**, 241–247 (1997).
30. P. Bunting, A. Rosenqvist, R. Lucas, L. M. Rebelo, L. Hilarides, N. Thomas, A. Hardy, T. Itoh, M. Shimada, C. Finlayson, The global mangrove watch—A new 2010 global baseline of mangrove extent. *Remote Sens. (Basel)* **10**, 1669 (2018).
31. T. Hastie, R. Tibshirani, Generalized additive models (with discussion). *Stat. Sci.* **1**, 297–310 (1986).
32. J. Knape, Decomposing trends in Swedish bird populations using generalized additive mixed models. *J. Appl. Ecol.* **53**, 1852–1861 (2016).
33. E. J. Pedersen, D. L. Miller, G. L. Simpson, N. Ross, Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ* **7**, e6876 (2019).
34. A. Guisan, T. C. Edwards Jr., T. Hastie, Generalized linear and generalized additive models in studies of species distributions: Setting the scene. *Ecol. Model.* **157**, 89–100 (2002).
35. S. N. Wood, *Generalized Additive Models: An Introduction with R* (CRC Press, 2017).
36. G. Marra, S. N. Wood, Practical variable selection for generalized additive models. *Comput. Stat. Data Anal.* **55**, 2372–2387 (2011).
37. J. Durbin, G. S. Watson, Testing for serial correlation in least squares regression: I. *Biometrika* **37**, 409–428 (1950).
38. K. Noguchi, Y. R. Gel, C. R. Duguay, Bootstrap-based tests for trends in hydrological time series, with application to ice phenology data. *J. Hydrol.* **410**, 150–161 (2011).
39. V. Lyubchich, Y. R. Gel, A local factor nonparametric test for trend synchronism in multiple time series. *J. Multivar. Anal.* **150**, 91–104 (2016).
40. R. C. Team (R Foundation for Statistical Computing, 2020).

Acknowledgments

Funding: T.D.P. is supported by a Macquarie University Research Fellowship (Grant No. MQRF0001124-2021). Imagery in the conceptual diagram was sourced from the Integration and Application Network, University of Maryland Center for Environmental Science, including artwork by T. Saxby. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. **Author contributions:** Conceptualization: N.S. and L.L. Data curation: L.L., E.A., T.D.P., and I.D.H. Formal analysis: N.S., L.W., T.D.P., and I.D.H.

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

Project administration: N.S. Supervision: N.S. Writing—original draft: N.S. Writing—review and editing: N.S., K.R., J.J.K., and R.L. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

Submitted 17 February 2022
Accepted 28 July 2022
Published 14 September 2022
10.1126/sciadv.abo6602

Downloaded from https://www.science.org at Macquarie University on June 23, 2024

Estuaries and Coasts (2014) 37:67–78
DOI 10.1007/s12237-013-9664-6

Managed Retreat of Saline Coastal Wetlands: Challenges and Opportunities Identified from the Hunter River Estuary, Australia

Kerrylee Rogers · Neil Saintilan · Craig Copeland

Received: 5 January 2013 / Revised: 14 June 2013 / Accepted: 17 June 2013 / Published online: 12 July 2013
© Coastal and Estuarine Research Federation 2013

Abstract We analyse the potential impacts of sea-level rise on the management of saline coastal wetlands in the Hunter River estuary, NSW, Australia. We model two management options: leaving all floodgates open, facilitating retreat of mangrove and saltmarsh into low-lying coastal lands; and leaving floodgates closed. For both management options we modelled the potential extent of saline coastal wetland to 2100 under a low sea-level rise scenario (based on 5 % minima of SRES B1 emissions scenario) and a high sea-level rise scenario (based on 95 % maxima of SRES A1FI emissions scenario). In both instances we quantified the carbon burial benefits associated with those actions. Using a dynamic elevation model, which factored in the accretion and vertical elevation responses of mangrove and saltmarsh to rising sea levels, we projected the distribution of saline coastal wetlands, and estimated the volume of sediment and carbon burial across the estuary under each scenario. We found that the management of floodgates is the primary determinant of potential saline coastal wetland extent to 2100, with only 33 % of the potential wetland area remaining under the high sea-level rise scenario, with floodgates closed, and with a 127 % expansion of potential wetland extent with floodgates open and levees breached. Carbon burial was an additional benefit of accommodating landward retreat of wetlands, with an additional 280,000 tonnes of carbon buried under the high sea-level rise scenario with floodgates open (775,075 tonnes with floodgates open and 490,280 tonnes with floodgates closed). Nearly all of the Hunter Wetlands National Park, a Ramsar wetland, will be lost under the high sea-level rise scenario, while there is potential for expansion of the wetland area by 35 % under the low sea-level rise scenario, regardless of floodgate management. We recommend that National Parks, Reserves, Ramsar sites and other static conservation mechanisms employed to protect significant coastal wetlands must begin to employ dynamic buffers to accommodate sea-level rise change impacts, which will likely require land purchase or other agreements with private landholders. The costs of facilitating adaptation may be offset by carbon sequestration gains.

Keywords Saline coastal wetland · Sea-level rise · Carbon sequestration · Elevation model · Sediment accretion · Threshold

K. Rogers (✉)
School of Earth and Environmental Science,
University of Wollongong, Wollongong, Australia
e-mail: kerrylee@uow.edu.au

N. Saintilan
Rivers and Wetlands Unit, New South Wales Office of Environment and Heritage, PO Box A290, Sydney South, NSW 1232, Australia

C. Copeland
Department of Primary Industries—Fisheries, Conservation Action Unit, 1243 Bruxner Highway, Wollongbar, NSW 2477, Australia

Introduction

The ecological and environmental services provided by saline coastal wetlands have been recognized for some time (Costanza et al. 1998; Costanza et al. 1989). Depending on their situation, these wetlands may act to dampen flood waters, recycle nutrients, provide timber and stabilize banks (Ewel et al. 1998; Lee et al. 2006). They provide essential habitat and contribute to the sustenance of a range of biota including commercially and recreationally important fish, invertebrates, waterbirds, bats and macropods (e.g. kangaroos and wallabies) (Kwak and Zedler 1997; Mazumder et al. 2006; Spencer et al. 2009). Recent reviews have documented the efficiency of saline coastal wetlands as carbon sinks, with more carbon sequestered per unit area than any other natural ecosystem type (Alongi 2012; McLeod et al. 2011). However,

saline coastal wetlands (specifically mangrove and saltmarsh) throughout the world are continuing to diminish in size as a consequence of the construction of levees, drains and floodgates. The conversion of substantial areas of saline coastal wetland to aquaculture has also occurred in recent decades (see for example Primavera 2006). Australia has a long history of saline coastal wetland drainage and reclamation. In coastal New South Wales the bulk of this drainage work had been completed by 1969 and Goodrick (1970) established that there had been a loss of 41,000 ha of fresh and saline wetlands principally due to drainage. Over 4,200 structures with the potential to impede tidal exchange have been identified in this area (Williams and Watford 1997) and these structures have promoted the establishment of pasture grasses and macrophytes more suited to brackish or freshwater conditions. These brackish and freshwater communities do not support coastal fisheries, are likely to be less efficient in the retention of carbon (Poffenbarger et al. 2011) and have been sources of poor water quality that has caused fish kills from acidification (Sammut et al. 1995) and deoxygenation (Walsh et al. 2004).

The Convention on Wetlands (Ramsar) has provided a framework for contracting parties (162 national governments) to list wetlands of international significance and voluntarily commit to their preservation. Other saline coastal wetlands are dependent upon national and local planning and legal frameworks, such as no net loss (USA), and local protected area legislation. In Australia, with the exception of wetlands listed as internationally important under the Ramsar Convention, wetland protection largely occurs at a state level through the acquisition of land as part of the reserve system, such as National Parks, or filters down to local and regional levels through legislation and policy.

Unfortunately, in Australia neither the Ramsar framework nor State policies deal well with the preservation of dynamic landscapes. Wetlands listed under the Ramsar Convention have official management boundaries defined as polygons drawn at the time of listing. Similarly, wetlands within reserves or protection zones are frequently managed according to gazetted boundaries. These boundaries may be derived from photography captured in the past and in the time since gazettal, boundaries may change, and have the potential to change at an accelerating rate as sea levels rise. While these planning and conservation instruments have served saline coastal wetlands well in the past, their utility in the conservation of critically important coastal ecosystems will diminish over time if they fail to accommodate the retreat of wetlands at a local scale.

Despite planning for saline coastal wetland protection in Australia being based on policy and legislation at state jurisdictions, planning actions that promote in situ adaptation and migration of saline coastal wetlands with sea-level rise is largely undertaken at the local scale (see for example Burley et al. 2012; Shoo et al. 2013). However, the need for effective coastal wetland legislation, policy and management is becoming even more imperative. The Intergovernmental Panel on Climate Change (IPCC) projected sea-level rise of between 18 and 59 cm above present levels by the end of the twenty-first century (Meehl et al. 2007). However, recent research indicates that this may underestimate sea-level rise, with current observations tracking the highest scenarios (Nicholls et al. 2011) and revised estimates of sea-level rise at the end of the century in the order of 47 to 100 cm (Horton et al. 2008), 30 to 215 cm (Grinsted et al. 2010) and 59 to 180 cm (Jevrejeva et al. 2010).

Saline coastal wetlands may have some capacity to adapt to accelerated sea-level rise and hydrological alterations through in situ processes that maintain their elevation relative to water levels. There has been considerable research into these processes over recent years, with results stressing the importance of sedimentation (Oliver et al. 2012; Rogers et al. 2012), and also the accumulation of root mass (McKee 2011; McKee et al. 2007; Nyman et al. 2006) as strategies by which saline coastal wetlands may adapt to sea-level rise. The latter has attracted interest as a mechanism for the burial of atmospheric carbon, with the associated benefit of offsetting emissions (Chmura et al. 2003; Duarte et al. 2005). As sea-level rise is likely to impact the resilience of these valuable ecosystems it is timely that consideration be given to appropriate management actions that will promote in situ adaptation of saline coastal wetlands, and their associated benefits.

In this paper we model sea-level rise impacts and adaptation strategies for an internationally important wetland. The Hunter River, NSW, Australia, supports an extensive temperate saline coastal wetland system comprising mangrove, saltmarsh and mixed mangrove–saltmarsh habitats. A large portion of these wetlands (4,257 ha) are formally protected within the Hunter Wetlands National Park and this includes over 2,926 ha listed as internationally important under the Ramsar Convention in 1984. The distribution of these wetlands within the lower Hunter has been shaped by the legacy of a network of 176 levees, culverts and floodgates that were constructed in the period 1950–1980 to create land suitable for agriculture and industry and to protect this land from flooding under the Hunter Valley Flood Mitigation Scheme (Williams and Watford 1997; Winning and Saintilan 2009). Wetland areas behind levee banks have transitioned from saltmarsh to brackish reedswamps dominated by *Schoenoplectus subulatus*, *Typha orientalis* and *Phragmites australis* (Winning and Saintilan 2009). Part of this estuary is heavily developed, being the site of the city of Newcastle, as well as one of the largest coal-loading facilities in the world. The lower Hunter therefore presents a useful case study in the management of internationally important and highly dynamic wetlands in the context of strong development pressure and anticipated sea-level rise.

We apply sea level projections provided by the IPCC (Meehl et al. 2007) and Hunter (2010) to the accretion/elevation model developed by Rogers et al. (2012) for the Hunter River to explore the adaptation capacity, resilience and mitigation opportunities for saline coastal wetlands. In doing so, we test the effect of flood mitigation structures on the distribution of saline coastal wetlands under low and high sea-level rise scenarios, and consider the differing carbon burial benefits of options relating to the management of floodgates and levees. This modelling allows for the exploration of the costs and benefits of planning and management actions that can be implemented at both state and local scales that promote the maintenance of wetland extent.

This is the first paper to quantify carbon burial benefits associated with contrasting sea-level rise adaptation options for saline coastal wetlands. We model two management options: (1) opening all floodgates and levees, facilitating retreat of mangrove and saltmarsh into low-lying coastal lands; and (2) leaving floodgates closed and levees elevated to protect coastal lowlands. For both management options we modelled the extent of saline coastal wetland to 2100 under a low sea-level rise scenario and a high sea-level rise scenario. For this we applied a dynamic elevation model (Rogers et al. 2012), which factored in the accretion and vertical elevation responses of mangrove and saltmarsh to rising sea levels, using locally derived data on these processes. We then calculated the volume of sediment accumulated across the estuary under the two management options for each sea-level rise scenario, and converted this to carbon accumulated using published estimates for the same wetland system (from Howe et al. 2009).

Methods

Study Site

The Hunter River (151°48′ E, 32°55′ S) has a length of approximately 300 km and drains a relatively large catchment area of 22,000 km^2 (Fig. 1). The Hunter River forms a permanently open barrier estuary with a semi-diurnal tidal regime and a tidal range of 1.9 m at the river mouth. In geomorphological terms, the Hunter estuary is in a mature evolutionary stage (Roy et al. 2001). Saline coastal wetlands on the Hunter

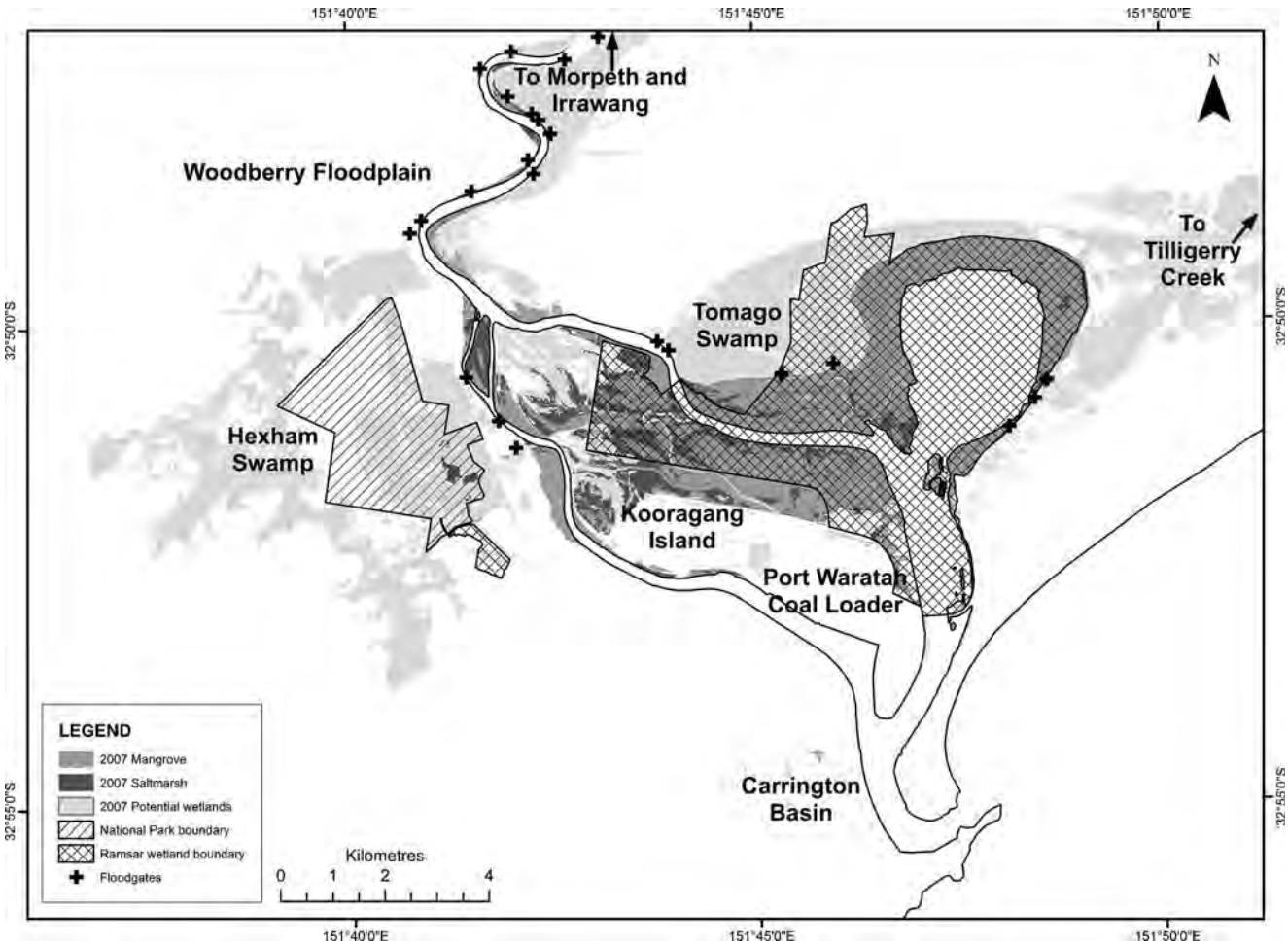


Fig. 1 Distribution of mangrove and saltmarsh on the Hunter River in 2007 and hydrologically connected areas with an elevation range of 0.1622 to 1.2015 m that are indicative of areas of potential saline coastal wetlands

River have undergone significant structural and morphological change since European occupation due to urban development as well as works associated with flood mitigation and drainage. Research by Rogers et al. (2006) indicates that incursion of mangroves into saltmarsh can be explained by relative sea-level rise in the region.

This study focuses on saline coastal wetlands located within the spatial extent of a light detection and ranging (LiDAR)-derived digital elevation model. Consequently, the analysis excludes saline coastal wetlands extending northeast from Fullerton Cove along Tilligerry Creek, and to the northwest on the Woodberry Floodplain, and at Morpeth and Irrawang.

Water Level Data

We used the maximum monthly water level model developed by Rogers et al. (2012) as a baseline for water level projections. This model was developed by time series analysis of monthly maximum water levels obtained from the Tomaree ocean level gauge using ARIMA modelling techniques. The model was selected as it maintained the upward trend in water level and accounted for seasonal trends associated with high spring tides in June/July and December/January. The maximum monthly water level predicted by the model for January 2010 was 2.9851 m and this was used as a baseline for water level projections.

Hunter (2010) provides minima (5th percentile) and maxima (95th percentile) projections of sea-level rise according to SRES scenarios from the IPCC fourth assessment report (Meehl et al. 2007) at decadal resolution to 2100. Two sea level projections from Hunter (2010) were selected for application to the landscape elevation model so as to project the full range of IPCC scenarios:

- Projections of sea level for 5th percentile minima according to the B1 emissions scenario, which has a projected sea-level rise between 1990 and 2100 of 18.5 cm.
- Projections of sea level for 95th percentile maxima according to the A1FI emissions scenario, which has a projected sea-level rise between 1990 and 2100 of 81.9 cm.

These scenarios were selected to capture the range of possible sea-level rise projections presented by the IPCC. These scenarios were disaggregated further to annual resolution by applying a quadratic curve of fit to each trend. Predicted values for each annual increment were added to the baseline water level value for January 2010 to generate projected maximum monthly water level values for the Tomaree water level gauge that corresponded to the 5th percentile minima according to the B1 emissions scenario and 95th percentile maxima according to the A1FI emissions scenario.

Accretion and Elevation Data

A standard technique to assess the in situ vulnerability of saline coastal wetlands to sea-level rise is the Surface Elevation Table/Marker Horizon (SET/MH) technique (Cahoon et al. 2000). The SET/MH technique quantifies the rate of sedimentation within a wetland and the extent to which that sedimentation contributes to raising the elevation of the wetland in response to sea-level rise. A network of SETs and MHs was established on Kooragang Island, Hunter River, in 2000 to investigate the vulnerability of these wetlands to sea-level rise. Data from the network was used to develop an accretion/elevation model that was driven by catchment scale processes such as water level and rainfall and local factors such as elevation and distance to waterways (Rogers et al. 2012). This model can be used to explore management options and planning guidance that facilitates adaptation of mangrove and saltmarsh on the Hunter River to sea-level rise. Increasingly, SET data are also being used to estimate the rate of carbon sequestration in saline coastal wetlands, and estimates of the rate of carbon burial in mangrove and saltmarsh from the Hunter SET dataset have recently been published (Howe et al. 2009).

Landscape Elevation Model

A digital elevation model (DEM) based on light detection and ranging data collected in January 2007, which reportedly has an accuracy of ±15 cm (Fugro Spatial Solutions, Pty, Ltd 2007), was used as the basis for the landscape model and to provide an understanding of the relationship between saline coastal wetland elevation and distribution. Distance to main channel was generated as a layer for input into the model.

Rogers et al. (2012) employed empirical wetland surface elevation and accretion data collected from mangrove and saltmarsh communities on the Hunter River to develop the following expression (r^2=0.8643, assumption of normality true) to explain changes in accretion occurring on the Hunter River estuary between January 2002 and May 2010:

$$A = -18.0118\,V + 0.0037\,W + 33.6177\,X - 0.0034\,Y + 0.0095\,Z - 0.0123\,(V - 0.6958)\,(W - 1880.8519) - 59.4570\,(V - 0.6958)\,(X - 2.9220) + 0.0114\,(W - 1880.8519)\,(X - 2.9220) - 0.1735\,(V - 0.6958)\,(W - 1880.8519)(X - 2.9220) - 80.8973$$

Where:

A	Vertical accretion (mm)
V	Elevation
W	Time
X	6-month average water level
Y	Distance
Z	Rainfall intensity

The model developed by Rogers et al. (2012) is a relatively simple equilibrium model, whereby sediment volume (both

organic and mineral components) is considered to be a function of relative elevation, which is influenced by a range of processes operating within catchments and estuaries, such as rainfall and water level. While Rogers et al. (2012) recognize that increasingly more sophisticated (and complex) models are available, they intentionally developed a simple model that: (1) utilized accessible information; and (2) could be used to assess planning and management scenarios.

This model assumes that accretion varies in proportion to a number of drivers that could be readily projected into the future; namely water level, distance from the main channel and rainfall intensity, which was defined as the total monthly rainfall from four rainfall gauges within the Hunter River catchment; Cessnock Airport (151.34° E, 32.79° S), Williamtown RAAF (151.84° E, 32.79° S), Jerrys Plains Post Office (150.91° E, 32.50° S) and Scone Airport (150.83° E, 32.03° S) gauges. Elevation was subsequently estimated by the addition of accretion to the previous elevation model. The model can be employed spatially within ARCGIS (ESRI® ARCMAP™ 10.0), with the LiDAR-derived DEM used as the benchmark elevation model. Rogers et al. (2012) justify excluding the contribution of fetch, wind shear and wave action due to the geomorphic setting of the wetlands within the Hunter estuary. This model also assumed that accretion was negligible at the landward wetland boundary, rainfall intensity is constant over the study period and equal to the long-term average rainfall for the region; and the distance to the sediment source is constant over the study period (Rogers et al. 2012).

In ARCGIS, we applied projected water level data to the model expression developed by Rogers et al. (2012) to generate landscape models of accretion and elevation according to the two selected scenarios; 5th percentile minima according to the B1 emissions scenario and 95th percentile maxima according to the A1FI emissions scenario. These scenarios are henceforth termed the low sea-level rise scenario (5 % minima of SRES B1 emissions scenario) and high sea-level rise scenario (95 % maxima of SRES A1FI emissions scenario). As elevation was a driver within the accretion model and water level was projected at annual increments, models of accretion and elevation were developed at annual increments to 2100. In accordance with Rogers et al. (2012), the accretion model was limited to the area of inundation and was assumed to be negligible in terrestrial areas.

Rogers et al. (2012) grouped mangrove and saltmarsh elevation distributions due to the overlapping elevation range of these communities in 2007 and estimated that mangrove and saltmarsh on the Hunter River occurred at a DEM elevation range of between 0.1622 and 1.2015 m. This accounts for 95 % of DEM cells within the mapped distribution of saline coastal wetlands. Approximately 2,442 ha of saline coastal wetland were delineated on the Hunter River in 2006. An additional 6,970 ha occurs within elevation ranges suitable for saline coastal wetlands (Fig. 1); however, it is important to note that the delineation of the potential extent of wetlands was limited by the northeast and northwest extent of the DEM; hence, the potential extent of wetlands is likely to be greater than that projected on the DEM. These additional areas do not currently support saline coastal wetlands due to management structures, such as flood levees and watercourse floodgates, which limit tidal flows to these areas of essentially private land. The DEM elevation range of 0.1622 to 1.2015 m was used to project the potential distribution of saline coastal wetlands on the lower Hunter River at 2100 according to the selected sea-level rise scenarios. Potential wetland extent was excluded from built-up areas where future expansion would be limited, namely Carrington Basin and the Port Waratah Coal loader; and a 26 ha section of the Tomago floodplain which has been infilled since the original LiDAR survey was undertaken in 2007. This approach assumes that inundation is the primary requirement for future wetland establishment and does not account for other limiting factors. Factors limiting mangrove and saltmarsh establishment have been considered elsewhere (see for example Erfanzadeh et al. 2010; Krauss et al. 2008), and the re-establishment of efficient carbon burial has been shown to be dependent upon time (Osland et al. 2012).

We estimated the volume of sediment required to facilitate wetland elevation adjustment at 2100 by subtraction of the benchmark DEM from the generated landscape elevation models using the Cut Fill volumetric analysis tool within the Spatial Analysis extension. We also explored a 'floodgates closed' management scenario where floodgates were maintained with no management action taken to reinstate tidal exchange (by opening floodgates) to low-lying areas thereby arresting the retreat of saline coastal wetlands into areas occupied by freshwater wetlands and farmland. As wetland extent is currently maintained through a network of floodgates that control tidal flows, we assumed that these floodgates would remain viable under higher sea levels and would continue to inhibit tidal exchange in the future. We used the landward limit of the mapped saline coastal wetland extent in 2007 as a surrogate for the extent of wetlands at 2100 under the floodgates closed management scenario. This extent was used to extract the volume of sediment required for in situ adaptation of wetlands under a floodgates closed management scenario and low and high sea-level rise scenarios.

While there is evidence that rates of carbon burial may vary with the age of regenerating wetlands (Osland et al. 2012), we assumed that carbon burial was constant over time. We also focussed on carbon burial and did not include other components of the carbon cycle that may offset carbon burial, such as gas efflux occurring in response to carbon decomposition (Adams et al. 2012; Kirwan and Mudd 2012). Hence, we assumed that carbon burial is proportional to accretion, and converted the volume of sediment into carbon content using estimates of total carbon density (Mg m^{-3}) provided by Howe

et al. (2009) for the Hunter saline coastal wetlands. These estimates distinguished between natural wetlands and disturbed wetlands, the disturbed category consisting of floodplains modified by agricultural activity into which tidal flows had been reinstated. These wetlands were found to have lower carbon content by approximately 50 %, and we used these estimates as they better represented the wetlands likely to be created under the "floodgates open" scenarios. Howe et al. (2009) estimated carbon density at 0.0301 Mg m^{-3} for mangrove and 0.0420 Mg m^{-3} for saltmarsh in disturbed sites. As we did not distinguish between mangrove and saltmarsh in our modelling we used an average figure of 0.03605 Mg m^{-3} for total carbon density.

Results

Landscape Elevation Model

Based on projected sea-level rise under the low sea-level rise scenario the landscape elevation model projected a 20 % increase in the area that may support mangrove and saltmarsh by 2100, henceforth identified as projected potential saline coastal wetland area, with all floodgates open (Table 1, Fig. 2). This expansion occurred incrementally at both the upper and lower boundaries of the projected potential saline coastal wetland area (Fig. 4). The model also indicated an expansion in the area of potential saline coastal wetland within the Ramsar area of 566 ha and within the Hunter Wetlands National Park of 1,108 ha. The increase in elevation of the wetland surface by 2100 equates to a soil volume (both autochthonous and allochthonous) of 1.67×10^7 m^3, corresponding to 602,035 tonnes of carbon buried.

Under the high sea-level rise scenario the model projected a decrease in potential saline coastal wetland area in the order of 56 % by 2100 with all floodgates open (Fig. 3). Approximately 2.15×10^7 m^3 of soil volume is required to facilitate wetland elevation adjustment by 2100 under the high sea-level rise scenario, corresponding to 775,075 tonnes of carbon sequestered. The limited capacity of saline coastal wetlands to respond in situ to sea-level rise is evident under a high sea-level rise scenario. Specifically, we found that the projected potential saline coastal wetland area increased incrementally at both the upper and lower boundaries of the projected saline coastal wetland extent until 2060; after 2060 marked submergence of lower intertidal environments was evident. By 2100, projected potential saline coastal wetlands primarily occurred in areas that did not support saline coastal wetlands in 2007. The model indicated that only 202 ha of potential saline coastal wetland will occur within the Ramsar area, a decrease of 1,393 ha from the present extent. Similarly, only 618 ha would remain in the national park, representing a decrease of 992 ha from the present extent.

The majority of wetland conversion by 2100 requires management actions that facilitate the reinstatement of tidal exchange and the subsequent conversion of generally privately owned grazing land to wetland. Based on the floodgates closed management scenario we estimated that approximately 1.08×10^7 m^3 of material, comprising both mineral and organic matter, would be required to facilitate wetland elevation adjustment under the low sea-level rise scenario, while approximately 1.36×10^7 m^3 of sediment is required under the high sea-level rise scenario. This corresponds to carbon burial of 389,349 and 490,280 tonnes, respectively.

Discussion

Wetland Adaptation and Resilience

We applied a low sea-level rise scenario to a model developed using empirical values of accretion and elevation. This demonstrated that saline coastal wetlands may have some capacity to build elevation at rates equivalent to sea-level rise (Fig. 2), in this case sea-level rise ranging from 1.2–2.2 mm-$year^{-1}$. According to the low sea-level rise scenario the model projected landward retreat of potential saline coastal wetland areas at rates approximately equivalent to sea-level rise. The seaward boundary exhibited very little change with minimal expansion into estuarine channels. Sources of material contributing to accretion at lower elevations that enable build-up of the wetland surface may include:

I. Mineral and organic matter from terrigenous sources that are transported to the estuary (or directly to wetlands) by overland flow are delivered to saline coastal wetlands by tidal flow and deposited when tidal flow diminishes.
II. Maintenance of lower elevation saline coastal wetlands may relate to 'roll-over' of the estuary morphology

Table 1 Estimated wetland area and carbon burried to 2100 in the lower Hunter estuary under two emissions and two management scenarios

	High emissions, floodgates open	High emissions, floodgates closed	Low emissions, floodgates open	Low emissions, floodgates closed
Wetland area (ha)	2,780	498	8,056	3,030
Carbon burial (tonnes)	775,075	490,280	602,035	389,349

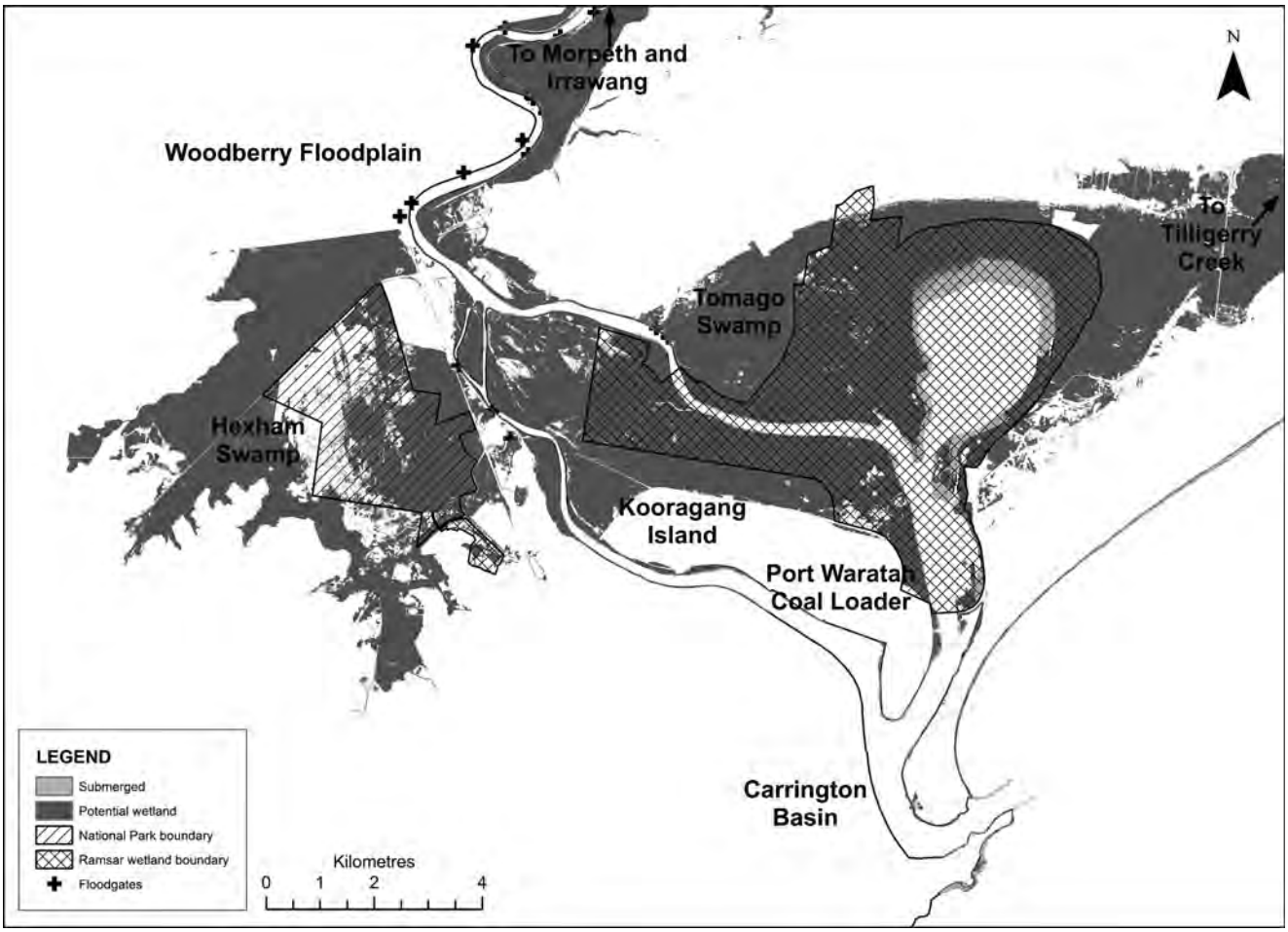


Fig. 2 Potential saline coastal wetlands areas at 2100 based on a low sea-level rise scenario (floodgates open). Saline coastal wetlands projection based on modelled hydrologically connected areas with an elevation between 0.1622 and 1.2015 m at 2100. The sea-level rise scenario employed in the model was based on a low sea-level rise projection derived from the 5th percentile minima sea-level rise projection under the IPCC B1 emissions scenario

upwards and landwards, similar to the model proposed by Allen (1990) for the Severn Estuary, UK and advocated by Pethick (2001). In this model, internal exchange and movement of fine sediment facilitates the removal of sediment from older deposits in the lower estuary to newer wetland areas so that wetlands maintain their position in the energy frame.

III. Wetland elevation gain within both mangrove and saltmarsh has been demonstrated to relate to expansion of the root zone and peat development (Bricker-Urso et al. 1989; McKee 2011; McKee et al. 2007; Nyman et al. 2006).

Our model results reflect the model applications of Kirwan et al. (2010) who demonstrated that marshes generally respond well to low rates of sea-level rise, but survival at rates exceeding 20 mm year^{-1} was dependent upon tidal range exceeding 3 m and tidal flows with high suspended sediment concentrations of 30–100 mg/L. Persistence of saline coastal wetlands at high rates of sea level-rise is not unprecedented; Woodroffe (1990) demonstrated that mangrove shorelines persisted at rates of sea-level rise in the order of 10–15 mm year^{-1} during the Holocene, and it has been demonstrated elsewhere that wetland accretion kept pace with sea-level rise over the Holocene (Alongi 2008; Fujimoto et al. 1996; Hashimoto et al. 2006; Krauss et al. 2003; Lynch et al. 1989; Miyagi et al. 1999).

The projected decline of potential saline coastal wetlands at higher rates of sea-level rise is substantial; with rates of sea-level rise exceeding the capacity of the wetlands to proportionally build elevation. This is consistent with the modelling of Traill et al. (2011) who demonstrated similar losses of seaward mangroves and landward expansion of wetlands. According to the high sea-level rise scenario the model projected extensive submergence of saline coastal wetlands, commencing around 2060 (Fig. 3) when rates of

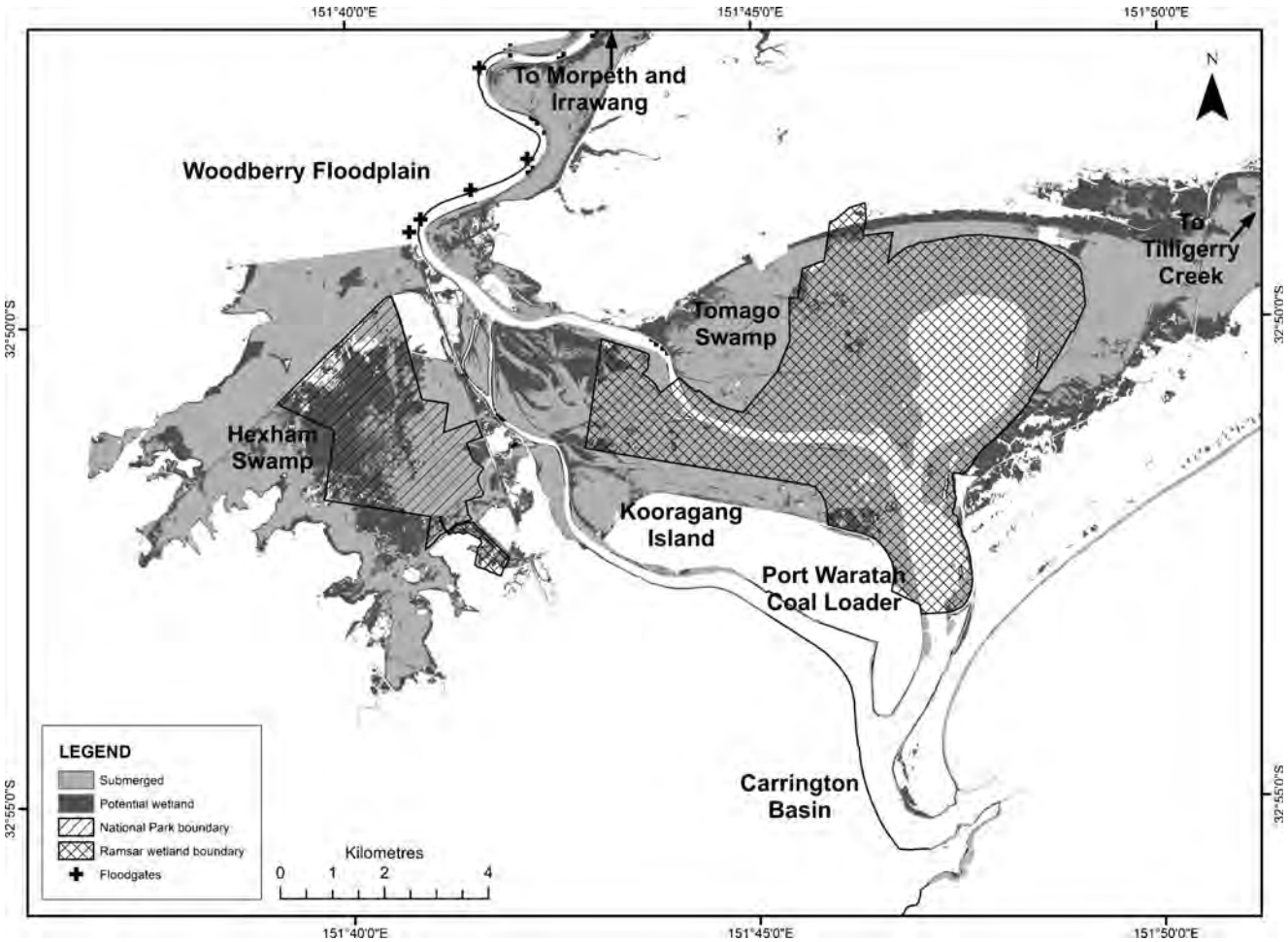


Fig. 3 Potential saline coastal wetlands areas at 2100 based on a high sea-level rise scenario (floodgates open). Saline coastal wetlands projection based on modelled hydrologically connected areas with an elevation between 0.1622 and 1.2015 m at 2100. The sea-level rise scenario employed in the model was based on a high sea-level rise projection derived from the 95th percentile maxima sea-level rise projection under the IPCC A1FI emissions scenario

sea-level rise began to exceed 9 mm year^{-1}. Based upon a high sea-level rise scenario our model demonstrates that when adaptation is facilitated by the reinstatement of tidal exchange, wetland retreat and elevation adjustment continues despite significant submergence under the high sea-level rise scenario. However, the wetland system may cross a resilience threshold by 2070 and rapidly transition to a new dynamic state of markedly less extent over a 30-year period unless adaptation measures are implemented. Though, we also recognize that the model presented here largely focusses on wetland geomorphology, and there may be some capability for biological responses to counteract geomorphological responses and inhibit (or slow) transition to new states. Upward adjustment of marsh surfaces facilitated by increased plant productivity and associated with increasing rates of relative sea-level rise have been demonstrated (Morris et al. 2002).

While our model application demonstrated the resilience of saline coastal wetlands, extended persistence beyond 2100 under high rates of sea-level rise may require significant mitigation measures to reduce the rate of sea-level rise and adaptation to reduce vulnerability. Active management of floodgate opening may be used to control tidal inundation and limit submergence in vulnerable areas located behind floodgates. Adaptation actions that manipulate accretion and wetland elevation building processes may be employed. Manipulation of elevation building processes through the addition of sediment (Ford et al. 1999) has been successfully trialled elsewhere. The success of nutrient addition in promoting plant growth and building wetland elevations is variable; McKee et al. (2007) observed increased root accumulation and elevation gain following nutrient addition of mangroves in the Caribbean region, while Lovelock et al. (2011) observed significant subsidence in nutrient-enriched mangroves and saltmarsh in Moreton Bay.

Accommodating wetland retreat has the additional benefit of carbon sequestration, as saline coastal wetlands are particularly efficient in the capture and retention of carbon (Alongi 2012; McLeod et al. 2011). The volume of carbon buried resulting

from wetland accommodation of sea-level rise is a function of lateral extension and vertical accretion. Vertical accretion will be driven by geomorphic and biological responses to sea-level rise, at least until the point of submergence, while lateral extension will be a function of hinterland topography and opportunities for migration afforded by the presence or absence of hard structures. Our modelling, incorporating the carbon density data of Howe et al. (2009), show that the scenario with the greatest rate of carbon burial is the high sea-level rise scenario with all floodgates open (775,075 tonnes carbon buried in the lower Hunter to 2100: Table 1).

Implications for Wetland Management

This paper considers two management options: leaving all floodgates open, facilitating retreat of mangrove and saltmarsh into low-lying coastal lands; and leaving floodgates closed. We modelled a significant decline in wetland extent under the floodgates closed option, which would induce a significant decline in ecosystem service (Costanza et al. 1998). Under a floodgates open management option, our modelling indicated that wetlands may have some capacity to retreat without impediment. The gains in ecosystem service under this management option are likely to be substantial. In particular, carbon burial gains may be approximately 30 % greater under a floodgates open management option (Fig. 4).

Unlike many terrestrial carbon sinks, coastal wetlands are particularly efficient at sequestering carbon as mangrove and saltmarsh soils do not become carbon saturated and continue to accrete sediments over long periods of time; anoxic saline conditions slow down the rate of decay of organic material and inhibit the release of greenhouse gases; and saline soil conditions, particularly the presence of sulphates, minimize the release of methane to the atmosphere (Duarte et al. 2005; Magenheimer et al. 1996; McLeod et al. 2011). Carbon sequestration has been a recognized forest management strategy for some time (Silver et al. 2000), but has yet to be fully explored as a strategy for coastal wetland management. In a 'carbon economy', the economic cost of wetland retreat and conversion of grazing land to coastal wetland may be off-set by the economic gains achieved through carbon sequestration. In this case, the decision to keep floodgates closed would forgo approximately 210,000 and 280,000 tonnes of carbon burial under the low and high sea-level rise scenarios respectively, an opportunity cost of $4–6 million in contemporary offset markets.

Legal and policy frameworks for wetland conservation globally are largely preservationist, grounded in the assumption that assets are stationary and can be defined in perpetuity as mappable areas. This approach is becoming increasingly discredited as a response to global environmental change (Craig 2010). Sea-level rise will diminish and in some cases obliterate the identity of relevant regulatory objects such as protected wetlands. The Hunter River case study described in this paper illustrates the limited capacity of both International (e.g. Ramsar Convention), National and State jurisdictional planning mechanisms to adequately protect critically important saline coastal wetlands in the face of climate change.

Under the high sea-level rise scenario, nearly all of the existing Ramsar wetland extent is lost by 2100. Presently, the

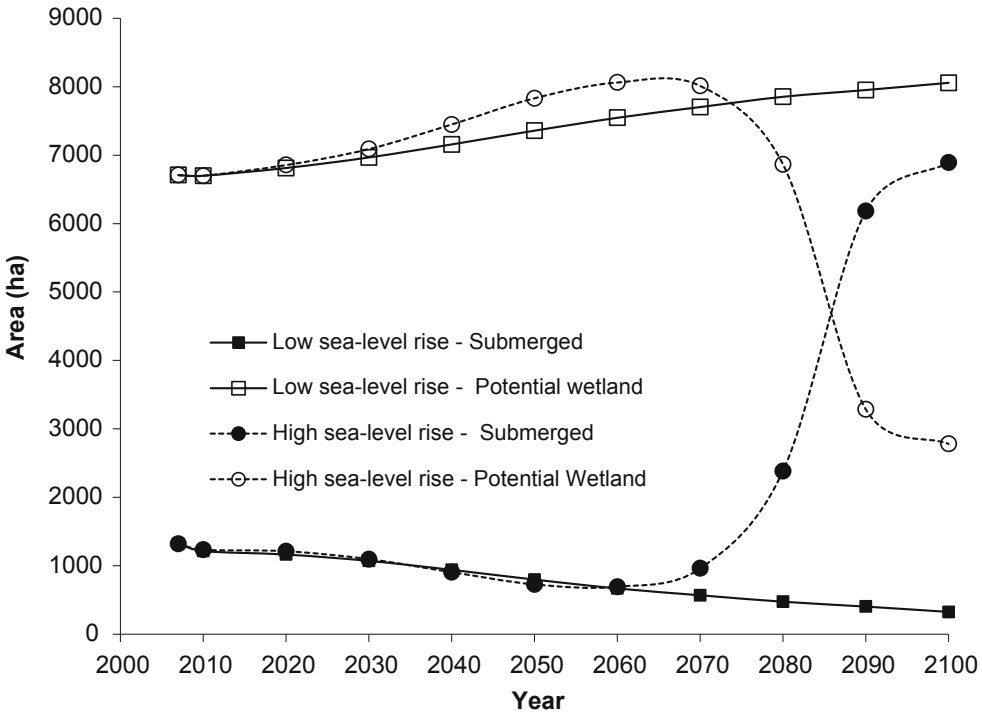


Fig. 4 Projected change in area of potential saline coastal wetlands and submerged area on the Hunter River between 2007 and 2100 based on a low and high sea-level rise scenario and all floodgates open. Submerged is defined as area below the elevation occupied by saline coastal wetland

Australian Government policy does not allow for notification to the Ramsar Convention under Article 3.2 of a change in ecological character where the principal cause is climate change (DEWHA 2009), even though Ramsar Resolution X.16 does not exclude climate change as a driver of altered ecological condition (Pittock et al. 2010). Opening of floodgates facilitates wetland retreat, but there is no mechanism in the Ramsar framework whereby the retreating wetland retains the status of international significance, a situation which progressively removes the wetland from Federal protection under the Federal *Environmental Protection and Biodiversity Conservation Act* (1999), which seeks to protect sites of international significance. The Ramsar Contracting Parties have not been able to provide clear guidance on how climate change should be dealt with under the Convention, though Resolution XI.14 from the recent COP 11 meeting (2012) recognizes the need to address the issue, referring the issue to the Scientific and Technical Review Panel for further consideration (Ramsar 2012).

In NSW (and elsewhere), State and local government planning instruments define the wetland as a mapped extent. The relevant maps were produced on the basis of aerial photography captured in the 1970s, and significant changes have already occurred since (Rogers and Saintilan 2002). There is currently no state level policy regarding buffers and accommodation space for coastal ecosystems impacted by sea-level rise. Hence, the primary level of planning control relevant to saline coastal wetland responses to sea-level rise in NSW is therefore via local government assessment of development applications.

We also identified that nearly all existing wetland within National Park boundaries is projected to be lost under the high sea-level rise scenario. In NSW, reserves are managed according to boundaries that have been gazetted. However, there may be some capacity to alter National Park boundaries to facilitate wetland adaptation to sea-level rise; relevant authorities (e.g. NSW National Parks and Wildlife Service) may acquire land for reservation or adjust the boundaries of existing reserves. The NSW National Park Establishment Plan (DECCW 2008) indicates that assessments of the adequacy of reserve systems within a bioregion should consider 'the likely impact of climate change on the resilience of the reserve system'. In NSW, the current statement of intent for reserve systems in the coast and coastal ranges bioregion of NSW indicates that 'fine-tuning and building-up of existing reserves' may include 'high priority intertidal, estuarine and lakebed areas which adjoin existing coastal and estuarine reserves' and 'areas that help buffer DECC public reserves from adjoining land uses that may be threatening reserve viability'.

In the Hunter region the bulk of the land that could be used to mitigate the impact of sea-level rise on intertidal wetlands is currently in private ownership. Elsewhere in NSW rehabilitation of saline coastal wetlands on private land has been achieved through either land purchase (e.g. Yarrahapinni and Hexham Wetlands) or through improved floodgate opening following landholder agreement. This latter method is only successful if there is no impact on landholders or more generally where the management change provides some benefits to the landholders through improved management of acid sulphate soils, increased wetland pasture or improved in-drain weed maintenance. Floodgate opening at sites in the lower Hunter River would result in damage to existing land uses and as such land purchase or other financial agreements would be the only possible course of action to facilitate wetland migration.

We make the following recommendations which should be broadly applicable to facilitating saline coastal wetland responses to sea-level rise nationally and internationally:

1. Saline coastal wetlands, and in particular those within a reserve system such as Ramsar or national parks, should be assisted in climate change resilience by the designation where possible of appropriate buffers for landward retreat. In the case of Ramsar wetlands, Ecological Character Descriptions should describe the wetland as a four-dimensional entity by recognising their latitudinal, longitudinal and elevation boundaries and the projected trajectory of these boundaries over time. Similarly, a comprehensive, adequate and representative public reserve system, such as national parks, should consider the trajectory of reserve boundaries over time.
2. The true cost of levee and floodgate maintenance be factored in cost–benefit analyses of coastal land protection, and that this includes the opportunity cost of wetland loss to carbon sequestration and ecological benefits, and the ongoing maintenance cost of the levee, including the accumulating liability for coastal flooding as sea levels rise.
3. The full range of adaptation pathways of saline coastal wetlands should be considered when promoting wetland resilience. Both mineral and organic sediment sequestration is essential for in situ adaptation of saline coastal wetlands. Consideration should be given to actions that facilitate in situ elevation adjustment of wetlands, such as enhancing the productivity of vegetation; or replenishment or maintenance of sediment supply.
4. To achieve these outcomes scientists and natural resource managers at all levels of government should work with individual wetland managers to identify likely wetland retreat pathways and potential management actions to facilitate wetland adaptation

Our analysis has exposed the limitations of current conservation and planning mechanisms in responding to the pressure of climate change in saline coastal wetlands, both in adapting to the reorientation of wetland boundaries or in facilitating mitigation through natural sequestration. Shoo et al. (2013)

propose the application of dynamic wetland boundaries and increased investment in reserves over time to maintain wetlands within the "preservation" network. This is a problem facing ecosystems more broadly, as Craig (2010) notes:

> "*climate change means that regulatory objectives based on pre-climate change characteristics of particular places can and will become obsolete. Climate change adaptation law must be able to accommodate this transforming ecological realities of particular places and not attempt to freeze ecosystems and their components into some prior state of being,"* p. 31

The modelling approach we have adopted provides the spatial output necessary for a considered approach to saline coastal wetland management, both in the presentation of flood risk, lands required for critical coastal processes and the likely benefit of carbon offsets associated with managed retreat. The implementation of coastal planning informed by these types of analysis will go some way to prevent the loss of opportunities for adaptive response and the wise management of wetlands throughout Australia.

Acknowledgements Max Finlayson is thanked for his comments on approaches to climate change adaptation under the Ramsar Convention. We also thank David Hanslow (NSW Office of Environment and Heritage) for helpful advice and three anonymous reviewers. Part of this research was funded by the NSW Environmental Trust with support provided by Kooragang Wetland Rehabilitation Project.

References

Adams, C.A., J.E. Andrews, and T. Jickells. 2012. Nitrous oxide and methane fluxes vs. carbon, nitrogen and phosphorous burial in new intertidal and saltmarsh sediments. *Science of The Total Environment* 434: 240–251.

Allen, J.R.L. 1990. The Severn Estuary in southwest Britain: Its retreat under marine transgression, and fine-sediment regime. *Sedimentary Geology* 66: 13–28.

Alongi, D.M. 2008. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science* 76: 1–13.

Alongi, D.M. 2012. Carbon sequestration in mangrove forests. *Carbon Management* 3: 313–322.

Bricker-Urso, S., S. Nixon, J. Cochran, D. Hirschberg, and C. Hunt. 1989. Accretion rates and sediment accumulation in Rhode Island salt marshes. *Estuaries and Coasts* 12: 300–317.

Burley, J., R. McAllister, K. Collins, and C. Lovelock. 2012. Integration, synthesis and climate change adaptation: A narrative based on coastal wetlands at the regional scale. *Regional Environmental Change* 12: 581–593.

Cahoon, D.R., P.E. Marin, B.K. Black, and J.C. Lynch. 2000. A method for measuring vertical accretion, elevation, and compaction of soft, shallow-water sediments. *Journal of Sedimentary Research* 70: 1250–1253.

Chmura, G.L., S.C. Anisfeld, D.R. Cahoon, and J.C. Lynch. 2003. Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles* 17: 1111.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, and M. van den Belt. 1998. The value of the world's ecosystem services and natural capital. *Ecological Economics* 25: 3–15.

Costanza, R., S.C. Farber, and J. Maxwell. 1989. Valuation and management of wetland ecosystems. *Ecological Economics* 1: 335–361.

Craig, R.K. 2010. "Stationary is Dead"—Long live transformation: five principles for climate change adaptation law. *Harvard Law Review* 34: 9–73.

DECCW. 2008. *New South Wales National Parks Establishment Plan: Directions for building a diverse and resilient system of parks and reserves under the National Parks and Wildlife Act*. Sydney: NSW Department of Environment, Climate Change and Water.

DEWHA. 2009. *National Guidelines for Notifying Change in Ecological Character of Australian Ramsar Sites (Article 3.2). "Module 3 of the National Guidllines for Ramsar Wetlands—Implementing the Ramsar Convention in Australia"*. Canberra: Department of Environment, Water, Heritage and the Arts.

Duarte, C.M., J. Middelburg, and N. Caraco. 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2: 1–8.

Erfanzadeh, R., A. Garbutt, J. Pétillon, J.-P. Maelfait, and M. Hoffmann. 2010. Factors affecting the success of early salt-marsh colonizers: Seed availability rather than site suitability and dispersal traits. *Plant Ecology* 206: 335–347.

Ewel, K.C., R.R. Twilley, and J.E. Ong. 1998. Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters* 7: 83–94.

Ford, M.A., D.R. Cahoon, and J.C. Lynch. 1999. Restoring marsh elevation in a rapidly subsiding salt marsh by thin-layer deposition of dredged material. *Ecological Engineering* 12: 189–205.

Fujimoto, K., T. Miyagi, T. Kikuchi, and T. Kawana. 1996. Mangrove habitat formation and response to holocene sea-level changes on Kosrae Island, Micronesia. *Mangroves and Salt Marshes* 1: 47–57.

Goodrick, G.N. 1970. *A Survey Of Wetlands Of Coastal New South Wales. In Technical Memorandum No. 5, September 1970, 36 pp. plus plates*. Canberra: CSIRO Division of Wildlife Research.

Grinsted, A., J. Moore, and S. Jevrejeva. 2010. Reconstructing sea level from paleo and projected temperatures 200 to 2100 AD. *Climate Dynamics* 34: 461–472.

Hashimoto, T.R., N. Saintilan, and S.G. Haberle. 2006. Mid-Holocene development of mangrove communities featuring Rhizophoraceae and geomorphic change in the Richmond River Estuary, New South Wales, Australia. *Geographical Research* 44: 63–76.

Horton, R., C. Herweijer, C. Rosenzweig, J. Liu, V. Gornitz, and A.C. Ruane. 2008. Sea-level rise projections for current generation CGCMs based on the semi-empirical method. *Geophysical Research Letters* 35, L02715.

Howe, A.J., J.F. Rodríguez, and P.M. Saco. 2009. Surface evolution and carbon sequestration in disturbed and undisturbed wetland soils of the Hunter estuary, southeast Australia. *Estuarine, Coastal and Shelf Science* 84: 75–83.

Hunter, J. 2010. Estimating sea-level extremes under conditions of uncertain sea-level rise. *Climatic Change* 99: 331–350.

Jevrejeva, S., J.C. Moore, and A. Grinsted. 2010. How will sea level respond to changes in natural and anthropogenic forcings by 2100? *Geophysical Research Letters* 37, L07703.

Kirwan, M.L., G.R. Guntenspergen, A. D'Alpaos, J.T. Morris, S.M. Mudd, and S. Temmerman. 2010. Limits on the adaptability of coastal marshes to rising sea level. *Geophysical Research Letters* 37, L23401.

Kirwan, M.L., and S.M. Mudd. 2012. Response of salt-marsh carbon accumulation to climate change. *Nature* 489: 550–553.

Krauss, K.W., J.A. Allen, and D.R. Cahoon. 2003. Differential rates of vertical accretion and elevation change among aerial root types in Micronesian mangrove forests. *Estuarine, Coastal and Shelf Science* 56: 251–259.

Krauss, K.W., C.E. Lovelock, K.L. McKee, L. López-Hoffman, S.M.L. Ewe, and W.P. Sousa. 2008. Environmental drivers in mangrove establishment and early development: A review. *Aquatic Botany* 89: 105–127.

Kwak, T.J., and J.B. Zedler. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia* 110: 262–277.

Lee, S.Y., R.J.K. Dunn, R.A. Young, R.M. Connolly, P.E.R. Dale, R. Dehayr, C.J. Lemckert, S. McKinnon, B. Powell, P.R. Teasdale, and D.T. Welsh. 2006. Impact of urbanization on coastal wetland structure and function. *Austral Ecology* 31: 149–163.

Lovelock, C., V. Bennion, A. Grinham, and D. Cahoon. 2011. The role of surface and subsurface processes in keeping pace with sea level rise in intertidal wetlands of Moreton Bay, Queensland, Australia. *Ecosystems* 14: 745–757.

Lynch, J.C., J.R. Meriwether, B.A. McKee, F. Vera-Herrera, and R.R. Twilley. 1989. Recent accretion in mangrove ecosystems based on ^{137}Cs and ^{210}Pb. *Estuaries* 12: 284–299.

Magenheimer, J., T. Moore, G. Chmura, and R. Daoust. 1996. Methane and carbon dioxide flux from a macrotidal salt marsh, Bay of Fundy, New Brunswick. *Estuaries and Coasts* 19: 139–145.

Mazumder, D., N. Saintilan, and R.J. Williams. 2006. Trophic relationships between itinerant fish and crab larvae in a temperate Australian saltmarsh. *Marine and Freshwater Research* 57: 193–199.

McKee, K.L. 2011. Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuarine, Coastal and Shelf Science* 91: 475–483.

McKee, K.L., D.R. Cahoon, and I.C. Feller. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* 16: 545–556.

McLeod, E., G.L. Chmura, S. Bouillon, R. Salm, M. BjÃ¶rk, C.M. Duarte, C.E. Lovelock, W.H. Schlesinger, and B.R. Silliman. 2011. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment* 9: 552–560.

Meehl, G.A., T.F. Stocker, W.D. Collins, P. Friedlingstein, A.T. Gaye, J.M. Gregory, A. Kitoh, R. Knutti, J.M. Murphy, A. Noda, S.C.B. Raper, I.G. Watterson, A.J. Weaver, and Z.-C. Zhao. 2007. Global climate projections. In *In Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller. Cambridge: Cambridge University Press.

Miyagi, T., C. Tanavud, P. Pramojanee, K. Fujimoto, and Y. Mochida. 1999. Mangrove habitat dynamics and sea-level change. A scenario and GIS mapping of the changing process of the delta and estuary type mangrove habitat in Southwestern Thailand. *Tropics* 8: 179–196.

Morris, J.T., P.V. Sundareshwar, C.T. Nietch, B. Kjerfve, and D.R. Cahoon. 2002. Responses of coastal wetlands to rising sea-levels. *Ecology* 83: 2869–2877.

Nicholls, R.J., N. Marinova, J.A. Lowe, S. Brown, P. Vellinga, D. de Gusmão, J. Hinkel, and R.S.J. Tol. 2011. Sea-level rise and its possible impacts given a 'beyond 4°C world' in the twenty-first century. *Philosophical Transactions of the Royal Society A—Mathematical, Physical and Engineering Sciences* 369: 161–181.

Nyman, J.A., R.J. Walters, R.D. Delaune, and W.H. Patrick Jr. 2006. Marsh vertical accretion via vegetative growth. *Estuarine, Coastal and Shelf Science* 69: 370–380.

Oliver, T., K. Rogers, C. Chafer, and C. Woodroffe. 2012. Measuring, mapping and modelling: an integrated approach to the management of mangrove and saltmarsh in the Minnamurra River estuary, south-east Australia. *Wetlands Ecology and Management* 20: 353–371.

Osland, M., A. Spivak, J. Nestlerode, J. Lessmann, A. Almario, P. Heitmuller, M. Russell, K. Krauss, F. Alvarez, D. Dantin, J. Harvey, A. From, N. Cormier, and C. Stagg. 2012. Ecosystem development after mangrove wetland creation: plant–soil change across a 20-year chronosequence. *Ecosystems* 15: 848–866.

Pethick, J. 2001. Coastal management and sea-level rise. *Catena* 42: 307–322.

Pittock, J., M. Finlayson, A. Gardner, and C. McKay. 2010. Changing character: the Ramsar Convention on Wetlands and climate change in the Murray Darling Basin, Australia. *Environmental Planning and Law Journal* 27: 401–425.

Poffenbarger, H., B. Needelman, and J. Megonigal. 2011. Salinity influence on methane emissions from tidal marshes. *Wetlands* 31: 831–842.

Primavera, J.H. 2006. Overcoming the impacts of aquaculture on the coastal zone. *Ocean and Coastal Management* 49: 531–545.

Ramsar. 2012. *Resolution XI.14. Climate change and wetlands: implications for the Ramsar Convention on Wetlands. In Resolutions of the 11th meeting of the Conference of Parties to the Convention on Wetlands*. Romania: Ramsar.

Rogers, K., and N. Saintilan. 2002. Remapping of the SEPP14 wetlands in the Shoalhaven district. *Wetlands (Australia)* 20: 55–65.

Rogers, K., N. Saintilan, and C. Copeland. 2012. Modelling wetland surface elevation and its application to forecasting the effects of sea-level rise on estuarine wetlands. *Ecological Modelling* 244: 148–157.

Rogers, K., K.M. Wilton, and N. Saintilan. 2006. Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf Science* 66: 559–569.

Roy, P.S., R.J. Williams, A.R. Jones, I. Yassini, P.J. Gibbs, B. Coates, R.J. West, P.R. Scanes, J.P. Hudson, and S. Nichol. 2001. Structure and function of South-east Australian Estuaries. *Estuarine, Coastal and Shelf Science* 53: 351–384.

Sammut, J., M.D. Melville, R.B. Callinan, and G.C. Fraser. 1995. Estuarine acidification: impacts on aquatic biota of draining acid sulphate soils. *Australian Geographical Studies* 33: 89–100.

Shoo, L.P., J. O'Mara, K., Perhans, J.R., Rhodes, R.K., Runting, S., Schmidt, L.W., traill, L.C., Weber, K.A., Wilson, C.E., Lovelock. (2013). Moving beyond the conceptual: specificity in regional climate change adaptation actions for biodiversity in South East Queensland, Australia. *Regional Environmental change*. doi:10.1007/s10113-012-0385-3

Silver, W.L., R. Ostertag, and A.E. Lugo. 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration Ecology* 8: 394–407.

Spencer, J., V. Monamy, and M. Breitfuss. 2009. Saltmarsh as habitat for birds and other vertebrates. In *Australian saltmarsh ecology*, ed. N. Saintilan, 149–166. Collingwood: CSIRO.

Traill, L.W., K. Perhans, C.E. Lovelock, A. Prohaska, S. McFallan, J.R. Rhodes, and K.A. Wilson. 2011. Managing for change: wetland transitions under sea-level rise and outcomes for threatened species. *Diversity and Distributions* 17: 1225–1233.

Walsh, S., Copeland, C., Westlake M. 2004. Major fish kills in the Northern Rivers of NSW in 2001: causes, impacts and responses. In Fisheries Final Report Series No. 68: NSW Department of Primary Industries

Williams, R.J., Watford, F.A. 1997. Change in the distribution of mangrove and saltmarsh in Berowra and Marramarra Creeks. 1941–1992. In Report to Hornsby Shire Council. Cronulla, NSW: NSW Fisheries Office of Conservation, Fisheries Research Institute

Winning, G., and N. Saintilan. 2009. Vegetation changes in Hexham Swamp, Hunter River, New South Wales, since the construction of floodgates in 1971. *Cunninghamia* 11: 185–194.

Woodroffe, C.D. 1990. *The impact of sea-level rise on mangrove shorelines*. Letchworth, ROYAUME-UNI: Turpin.

forests

MDPI

Article

Mapping Mangrove Above-Ground Carbon Using Multi-Source Remote Sensing Data and Machine Learning Approach in Loh Buaya, Komodo National Park, Indonesia

Seftiawan Samsu Rijal [1], Tien Dat Pham [2,*], Salma Noer'Aulia [1], Muhammad Ikbal Putera [3] and Neil Saintilan [2]

[1] Marine Science Study Program, Faculty of Fisheries and Marine Science, Universitas Brawijaya, Malang 65145, Jawa Timur, Indonesia
[2] School of Natural Sciences, Faculty of Science and Engineering, Macquarie University, Sydney, NSW 2109, Australia
[3] Komodo National Park, Ministry of Environment and Forestry Republic of Indonesia, Labuan Bajo 86554, Nusa Tenggara Timur, Indonesia
* Correspondence: tiendat.pham@mq.edu.au

Abstract: Mangrove forests provide numerous valuable ecosystem services and can sequester a large volume of carbon that can help mitigate climate change impacts. Modeling mangrove carbon with robust and valid approaches is crucial to better understanding existing conditions. The study aims to estimate mangrove Above-Ground Carbon (AGC) at Loh Buaya located in the Komodo National Park (Indonesia) using novel Extreme Gradient Boosting (XGB) and Genetic Algorithm (GA) analyses integrating multiple sources of remote sensing (optical, Synthetic Aperture Radar (SAR), and Digital Elevation Model (DEM)) data. Several steps were conducted to assess the model's accuracy, starting with a field survey of 50 sampling plots, processing the images, selecting the variables, and examining the appropriate machine learning (ML) models. The effectiveness of the proposed XGB-GA was assessed via comparison with other well-known ML techniques, i.e., the Random Forest (RF) and the Support Vector Machine (SVM) models. Our results show that the hybrid XGB-GA model yielded the best results (R^2 = 0.857 in the training and R^2 = 0.758 in the testing phase). The proposed hybrid model optimized by the GA consisted of six spectral bands and five vegetation indices generated from Sentinel 2B together with a national DEM that had an RMSE = 15.40 Mg C ha^{-1} and outperformed other ML models for quantifying mangrove AGC. The XGB-GA model estimated mangrove AGC ranging from 2.52 to 123.89 Mg C ha^{-1} (with an average of 57.16 Mg C ha^{-1}). Our findings contribute an innovative method, which is fast and reliable using open-source data and software. Multisource remotely sensed data combined with advanced machine learning techniques can potentially be used to estimate AGC in tropical mangrove ecosystems worldwide.

Keywords: mangroves; Above-Ground Carbon (AGC); remote sensing; Sentinel; machine learning; Indonesia

check for updates

Citation: Rijal, S.S.; Pham, T.D.; Noer'Aulia, S.; Putera, M.I.; Saintilan, N. Mapping Mangrove Above-Ground Carbon Using Multi-Source Remote Sensing Data and Machine Learning Approach in Loh Buaya, Komodo National Park, Indonesia. *Forests* **2023**, *14*, 94. https://doi.org/10.3390/f14010094

Academic Editors: Andrzej Węgiel and Adrian Łukowski

Received: 29 November 2022
Revised: 29 December 2022
Accepted: 30 December 2022
Published: 4 January 2023

Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Mangroves provide many important ecological and provisioning services including the sequestration of atmospheric CO_2 [1], protection of shorelines from the impact of waves, storm surges, and shoreline erosion [2], and habitat for organisms including shorebirds and commercially important fish [3,4], such that total ecosystem value has been estimated at more than a million dollars per year [5,6]. Despite their valuable contributions, these forests have been lost all over the world due to multiple factors, though primarily human disturbance, especially in Southeast Asia [7]. Previous studies by Fauzi [8] and Latiff [9] revealed that mangrove forests were converted into agriculture, aquaculture, infrastructure, and

other land use. Understanding the driving forces and the efficacy of conservation and rehabilitation activities is a central consideration in sustainable mangrove forest replantation and management [10].

One of the fundamental aspects of the sustainable conservation of mangrove forests is to understand their spatial distribution and rates of change, the subject of several previous studies [11–13]. However, these forests are associated with a wide range of biophysical parameters that can be related to ecosystem health, interactions, functions, and dynamics [14]. Measuring biophysical parameters of mangroves such as their ability to sequester carbon can be achieved with accuracy using allometric equations applied to field-based measures from designated plots [15]. However, this method is laborious and time-consuming, and often logistically challenging due to the complexity of the mangrove environment, consisting of dynamic tidal levels [16] and tidal cycles [17], and dangerous fauna [18]. Therefore, the development of effective and efficient mangrove carbon estimates is needed.

Remote sensing is an important complementary tool in offering a synoptical overview, high spectral and spatial resolution, and ease of data capture to overcome some of the limitations of time, labor cost, and inaccessibility facing mangrove carbon measurement [19]. The use of remotely sensed optical and Synthetic Aperture Radar (SAR) images incorporated with field-based sampling has been successfully applied to develop mangrove carbon models calibrated by empirical measures [20]. However, a concern for previous studies has been the need for improved accuracy in mangrove carbon models [21]. This issue has driven previous studies to build many models from linear/multi-linear regression from single or combinations of remote sensing image transformations to map mangrove above-ground biomass and above-ground carbon. Furthermore, they may also integrate optical and SAR data to achieve better model prediction [22].

Several optical and SAR remote sensing satellite image libraries are available online and free access, especially for coarse (30 m) and medium-high (20–10 m) spatial resolutions, for instance, generations of Landsat and Sentinel missions [23–25]. Landsat yields satisfactory results when used for mangrove extent mapping and temporal changes [26,27]. However, it only works well for large geographical areas and shows inconsistencies in application over finer mapping scales [28]. Sentinel, which brings optical and SAR wavelength with higher spatial resolution, has proven to map mangroves well at large scales [22,28].

The emergence of high-performance computing [29,30], and the use of Machine Learning (ML) techniques can assist in the development of mangrove biomass and carbon maps based on remotely sensed variables [31–34]. In this study, we aim to test a novel ML method, which was proposed by Pham et al. [35] to map and quantify mangrove above-ground carbon (AGC) in Indonesian mangroves using multisource free-of-charge remotely sensed datasets. Pham et al. [35] developed a novel ML model by integrating the extreme gradient boosting regression (XGB) and genetic algorithm (GA) to map AGB mangroves in Northern Vietnam using optical and SAR data combined with field sampling.

The current work aims to test the effectiveness and robustness of the method using free-of-charge multisource remote sensing data and to extend this approach to other tropical mangrove environments. The results of this study show the ability of the innovative mapping technique using open-source software to perform a mangrove's carbon while reflecting the optimum features selection to be used.

2. Materials

2.1. Study Area

Established on 6th March 1980, Komodo National Park is one of the earliest national parks in Indonesia. The Komodo National Park is an archipelagic national park with a total area of 173,300 ha located at Manggarai Barat Regency, Province of Nusa Tenggara Timur. It has five major islands: Rinca Island, Padar Island, Komodo Island, Gili Motang Island, Nusa Kode Island, and 142 smaller islands [36].

The Komodo National Park has seven different ecosystem types: the quasi-cloud forests (16,706.20 ha), tropical deciduous (monsoon) forests (5026.48 ha), open grassland

total area of 173,300 ha located at Manggarai Barat Regency, Province of Nusa Tenggara Timur. It has five major islands: Rinca Island, Padar Island, Komodo Island, Gili Motang Island, Nusa Kode Island, and 142 smaller islands [36].

The Komodo National Park has seven different ecosystem types: the quasi-cloud forests (16,706.20 ha), tropical deciduous (monsoon) forests (5026.48 ha), open grassland and woodland savannah (33,788.36 ha), mangroves (1030.30 ha), seagrasses (3967.18 ha), coral reefs (825.61 ha), and the open ocean (111,955.87 ha) [37]. Each ecosystem in the park is unique compared to one another and has a high biodiversity variety, most importantly Loh Buaya Resort.

Loh Buaya is a local name for 'Crocodile Bay', which is located on Rinca Island (latitude of 8°32′36″ S; longitude of 119°29′22″ E). Komodo National Park is comprised of 23% terrestrial and 77% aquatic environments. Komodo National Park supports up to 23 species of mangrove [37,38], though to the best of our knowledge no published species list exists.

2.2. Field Survey

Data were collected from 50 plots sampling across four dominant species of mangroves found in the study area (*Ceriops decandra*, *Lumnitzera racemosa*, *Rhizophora apiculata*, and *Rhizophora mucronata*). Plots consisted of 10 m × 10 m squares established during the field campaign of July 2022 (dry season) using a technique by Dharmawan et al. [39] (Figure 1). Measurement in every plot comprised coordinate tagging using a handheld Global Positioning System (GPS; Garmin GPSMAP 64s series with ±3 m accuracy), Girth at Breast Height (GBH), percentage of canopy cover using hemispherical photography, mangroves species, and substrate identification. MonMang, a smartphone logbook application for mangrove surveys developed by Lembaga Ilmu Pengetahuan Indonesia (LIPI) [40] was used to record field data.

(**a**)

Figure 1. *Cont.*

(**b**)

(**c**)

Figure 1. Mangrove field measurement: (**a**) mangrove situated at the study area, (**b**) preparing plot measurements using a rope, (**c**) GBH measurement which is then converted to Diameter of Breast Height (DBH). (Photos taken by Salma Noer 'Aulia during field survey).

2.3.2. Biomass and Carbon Estimations

Mangrove GBH was divided by 3.14 to convert into DBH value, and Above-Ground Biomass (AGB) was calculated using the allometric equation (Equation (1)) of Komiyama [41] derived for Southeast Asian mangroves. Therefore, this equation is relevant to use in the study area. The equation is as follows:

$$AGB\ (Mg\ ha^{-1}) = 0.251\rho(DBH)^{2.46} \quad (1)$$

where:

ρ: Wood density corresponding to the mangrove species, based on the ICRAF database [42]

DBH: Diameter at Breast Height (mean value of different individual trees in every single sampling plot)

According to the Indonesian National Standards for measuring and calculating forest carbon (SNI:7724-2011) [43], about 47% of biomass is carbon. The Above-Ground Carbon (AGC) value was therefore calculated by (Equation (2)).

$$AGC\ (MgC\ ha^{-1}) = AGB \times 0.47 \quad (2)$$

2.4. Earth Observations (EO) Data

Several earth observation datasets were used in this study including Sentinel-1A (S1A), Sentinel-2B MultiSpectral Instrument (S2B MSI), and Digital Elevation Model Nasional (DEMNAS)/Indonesian Digital Elevation Model to estimate mangrove AGC. S1A is a Synthetic Aperture Radar (SAR) satellite with Level-1 Ground Resolution Distance (GRD) equipped with the frequency of C-band (5.405 GHz) and uses the polarizations of VV (Vertical transmit-Vertical receiving) and VH (Vertical transmit-Horizontal receiving) [44]. S2B MSI level-1C has twelve bands, ranging from 443 nm (coastal band), 492 nm (blue band), 560 nm (green band), 665 nm (red band), 704–783 nm (three red-edge bands), 832 nm (near-infrared (NIR) band), 865 (narrow-NIR band), and 1614–2202 nm (short-wavelength infrared (SWIR) band). Each of the S2B bands has a different spatial resolution ranging from 10–20 m [24]. Both S1A and S2B MSI were acquired on the 20th and 18th July 2022, respectively. DEMNAS was produced by the Government of Indonesia in 2018 using a combination of Interferometry SAR, TERRASAR-X, ALOS PALSAR, and mass point data from stereo-plotting. The spatial resolution for the DEMNAS is about 8.33 m with vertical accuracy of 3.6 m [45,46].

The S1A and S2B MSI were downloaded from the Copernicus Open Access Hub (https://scihub.copernicus.eu/, accessed on 16 September 2022), while DEMNAS was acquired from Tanah Air (https://tanahair.indonesia.go.id/demnas/#/, accessed on 5 October 2022). All the EO datasets are free and open to the public (Table 1).

Table 1. The Earth Observations Data used in this study.

Earth Observations Data	Scene ID	Acquisition Date (Date/Month/Year)	Processing Level	Spatial Resolution (m)	Spectral/Polarization Used
S1A SAR	S1A_05460F	20 July 2022	Level-1 GRD	20	C Band (VV and VH polarizations)
S2B MSI	S2B_MSI_T50LQR	18 July 2022	Level-1C	10–20	11 multispectral bands
DEMNAS	2007-33_v1.0	2018	-	8.33	-

3. Methods

We adopted an innovative ML framework introduced by Pham et al. [35] to estimate mangrove AGC. However, in this study, a combination of multiple EO source data with free-of-charge Sentinel-2B and Sentinel-1A imagery and a national DEM as elevation data was used to improve the prediction accuracy. Several steps were conducted to derive and test models as follows: (1) Pre-processing and processing of the multiple EO sources, (2) Creating training and testing datasets by combining field sampling data and EO data extraction, (3) Evaluating Machine Learning models, (4) Selecting the optimal variables using the Genetic Algorithm and the highest ML model, (5) Model re-evaluation for mangrove AGC estimations in the study area. The flowchart of this study is shown in Figure 2.

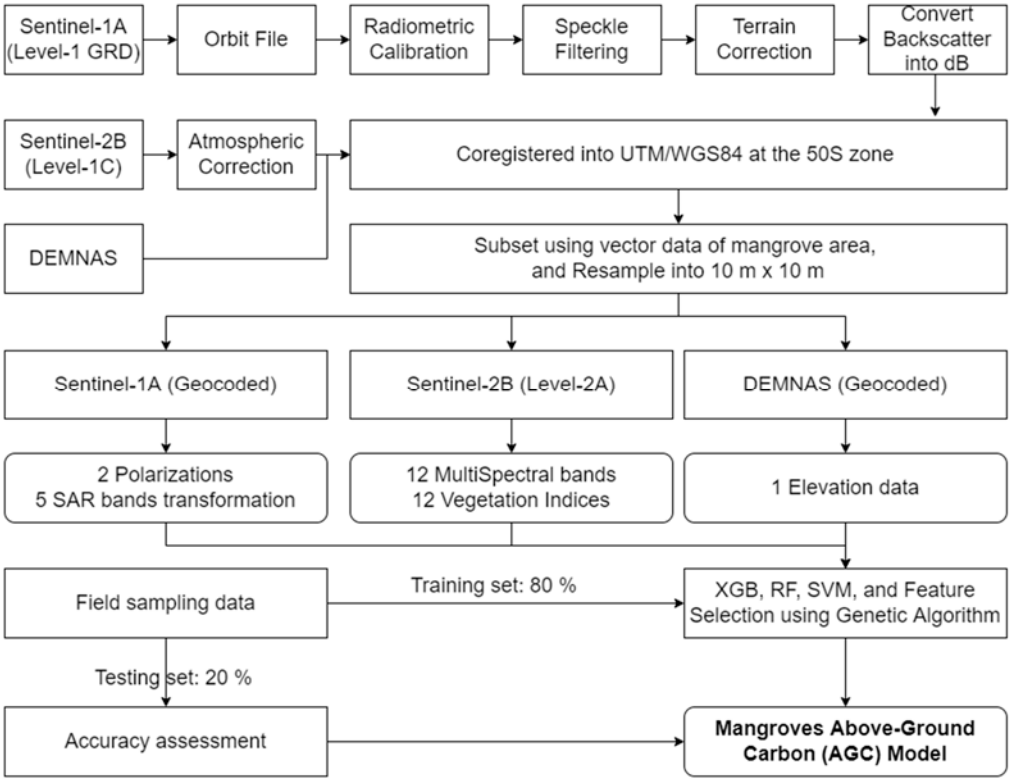


Figure 2. Flowchart for mangrove AGC retrieval developed in the study.

3.1. EO Image Processing

3.1.1. EO Image Pre-Processing

The S1A was processed in several steps, including applying the orbit file to update more accurately satellite orbit position, radiometric calibration to convert the intensity value of VV and VH into sigma nought (σ°), which can represent the actual backscatter of the object, speckle filtering to reduce the granular noise on the image, terrain correction to register the imagery from sensor geometry into the projection coordinate, and converting backscatter value into decibel (dB) units. The S2B level-1C already has the Top of Atmosphere (TOA) value and has been geometrically and radiometrically corrected [24]. To gain the Bottom of Atmospheric (BOA) reflectance (Level-2A), The S2B level-1C was converted using the Sen2Cor algorithm [22,35]. All the EO data (S1A, S2B, and DEMNAS) were clipped using the vector data of the mangrove area in Loh Buaya, co-registered into UTM/WGS84 at the 50S zone, and resampled into 10 m corresponds to the field plots size. According to Kamal [47], matching the size of plots with the image pixel resolution will improve the accuracy of mangrove identification. All data were processed using European Space Agency (ESA) SNAP software.

3.1.2. EO Image Transformations

Optical satellite imagery has been widely used to estimate mangrove carbon [16,48,49]. In tropical latitudes, minimum cloud coverage of optical imagery may be difficult to access. Therefore, previous studies have substituted optical imagery with SAR imagery for carbon estimation [50,51] or the combination of optical and SAR [22,52]. Further, a DEM may also be used to improve the accuracy of forest carbon estimates [53–55]. In this study, we employed a total of 32 variables consisting of 2 polarizations of S1A, 5 SAR bands transformations of S1A, 12 bands of S2B, 12 Vegetation Indices (VIs) of S2B, and an elevation model (DEMNAS) (Table 2). The SAR band transformations and VIs are sensitive to the plant and vegetation characteristics [16,56,57]. The total number of optimal inputs for predicting the AGC model was 12 variables composed of 5 VIs (NDVI, GNDVI, NDI45,

SAVI, MCARI), the elevation model (DEMNAS), and 6 bands (B4, B5, B7, B8A, B11, and B12). The variables were normalized before further processing.

Table 2. Overview of variables used in this study.

Band/Polarizations/Index	Central Wavelength/Formula	References	Sensor
VH	Horizontally polarized backscatter	[58]	S1A
VV	Vertically polarized backscatter	[58]	S1A
VH/VV	SAR polarization ratio	[44,59]	S1A
VV/VH	SAR polarization ratio	[44,59]	S1A
(VV+VH)/2	SAR polarization ratio	[44,59]	S1A
VV, VH GLCM	SAR image transformations	[60]	S1A
VV, VH PCA	SAR image transformations	[61]	S1A
B1—Coastal Aerosol	442.2	[62]	S2B
B2—Blue	492.1	[62]	S2B
B3—Green	559.0	[62]	S2B
B4—Red	664.9	[62]	S2B
B5—Red Edge 1	703.8	[62]	S2B
B6—Red Edge 2	739.1	[62]	S2B
B7—Red Edge 3	779.7	[62]	S2B
B8—Near InfraRed (NIR)	832.9	[62]	S2B
B8A—Narrow NIR	864.0	[62]	S2B
B9—Water Vapor	943.2	[62]	S2B
B11—Short Wave InfraRed (SWIR-1)	1610.4	[62]	S2B
B12—Short Wave InfraRed (SWIR-2)	2185.7	[62]	S2B
Ratio Vegetation Index (RVI)	$\frac{\text{NIR}}{\text{Red}}$	[63]	S2B
Normalized Difference Vegetation Index (NDVI)	$\frac{\text{NIR} - \text{Red}}{\text{NIR} + \text{Red}}$	[64]	S2B
Green NDVI (GNDVI)	$\frac{\text{NIR} - \text{Green}}{\text{NIR} + \text{Green}}$	[65]	S2B
Normalized Difference Index using Bands 4 and 5 (NDI45)	$\frac{\text{Red Edge (B5)} - \text{Red}}{\text{Red Edge (B5)} + \text{Red}}$	[66]	S2B
Soil-Adjusted Vegetation Index (SAVI)	$(1 + \text{L})\left(\frac{\text{NIR} - \text{Red}}{\text{NIR} + \text{Red} + \text{L}}\right)$ L = 0.5 in most conditions	[67]	S2B
Inverted Red-Edge Vegetation Index (IRECI)	$\frac{\text{Red Edge (B7)} - \text{Red}}{\text{Red Edge (B5)} / \text{ Red Edge (B6)}}$	[68]	S2B
Modified Chlorophyll Absorption in Reflectance Index (MCARI)	$\begin{bmatrix}(\text{Red Edge (B5)} - \text{Red}) - 0.2\\ * (\text{Red Edge (B5)} - \text{Green})\end{bmatrix}$ $* (\text{Red Edge (B5)} - \text{NIR})$	[69]	S2B
Modified Soil-Adjusted Vegetation Index (MSAVI)	$(1 + \text{L}) * (\text{NIR} - \text{Red}) / (\text{NIR} + \text{Red} + \text{L})$ L = 0.5 in most conditions	[70]	S2B
The Second Modified Soil-Adjusted Vegetation Index (MSAVI2)	$\left(\frac{1}{2}\right) * (2{*}\text{NIR} + 1 -$ $\text{Sqrt}\left(\begin{matrix}(2{*}\text{NIR} + 1) * (2{*}\text{NIR} + 1) -\\ 8 * (\text{NIR} - \text{Red})\end{matrix}\right)$	[70]	S2B

Table 2. *Cont.*

Band/Polarizations/Index	Central Wavelength/Formula	References	Sensor
Different Vegetation Index (DVI)	$NIR - Red$	[71]	S2B
Perpendicular Vegetation Index (PVI)	$Sin(a)*NIR - Cos(a)*Red$ a = angle between the soil line and the NIR axis, in degrees	[71]	S2B
The Second Enhanced Vegetation Index (EVI-2)	$2.5\left(\frac{NIR - Red}{NIR + 2.4*Red + 1}\right)$	[68]	S2B
Elevation Data	-	[45]	DEMNAS

3.2. Machine Learning Algorithms

3.2.1. Random Forest (RF)

The RF algorithm was developed by Breiman [72] for supervised classification and regression tasks, applying bootstrap sampling and bagging trees in the ensemble learning family. The RF model can effectively handle non-linear data without overestimation during the training and testing phases. In the RF model, approximately 2/3 of the total samples (in-bag) are used during the training phase and the remaining 1/3 of the total samples (out-of-bag, OOB) is used for the testing phase.

In the RF benchmark, a maximum depth, a minimum sample leaf, a minimum sample split, a maximum feature, and the number of trees as well as the number of features m can be tuned to fit a specific dataset. These parameters were optimized using five-fold cross-validation (CV) in the Python environment.

3.2.2. Support Vector Machine (SVM)

The SVM algorithm was developed by Vapnik [73] based on the statistical learning theory for supervised classification and regression tasks. This algorithm has been widely applied in numerous domains such as image processing, computer vision, pattern recognition, and environmental monitoring. In the SVM model, the choice of different kernel functions largely influences the model performance. For this reason, we selected the radial basis function (RBF) kernel in this work to minimize the bias as suggested by the prior studies for the estimates of mangrove AGC [52,74].

The effectiveness of the estimate of mangrove AGC can be highly influenced by the hyperparameters. In the SVM benchmark, we configured three main parameters with an RBF kernel: the regularization parameter (C), Epsilon (ε), and the kernel width (γ) using five-fold CV using Python scripting.

3.2.3. Extreme Gradient Boosting (XGB)

The XGB algorithm uses the theory of boosting technique and belongs to the ensemble-based decision tree learning. Initially introduced by Chen and Guestrin [75], XGB has been effectively applied in both classification and regression tasks for the supervised-learning domains [76].

In the XGB model, two regularization terms L_1 and L_2 are added to the cost functions to improve the generalization, optimize performance, and reduce the overfitting problem. In the XGB benchmark, several hyperparameters such as the booster, a maximum depth, a minimum child weight, several trees, and a learning rate must be set and tuned beforehand.

3.3. Model Configuration, Implementation, and Accuracy Assessment

3.3.1. Configuration and Training

A total of 50 samples were split randomly into the training set (80%) and the testing set (20%) of the total samples. The former set was used to construct the ML models using the features derived from multiple source EO such as bands' reflectance, vegetation indices (VIs) derived from S2B, backscatters coefficients, and SAR transformation derived from

S1A C-band as well as the national DEM, whereas the latter dataset was used to assess the predictive performance of the ML models. All features were normalized using the normalization function in the Scikit-learn library in Python 3.7 [77].

3.3.2. Hyperparameters Tuning

ML models consist of several parameters, which control the learning process during the construction of any ML model. These parameters are called hyperparameters, which often need to be tuned or optimized to achieve the highest regression performance. In this work, the hyperparameters of the RF, the SVM, and the XGB models were tuned and maintained during the training and the testing phases using a grid-search with a five-fold CV in the Scikit-learn library [77].

3.3.3. Feature Selection Using the Genetic Algorithm (GA)

In the current study, the GA was implemented in the Python environment to automatically select the optimal number of variables for estimating mangrove AGC in the study area. The GA adopts Darwinian natural selection theory to automatically tune the hyperparameters of an ML model [78]. In the GA, the vector of parameter values, which is called an individual, is the most important pattern to define a solution in each generation.

First, all features generated from S1A C-band SAR and S2B (input variables) were tested with the three ML models using a grid search with a five-fold CV to tune the hyperparameter of each model. Second, the highest predictive ML model performance for estimating mangrove AGC with the lowest root-mean-square error (RMSE) was chosen. The GA was then used in conjunction with the best predictive model to select the optimal features derived from the S2B MSI, VIs, and S1A, SAR transformations generated from S1A, and national DEM data for mangrove AGC estimation. Finally, all of the chosen ML models were tested with the best features for comparison.

3.3.4. Accuracy Assessment

We used several criteria including RMSE and the coefficient of determination (R^2) for model evaluation and comparison of different ML algorithms for estimating mangrove AGC as they are well-known indices for assessing the performance of any regression model [52,79].

RMSE (Equation (3)) and R^2 (Equation (4)) are standard criteria for measuring errors of regression tasks, in which higher R^2 and lower RMSE values indicate the better regression model

$$\text{RMSE} = \sqrt{\sum_{i=1}^{n} \frac{(\hat{y}_i - y_i)^2}{n}}, \tag{3}$$

$$R^2 = 1 - \frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}{\sum_{i=1}^{n} \left(y_i - \bar{y}\right)^2}, \tag{4}$$

where $\hat{y}_i$ and y_i are the estimated and measured mangrove AGC for the ith plot, respectively; n is the total number of sampling plots, and $\bar{y}$ is the measured mean values of the mangrove AGC.

4. Results

4.1. Characteristics of Mangrove Forests

Mangroves in the study area (Figure 3) also had varying DBH, ranging from 7.48 cm in plot 5 (*Rhizophora apiculata*) to 19.21 cm in plot 27 (*Rhizophora mucronata*) with an average of 12.67 cm. Based on the calculated results of AGC listed in Table 3, the lowest carbon stock was 13.63 Mg C ha^{-1} in Plot 14 while the largest carbon stock was found in Plot 27 with 143.94 Mg C ha^{-1}. An average AGC was observed at approximately 57.51 Mg C ha^{-1}. The dominant species in the sampling plots were *Rhizophora apiculata*, which was common in 23 of the 50 plots. The calculation of carbon stock is influenced by DBH and wood density,

sity, therefore, although *Rhizophora apiculata* had the lowest DBH, this is not corresponding with the lowest carbon stock due to its wood density being higher than *Ceriops decandra*.

~~therefore, although *Rhizophora apiculata* had the lowest DBH, this is not corresponding with the lowest carbon stock due to its wood density being higher than *Ceriops decandra*.~~

(**a**) (**b**) (**c**)

(**d**)

Figure 3. Mangrove species at study area: (**a**) *Rhizophora apiculata*, (**b**) *Rhizophora mucronata*, (**c**) *Ceriops decandra*, and (**d**) *Lumnitzera racemosa*. (Photos taken by Salma Noer 'Aulia during field survey).

~~**Figure 3.** Mangrove species at study area: (**a**) *Rhizophora apiculata*, (**b**) *Rhizophora mucronata*, (**c**) *Ceriops decandra*, and (**d**) *Lumnitzera racemosa*. (Photos taken by Salma Noer 'Aulia during field survey).~~

Table 3. Identification of mangrove characteristics in the study area.

Plot	Longitude (E)	Latitude (S)	DBH (cm)	AGC (Mg C ha^{-1})	Dominant Species	Canopy Cover (%)	Substrate
1	119°42′56.62″	8°39′13.42″	11.86	43.99	*Rhizophora mucronata*	77.29	Sandy Mud
2	119°42′56.72″	8°39′12.22″	14.62	76.36	*Rhizophora apiculata*	73.94	Sandy Mud
3	119°42′56.58″	8°39′11.25″	12.98	57.05	*Rhizophora apiculata*	84.32	Sandy Mud

~~**Table 3.** Identification of mangrove characteristics in the study area.~~

~~| Plot | Longitude (E) | Latitude (S) | DBH (cm) | AGC (Mg C ha^{-1}) | Dominant Species | Canopy Cover (%) | Substrate |~~
~~| 1 | 119°42′56.62″ | 8°39′13.42″ | 11.86 | 43.99 | *Rhizophora mucronata* | 77.29 | Sandy Mud |~~
~~| 2 | 119°42′56.72″ | 8°39′12.22″ | 14.62 | 76.36 | *Rhizophora apiculata* | 73.94 | Sandy Mud |~~
~~| 3 | 119°42′56.58″ | 8°39′11.25″ | 12.98 | 57.05 | *Rhizophora apiculata* | 84.32 | Sandy Mud |~~

Table 3. *Cont.*

Plot	Longitude (E)	Latitude (S)	DBH (cm)	AGC (Mg C ha^{-1})	Dominant Species	Canopy Cover (%)	Substrate
4	119°42′55.84″	8°39′10.41″	11.94	46.39	*Rhizophora apiculata*	86.24	Muddy Sand
5	119°42′55.23″	8°39′9.68″	7.48	14.72	*Rhizophora apiculata*	72.96	Muddy Sand
6	119°42′56.71″	8°39′9.97″	10.40	31.79	*Rhizophora mucronata*	72.03	Sandy Mud
7	119°42′57.61″	8°39′9.55″	8.49	18.97	*Lumnitzera racemosa*	83.21	Sand
8	119°42′57.48″	8°39′10.84″	9.38	24.21	*Lumnitzera racemosa*	73.54	Sand
9	119°42′57.59″	8°39′11.79″	14.53	72.37	*Rhizophora mucronata*	68.97	Sand
10	119°42′57.47″	8°39′12.99″	10.75	34.52	*Rhizophora mucronata*	82.35	Sand
11	119°42′53.96″	8°39′8.82″	14.99	81.25	*Rhizophora apiculata*	69.04	Muddy Sand
12	119°42′59.76″	8°39′15.21″	12.77	45.08	*Ceriops decandra*	75.74	Muddy Sand
13	119°42′00.45″	8°39′15.82″	16.02	78.70	*Ceriops decandra*	70.34	Muddy Sand
14	119°42′58.88″	8°39′16.17″	7.85	13.63	*Ceriops decandra*	79.69	Sand
15	119°42′59.53″	8°39′16.80″	9.86	23.82	*Ceriops decandra*	76.73	Muddy Sand
16	119°42′58.63″	8°39′17.75″	14.04	66.51	*Rhizophora mucronata*	78.24	Muddy Sand
17	119°42′57.87″	8°39′17.01″	14.64	73.76	*Rhizophora mucronata*	80.04	Muddy Sand
18	119°42′56.89″	8°39′16.25″	14.43	73.98	*Rhizophora apiculata*	83.12	Muddy Sand
19	119°42′54.96″	8°39′16.22″	10.82	36.41	*Rhizophora apiculata*	85.28	Muddy Sand
20	119°42′55.90″	8°39′17.12″	13.20	59.42	*Rhizophora apiculata*	82.14	Muddy Sand
21	119°42′56.89″	8°39′17.96″	10.65	35.06	*Rhizophora apiculata*	83.04	Muddy Sand
22	119°42′57.80″	8°39′18.85″	8.98	23.07	*Rhizophora apiculata*	81.54	Muddy Sand
23	119°42′56.89″	8°39′19.91″	8.89	21.64	*Rhizophora mucronata*	77.4	Sandy Mud
24	119°42′56.02″	8°39′18.94″	9.37	25.56	*Rhizophora apiculata*	83.3	Muddy Sand
25	119°42′54.93″	8°39′18.01″	8.79	17.98	*Ceriops decandra*	83.2	Muddy Sand
26	119°42′54.05″	8°39′17.21″	16.07	96.45	*Rhizophora apiculata*	78.41	Muddy Sand
27	119°42′53.87″	8°39′18.84″	19.21	143.94	*Rhizophora mucronata*	78.84	Muddy Sand
28	119°42′55.02″	8°39′19.88″	15.02	81.64	*Rhizophora apiculata*	87.64	Muddy Sand
29	119°42′55.97″	8°39′20.89″	10.83	35.14	*Rhizophora mucronata*	81.19	Muddy Sand
30	119°42′55.02″	8°39′21.84″	8.84	18.22	*Ceriops decandra*	81.61	Muddy Sand
31	119°42′53.78″	8°39′21.94″	17.04	111.42	*Rhizophora apiculata*	85.1	Muddy Sand
32	119°42′53.65″	8°39′20.50″	16.37	100.89	*Rhizophora apiculata*	82.38	Muddy Sand
33	119°42′53.10″	8°39′23.06″	15.70	90.97	*Rhizophora apiculata*	80.96	Muddy Sand
34	119°42′52.23″	8°39′24.30″	8.33	15.77	*Ceriops decandra*	83.63	Muddy Sand
35	119°42′50.21″	8°39′24.47″	12.67	50.76	*Lumnitzera racemosa*	82.9	Muddy Sand
36	119°42′51.24″	8°39′22.98″	8.97	18.90	*Ceriops decandra*	79.4	Muddy Sand
37	119°42′51.97″	8° 9′21.75″	13.29	58.13	*Rhizophora mucronata*	82.24	Muddy Sand
38	119°42′50.99″	8°39′20.23″	17.61	120.65	*Rhizophora apiculata*	88.28	Muddy Sand
39	119°42′50.10″	8°39′21.53″	14.59	75.95	*Rhizophora apiculata*	85.6	Muddy Sand
40	119°42′49.17″	8°39′22.71″	9.22	20.22	*Ceriops decandra*	79.62	Muddy Sand
41	119°42′49.07″	8°39′20.05″	14.68	77.18	*Rhizophora apiculata*	83.96	Muddy Sand

Table 3. *Cont.*

Plot	Longitude (E)	Latitude (S)	DBH (cm)	AGC (Mg C ha^{-1})	Dominant Species	Canopy Cover (%)	Substrate
42	119°42′50.11″	8°39′18.93″	13.36	58.89	*Rhizophora mucronata*	76.91	Muddy Sand
43	119°42′48.76″	8°39′18.03″	13.73	63.04	*Rhizophora mucronata*	85.35	Muddy Sand
44	119°42′47.52″	8°39′16.97″	18.22	131.36	*Rhizophora apiculata*	82.2	Sandy Mud
45	119°42′46.77″	8°39′15.50″	13.01	47.12	*Ceriops decandra*	82.87	Sandy Mud
46	119°42′45.96″	8°39′13.78″	14.98	81.12	*Rhizophora apiculata*	84.39	Sandy Mud
47	119°42′45.42″	8°39′12.29″	7.96	14.08	*Ceriops decandra*	81.1	Sandy Mud
48	119°42′43.83″	8°39′12.11″	15.53	83.73	*Lumnitzera racemosa*	77.42	Sandy Mud
49	119°42′44.60″	8°39′10.84″	18.10	129.16	*Rhizophora apiculata*	83.39	Muddy Sand
50	119°42′42.76″	8°39′8.20″	11.79	45.01	*Rhizophora apiculata*	82.41	Sandy Mud

4.2. Model Performance and Comparison

Table 4 and Figure 4 compare the model performance of the three ML techniques with all input variables derived from S2B MSI, VIs, and S1A together with SAR transformation as well as DEM and the proposed hybrid XGB-GA model with the optimal 12 features. The hybrid model XGB-GA yielded the highest performance in both the training phase (R^2 = 0.857) and the testing phase (R^2 = 0.758) and had an RMSE = 15.40 Mg C ha^{-1} for mangrove AGC estimation in the study site. The XGB-GA model incorporating the S2B (6 MS bands), and VIs (5 bands) together with DEM data achieved the highest performance, reflecting a good fit between the model estimates and field-based measurements. The next-highest performers in the testing phase were the XGB (R^2 = 0.572) and the RF (R^2 = 0.529) models. In contrast, the SVM model (R^2 testing = −0.039) was unsuitable for estimating the mangrove AGC at Loh Buaya (Table 4).

Table 4. Performance comparison of ML techniques on mangrove AGC estimation (bold values highlight the best-performing model).

No	Machine Learning Model	R^2 Training (80%)	R^2 Testing (20%)	RMSE (Mg C ha^{-1})
1	Extreme Gradient Boosting (XGB)	0.892	0.572	16.45
2	Support Vector Machine (SVM)	0.747	−0.039	38.74
3	Random Forests (RF)	0.807	0.529	18.11
4	Extreme Gradient Boosting optimized by Genetic Algorithm (XGB-GA)	**0.857**	**0.758**	**15.40**

Table 5 compares the effectiveness and performances of the XGB-GA model in four scenarios (SC) for mangrove AGC estimation using difference integrations of S2B, S1A, VIs, SAR transformations, and DEM data. The XGB-GA models using the different combinations of datasets had promising results in both four SC with the R^2 greater than 0.57 in the testing phase. The XGB optimized by the GA with 12 optimal features in SC3 produced the best accuracy with the highest R^2 of 0.758 and the lowest RMSE of 15.40 Mg C ha^{-1} as well as reduced overfitting problems in both the training and the testing phases.

		(80%)	(20%)	
1	Extreme Gradient Boosting (XGB)	0.892	0.572	16.45
2	Support Vector Machine (SVM)	0.747	-0.039	38.74
3	Random Forests (RF)	0.807	0.529	18.11
4	Extreme Gradient Boosting optimized by Genetic Algorithm (XGB-GA)	**0.857**	**0.758**	**15.40**

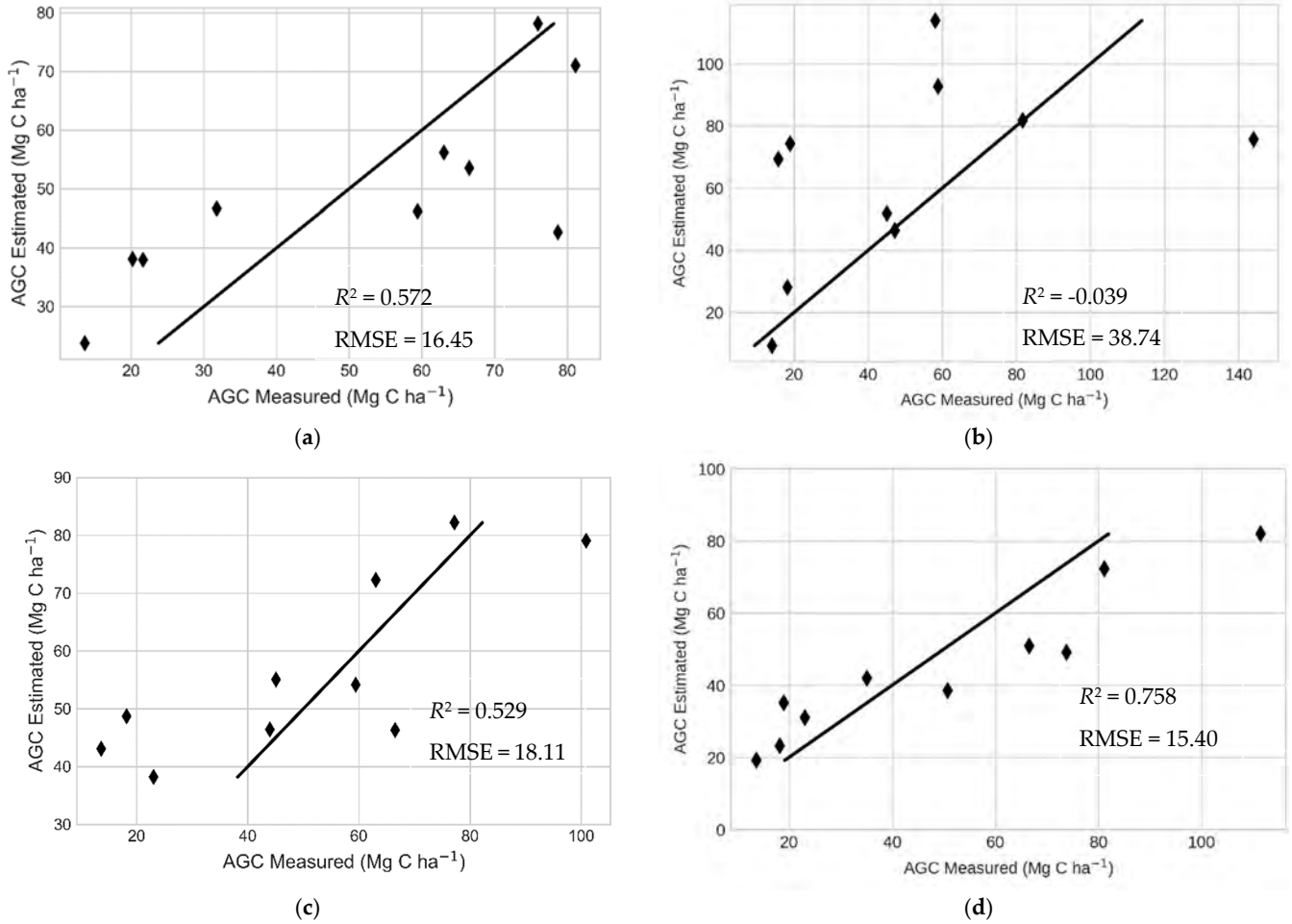


Figure 4. Scatter plots of the estimated (Y-axis) and measured (X-axis) mangrove AGC in the three ML models and the proposed hybrid XGB-GA model (**a**) XGB, (**b**) SVM, (**c**) RF, (**d**) XGB-GA.

Table 5. Performance of the XGB-GA model using different numbers of variables (bold values highlight the best-performing model).

Scenario (SC)	Number of Variables	R^2 Training Set	R^2 Testing Set	RMSE (Mg C ha^{-1})
SC1	14 variables (12 MS bands of S2B data + 2 backscatter coefficients VV and VH of S1A)	0.997	0.651	21.66
SC2	27 variables (12 MS bands of S2B + 12 VIs + 2 backscatter coefficients VV & VH of S1A + DEM)	0.892	0.572	16.45
SC3	12 optimal variables (6 MS bands of S2B + 5 VIs + DEM)	**0.857**	**0.758**	**15.40**
SC4	32 variables (2 backscatter coefficients VV & VH of S1A + 30 SAR transformations)	0.991	0.573	15.82

4.3. The Important Variables

Among the 12 multispectral bands of S2B, the Red Edge-3 (Band 7 at 779.7 nm), and the Red (Band 4 at 664.9 nm) were the most sensitive to mangrove AGC in the current study, followed by the two SWIR spectra (band 11 at 1610.4 nm and band 12 at 2185.7 nm). Interestingly, among the 12 VI indices, the Modified Chlorophyll Absorption in Reflectance Index (MCARI) and the Green Normalized Difference Vegetation Index (GNDVI) were also important variables for estimating mangrove AGC in the study area, followed by

the Soil-Adjusted Vegetation Index (SAVI) and the Normalized Difference Index (NDI45) (bands 4 and 5 of S2B) (see Figure 5). The DEM data showed that mangrove AGC was sensitive to elevation. It is noted that the VH and VV backscatter coefficients of the S1A C-band and their SAR transformations were likely less important and were eliminated in the final optimal 12 features selection using the GA algorithm (Figure 5).

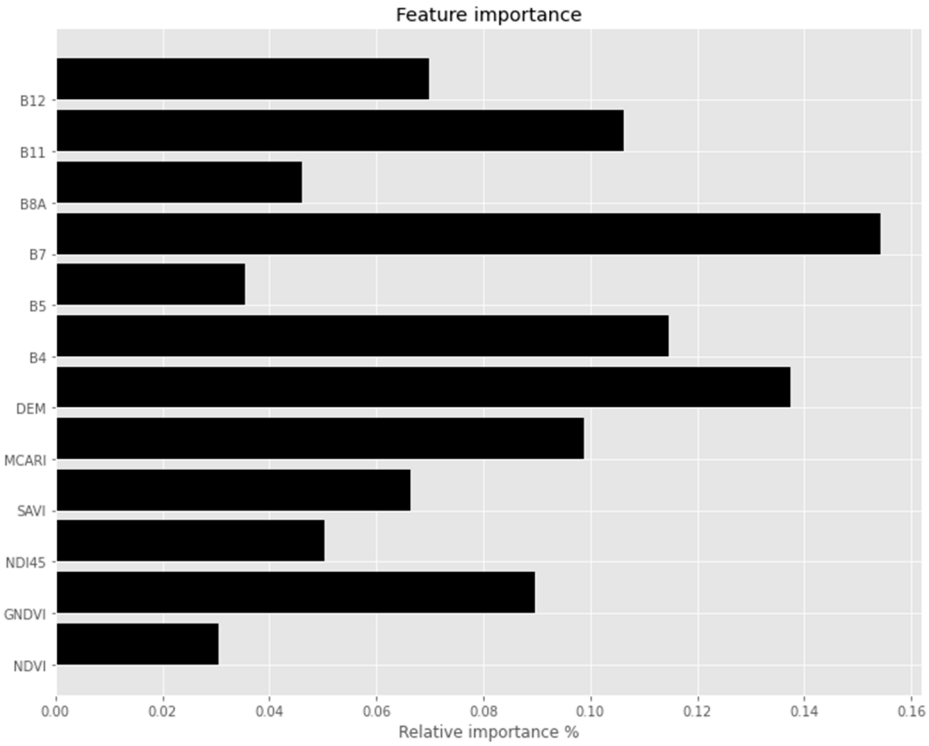


Figure 5. Variable importance of the optimal 12 features for mangrove AGC estimates.

4.4. Mangroves AGC Models

The prediction performance of the XGB-GA model for estimating mangrove AGC was improved by combining the S2B multispectral bands, VIs, and DEM datasets. Thus, the hybrid XGB-GA model was employed for generating mangrove AGC in the study area. The final results were computed to a raster in GeoTiff format for visualization. The AGC map was interpreted (Figure 6), showing the mangrove AGC ranging from 2.52 to 123.89 Mg C ha^{-1} (average = 57.16 Mg C ha^{-1}).

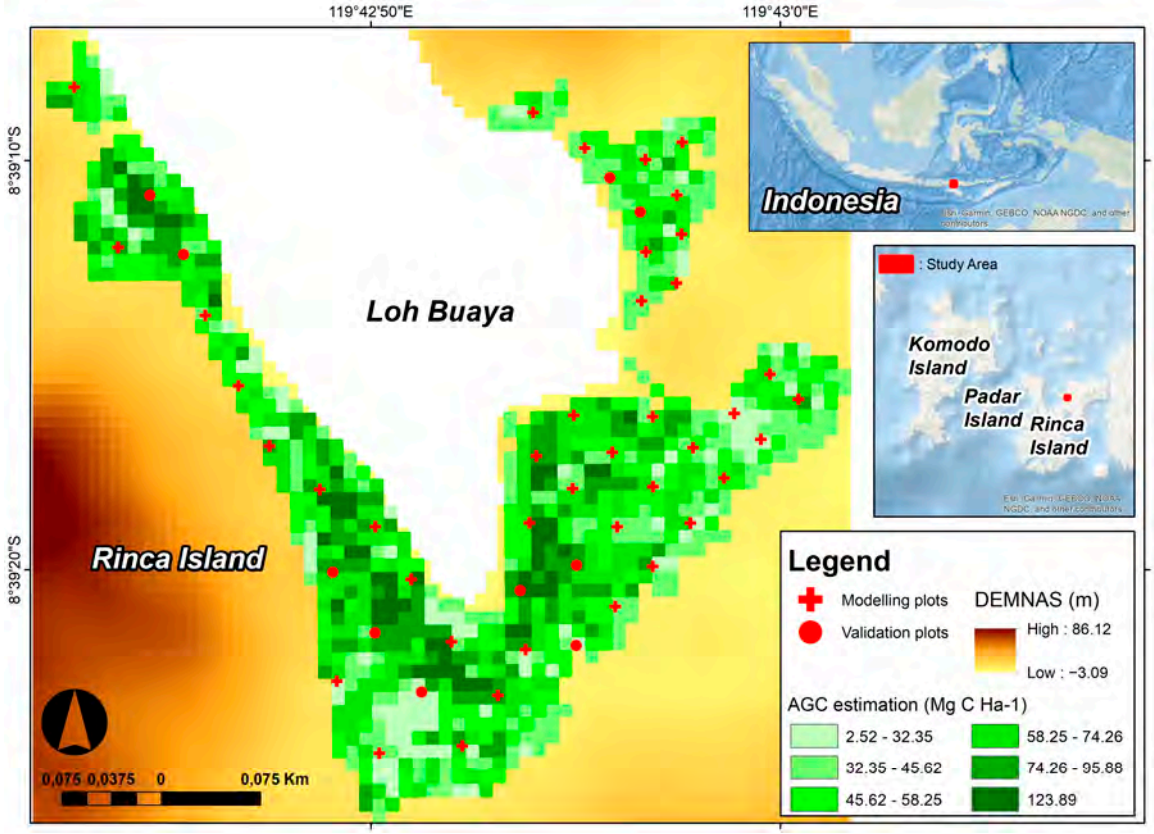


Figure 6. Spatial distribution of mangrove AGC at Loh Buaya.

5. Discussion

Rhizophora was the dominant genus in the study area, in common with other Indonesian mangroves forests at Karimun Jawa island [80,81], Bali island [82], and East Java [83], and is the dominant tropical genus [84]. Besides *Rhizophora* sp., other important species found in the study area included *Ceriops decandra* and *Lumnitzera racemosa*, their first observation in the area (c.f. Erdmann [37] and Suraji et al. [38]). The estimation of AGC calculation was controlled by tree density and girth [16,85], and also wood density [86]. Canopy cover provided a negligible contribution to biomass, though is likely to be sensitive to variation in hydroperiod [17] and influence forest productivity.

Our results show that the XGBR-GA model yielded the highest performance in the estimation of mangrove AGC, with an R^2 and an RMSE of 0.758 and 15.40 Mg C ha^{-1}, respectively. The lowest performing model was SVM, with an R^2 and an RMSE of −0.039 and 38.74 Mg C ha^{-1}. Both the XGB model (R^2 = 0.572) and the RF model (R^2 = 0.529) produced a relatively good performance for the estimates of mangrove AGC, indicating that the ensemble decision trees regression models were suitable for mapping mangrove AGC. As shown in Tables 4 and 5, the combined S2B and VIs as well as DEM data significantly improved the estimation of mangrove AGC in the study area. Backscatter coefficients and transformations generated from the dual polarimetric VV and VH of the S1A C-band were less important. These results are strongly consistent with a recent study in Northern Vietnam [35] and prove that the ML approach can also depict mangrove biomass/carbon with satisfying results compared to conventional parametric regression models. This is due to the ability to provide nearly unbiased error prediction and select effective variables [87,88]. Overall, the XGB-GA model performed well and outperformed the existing algorithms for estimating mangrove AGC in an Indonesian mangrove national park. Indonesian Government through the Ministry of Environment and Forestry has released an operational plan for FOLU (Forestry and Other Land Use) Net Sink to reduce greenhouse emission in 2030 [89] and mangrove has been mentioned for their potential for carbon absorption

ability. Therefore, this study could potentially support that policy using a state-of-the-art and scientific approach.

The XGB-GA model estimated the mangrove AGC at Loh Buaya ranging from 2.52 to 123.89 Mg C ha^{-1} with a mean of 57.16 Mg C ha^{-1}. These numbers fit well a range between 13.63 and 143.94 Mg C ha^{-1} with a mean measured mangrove AGC of 57.32 Mg C ha^{-1} (Table 3). In comparison to existing global coarse (30 m) mangrove biomass datasets [90], the results of this study produced a more suitable AGC range corresponding to field AGC data, with promising R2 and RMSE values. More accurate information on mangrove biomass is frequently produced by higher satellite spatial resolution [91]. This finding is consistent with the finding of Nguyen [92], who compared the ability of Sentinel-2 and Landsat-8 to map the AGB of mangroves in Vietnam. However, the proposed hybrid model was likely under-estimating at high observed carbon values and over-estimating at low observed carbon values. The scatterplot in Figure 4d depicts the prediction ability of the proposed hybrid XGB-GA model with optimal features to estimate the AGC of mangrove forests ranging from 10 to 100 Mg C ha^{-1} with the highest accuracy between 20 and 80 Mg C ha^{-1}. One possible reason could be the saturation levels for mangrove AGC estimates of S2B data, resulting in weak prediction performance at high AGC values and dense mangrove canopy densities observed in Indonesian mangrove ecosystems as reported by [88]. Further research focuses on the data integration and fusion between multispectral and longer wavelength SAR sensors, particularly integrating S2B and ALOS-2 PALSAR-2 to overcome the limitation saturation problem of the S2B sensor.

The results of variable importance in Figure 5 showed that the mangrove AGC at the Loh Buaya in Indonesia was largely retrieved from the Red band and the Red Edge bands. A similar observation was reported in other mangrove regions in Southeast Asian nations [87,93]. The Red and the Red Edge, and SWIR reflectance are more sensitive indicators to mangrove carbon stock volume than the visible reflectance [94]. Our results also revealed that the new vegetation index NDI45, which is generated from bands 4 and 5 of the S2B sensor, is probably correlated with mangrove AGC. The two SWIR spectra (bands 11 and 12) as well as the narrow NIR (band 8A) also play a vital role in estimating mangrove AGC. Noticeably, the MCARI derived from S2B was strongly correlated with mangrove AGC in the national park. The high quality of a national DEM also contributes to the hybrid ML model as it is strongly related to the distribution of mangrove canopy cover as shown in a recent study [17]. Furthermore, this is the first use of the national DEM for mangrove AGC estimation, though it is commonly used for disaster-related mapping, e.g., tsunami and tidal flood [95,96].

6. Conclusions

We incorporated S2B and S1A together with national DEM data into the XGB-GA model to estimate the mangrove AGC in an Indonesian mangrove area for the first time. The XGB-GA model outperformed other well-known ML models in mangrove AGC retrieval at Loh Buaya. The proposed hybrid XGB-GA with 12 optimal features estimated the mangrove AGC with the highest prediction accuracy for the first time in the Indonesian mangrove ecosystems (R^2 = 0.758, RMSE = 15.40 Mg C ha^{-1}). Interestingly, we found that new vegetation indices derived from the S2B data, such as the Normalized Difference Index (NDI45) and the Modified Chlorophyll Absorption in Reflectance Index (MCARI) were sensitively detected mangrove AGC in the Indonesian mangrove ecosystem.

Author Contributions: Conceptualization, S.S.R. and T.D.P.; methodology, S.S.R. and T.D.P.; software, S.S.R. and T.D.P.; validation, S.S.R. and T.D.P.; formal analysis, S.S.R. and T.D.P.; investigation, T.D.P. and S.N.; resources, S.N.; data curation, T.D.P. and S.N.; writing—original draft preparation, S.S.R. and T.D.P.; writing—review and editing, S.S.R., T.D.P. and N.S.; visualization, S.S.R. and T.D.P.; supervision, S.S.R. and M.I.P.; project administration, S.S.R. and S.N.; funding acquisition, S.S.R. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by Badan Penelitian dan Pengabdian Masyarakat (BPPM), FPIK Universitas Brawijaya through the scheme of Hibah Penelitian Dosen (Lecturer Research Grant) contract number 4717/UN10.F06/KS/2022.

Data Availability Statement: Not Applicable.

Acknowledgments: T.D.P. is supported by a Macquarie University Research Fellowship (Grant No. MQRF0001124-2021). The authors would like to thank local authorities for their generous assistance during the fieldwork and technical data process.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Kumari, A.; Rathore, M.S. Roles of Mangroves in Combating the Climate Change. In *Mangroves: Ecology, Biodiversity and Management*; Rastogi, R.P., Phulwaria, M., Gupta, D.K., Eds.; Springer Singapore: Gateway East, Singapore, 2021; pp. 225–255. ISBN 978-981-16-2494-0.
2. Hu, T.; Zhang, Y.Y.; Su, Y.; Zheng, Y.; Lin, G.; Guo, Q. Mapping the global mangrove forest aboveground biomass using multisource remote sensing data. *Remote Sens.* **2020**, *12*, 1690. [CrossRef]
3. Mumby, P.J.; Edwards, A.J.; Ernesto Arias-González, J.; Lindeman, K.C.; Blackwell, P.G.; Gall, A.; Gorczynska, M.I.; Harborne, A.R.; Pescod, C.L.; Renken, H.; et al. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **2004**, *427*, 533–536. [CrossRef]
4. Buelow, C.; Sheaves, M. A birds-eye view of biological connectivity in mangrove systems. *Estuar. Coast. Shelf Sci.* **2015**, *152*, 33–43. [CrossRef]
5. Hernández-Blanco, M.; Costanza, R.; Cifuentes-Jara, M. Economic valuation of the ecosystem services provided by the mangroves of the Gulf of Nicoya using a hybrid methodology. *Ecosyst. Serv.* **2021**, *49*, 101258. [CrossRef]
6. Marlianingrum, P.R.; Kusumastanto, T.; Adrianto, L.; Fahrudin, A. Valuing habitat quality for managing mangrove ecosystem services in coastal Tangerang District, Indonesia. *Mar. Policy* **2021**, *133*, 104747. [CrossRef]
7. Goldberg, L.; Lagomasino, D.; Thomas, N.; Fatoyinbo, T. Global declines in human-driven mangrove loss. *Glob. Chang. Biol.* **2020**, *26*, 5844–5855. [CrossRef]
8. Fauzi, A.; Sakti, A.; Yayusman, L.; Harto, A.; Prasetyo, L.; Irawan, B.; Kamal, M.; Wikantika, K. Contextualizing mangrove forest deforestation in southeast asia using environmental and socio-economic data products. *Forests* **2019**, *10*, 952. [CrossRef]
9. Latiff, A.; Faridah-Hanum, I. Mangrove Ecosystem of Malaysia: Status, Challenges and Management Strategies. In *Mangrove Ecosystems of Asia*; Faridah-Hanum, I., Latiff, A., Hakeem, K.R., Ozturk, M., Eds.; Springer New York: New York, NY, USA, 2014; pp. 1–22. ISBN 978-1-4614-8582-7.
10. Pendleton, L.; Donato, D.C.; Murray, B.C.; Crooks, S.; Jenkins, W.A.; Sifleet, S.; Craft, C.; Fourqurean, J.W.; Kauffman, J.B.; Marbà, N.; et al. Estimating Global "Blue Carbon" Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. *PLoS ONE* **2012**, *7*, e43542. [CrossRef]
11. Hutchison, J.; Manica, A.; Swetnam, R.; Balmford, A.; Spalding, M. Predicting Global Patterns in Mangrove Forest Biomass. *Conserv. Lett.* **2014**, *7*, 233–240. [CrossRef]
12. Hagger, V.; Worthington, T.A.; Lovelock, C.E.; Adame, M.F.; Amano, T.; Brown, B.M.; Friess, D.A.; Landis, E.; Mumby, P.J.; Morrison, T.H.; et al. Drivers of global mangrove loss and gain in social-ecological systems. *Nat. Commun.* **2022**, *13*, 6373. [CrossRef]
13. Friess, D.A.; Yando, E.S.; Abuchahla, G.M.O.; Adams, J.B.; Cannicci, S.; Canty, S.W.J.; Cavanaugh, K.C.; Connolly, R.M.; Cormier, N.; Dahdouh-Guebas, F.; et al. Mangroves give cause for conservation optimism, for now. *Curr. Biol.* **2020**, *30*, R153–R154. [CrossRef]
14. Sani, D.A.; Hashim, M.; Hossain, M.S. Remote sensing models used for mapping and estimation of blue carbon biomass in seagrass-mangrove habitats: A review. In Proceedings of the 39th Asian Conference on Remote Sensing (ACRS), Renaissance Kuala Lumpur Hotel, Lumpur, Malaysia, 15–19 October 2018; Volume 1, pp. 399–408.
15. Lamont, K.; Saintilan, N.; Kelleway, J.J.; Mazumder, D.; Zawadzki, A. Thirty-Year Repeat Measures of Mangrove Above- and Below-Ground Biomass Reveals Unexpectedly High Carbon Sequestration. *Ecosystems* **2020**, *23*, 370–382. [CrossRef]
16. Purnamasari, E.; Kamal, M.; Wicaksono, P. Comparison of vegetation indices for estimating above-ground mangrove carbon stocks using PlanetScope image. *Reg. Stud. Mar. Sci.* **2021**, *44*, 101730. [CrossRef]
17. Saintilan, N.; Lymburner, L.; Wen, L.; Haigh, I.D.; Ai, E.; Kelleway, J.J.; Rogers, K.; Pham, T.D.; Lucas, R. The lunar nodal cycle controls mangrove canopy cover on the Australian continent. *Sci. Adv.* **2022**, *8*, eabo6602. [CrossRef]
18. Jones, A.R.; Raja Segaran, R.; Clarke, K.D.; Waycott, M.; Goh, W.S.H.; Gillanders, B.M. Estimating Mangrove Tree Biomass and Carbon Content: A Comparison of Forest Inventory Techniques and Drone Imagery. *Front. Mar. Sci.* **2020**, *6*, 784. [CrossRef]
19. Tran, T.V.; Reef, R.; Zhu, X. A Review of Spectral Indices for Mangrove Remote Sensing. *Remote Sens.* **2022**, *14*, 4868. [CrossRef]
20. Pham, T.D.; Xia, J.; Ha, N.T.; Bui, D.T.; Le, N.N.; Tekeuchi, W. A Review of Remote Sensing Approaches for Monitoring Blue Carbon Ecosystems: Mangroves, Seagrasses and Salt Marshes during 2010–2018. *Sensors* **2019**, *19*, 1933. [CrossRef]

21. Wang, L.; Jia, M.; Yin, D.; Tian, J. A review of remote sensing for mangrove forests: 1956–2018. *Remote Sens. Environ.* **2019**, *231*, 111223. [CrossRef]
22. Nuthammachot, N.; Askar, A.; Stratoulias, D.; Wicaksono, P. Combined use of Sentinel-1 and Sentinel-2 data for improving above-ground biomass estimation. *Geocarto Int.* **2020**, *37*, 366–376. [CrossRef]
23. USGS. Imagery for Everyone . . . Timeline Set to Release Entire USGS Landsat Archive at No Charge. 2008. Available online: https://www.usgs.gov/media/files/2008-imagery-everyonetimeline-set-release-entire-usgs-landsat-0 (accessed on 1 November 2022).
24. European Space Agency. Sentinel-2 MSI—Technical Guide—Sentinel Online 2019. Available online: https://sentinels.copernicus.eu/web/sentinel/technical-guides/sentinel-2-msi (accessed on 5 September 2022).
25. European Space Agency. Sentinel-1 SAR User Guide. 2013. Available online: https://sentinel.esa.int/web/sentinel/user-guides/sentinel-1-sar (accessed on 1 November 2022).
26. Bunting, P.; Rosenqvist, A.; Hilarides, L.; Lucas, R.M.; Thomas, N.; Tadono, T.; Worthington, T.A.; Spalding, M.; Murray, N.J. Global Mangrove Extent Change 1996–2020: Global Mangrove Watch Version 3.0. *Remote Sens.* **2022**, *14*, 3657. [CrossRef]
27. Lagomasino, D.; Fatoyinbo, T.; Lee, S.; Feliciano, E.; Trettin, C.; Shapiro, A.; Mangora, M.M. Measuring mangrove carbon loss and gain in deltas. *Environ. Res. Lett.* **2019**, *14*, 25002. [CrossRef]
28. Liu, X.; Fatoyinbo, T.E.; Thomas, N.M.; Guan, W.W.; Zhan, Y.; Mondal, P.; Lagomasino, D.; Simard, M.; Trettin, C.C.; Deo, R.; et al. Large-Scale High-Resolution Coastal Mangrove Forests Mapping Across West Africa With Machine Learning Ensemble and Satellite Big Data. *Front. Earth Sci.* **2021**, *8*, 560933. [CrossRef]
29. Sidhu, N.; Pebesma, E.; Câmara, G. Using Google Earth Engine to detect land cover change: Singapore as a use case. *Eur. J. Remote Sens.* **2018**, *51*, 486–500. [CrossRef]
30. Nemani, R.; Votava, P.; Michaelis, A.; Melton, F.; Milesi, C. Collaborative Supercomputing for Global Change Science. *Eos Trans. Am. Geophys. Union* **2011**, *92*, 109–116. [CrossRef]
31. Argamosa, R.J.; Blanco, A.C.; Baloloy, A.B.; Candido, C.G.; Dumalag, J.B.; DImapilis, L.L.; Paringit, E.C. Modelling above Ground Biomass of Mangrove Forest Using Sentinel-1 Imagery. *ISPRS Ann. Photogramm. Remote Sens. Spat. Inf. Sci.* **2018**, *4*, 13–20. [CrossRef]
32. Diniz, C.; Cortinhas, L.; Nerino, G.; Rodrigues, J.; Sadeck, L.; Adami, M.; Souza-Filho, P.W.M. Brazilian Mangrove Status: Three Decades of Satellite Data Analysis. *Remote Sens.* **2019**, *11*, 808. [CrossRef]
33. Pham, T.D.; Le, N.N.; Ha, N.T.; Nguyen, L.V.; Xia, J.; Yokoya, N.; To, T.T.; Trinh, H.X.; Kieu, L.Q.; Takeuchi, W. Estimating mangrove above-ground biomass using extreme gradient boosting decision trees algorithm with fused sentinel-2 and ALOS-2 PALSAR-2 data in can Gio biosphere reserve, Vietnam. *Remote Sens.* **2020**, *12*, 777. [CrossRef]
34. Tian, Y.; Huang, H.; Zhou, G.; Zhang, Q.; Tao, J.; Zhang, Y.; Lin, J. Aboveground mangrove biomass estimation in Beibu Gulf using machine learning and UAV remote sensing. *Sci. Total Environ.* **2021**, *781*, 146816. [CrossRef]
35. Pham, T.D.; Yokoya, N.; Xia, J.; Ha, N.T.; Le, N.N.; Nguyen, T.T.T.; Dao, T.H.; Vu, T.T.P.; Pham, T.D.; Takeuchi, W. Comparison of machine learning methods for estimating mangrove above-ground biomass using multiple source remote sensing data in the red river delta biosphere reserve, Vietnam. *Remote Sens.* **2020**, *12*, 1334. [CrossRef]
36. UNESCO. Komodo National Park—UNESCO World Heritage Centre 2014. Available online: http://whc.unesco.org/en/list/685 (accessed on 3 November 2022).
37. Erdmann, A.M. *A Natural History Guide to Komodo National Park*; The Nature Conservancy: Virginia, UK, 2004; p. 198.
38. Suraji, S.; Hasan, S.; Suharyanto, S.; Yonvitner, Y.; Koeshendrajana, S.; Prasetiyo, D.E.; Widianto, A.; Dermawan, A. Nilai Penting Dan Strategis Nasional Rencana Zonasi Kawasan Taman Nasional Komodo. *J. Sos. Ekon. Kelaut. dan Perikan.* **2020**, *15*, 15–32. [CrossRef]
39. Dharmawan, I.W.E.; Suyarso; Yaya, I.U.; Prayudha, B.; Pramudji. *Panduan Monitoring Struktur Komunitas Mangrove Di Indonesia*, 1st ed.; Media Sains Nasional: Bogor, Indonesia, 2020; ISBN 9786239430603.
40. Dharmawan, I.W.; Sastrosuwondo, P. *Panduan Monitoring Status Ekosistem Mangrove di Indonesia*; COREMAP CITI LIPI: Jakarta, Indonesia, 2014.
41. Komiyama, A.; Poungparn, S.; Kato, S. Common allometric equations for estimating the tree weight of Common allometric equations for estimating the tree weight of mangroves. *J. Trop. Ecol.* **2005**, *21*, 471–477. [CrossRef]
42. World Agroforestry. ICRAF Database—Wood Density. 2016. Available online: http://db.worldagroforestry.org/wd (accessed on 5 October 2022).
43. Badan Standar Nasional. *Pengukuran dan Penghitungan Cadangan Karbon—Pengukuran Lapangan untuk Penaksiran Cadangan Karbon Hutan (Ground Based Forest Carbon Accounting)*; BSNI: Jakarta, Indonesia, 2011.
44. European Space Agency. User Guides—Sentinel-1 SAR—Polarimetry—Sentinel Online. 2022. Available online: https://sentinels.copernicus.eu/web/sentinel/user-guides/sentinel-1-sar/product-overview/polarimetry (accessed on 5 November 2022).
45. Badan Informasi Geospasial (BIG)/Indonesian Geospatial Information Agency. DEMNAS. 2022. Available online: https://tanahair.indonesia.go.id/demnas/#/demnas (accessed on 5 October 2022).
46. Susetyo, D.B.; Lumban-Gaol, Y.A.; Sofian, I. Prototype of national digital elevation model in Indonesia. *Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci.—ISPRS Arch.* **2018**, *42*, 687–692. [CrossRef]
47. Kamal, M.; Phinn, S.; Johansen, K. Assessment of multi-resolution image data for mangrove leaf area index mapping. *Remote Sens. Environ.* **2016**, *176*, 242–254. [CrossRef]

48. Wicaksono, P. Mangrove above-ground carbon stock mapping of multi-resolution passive remote-sensing systems. *Int. J. Remote Sens.* **2017**, *38*, 1551–1578. [CrossRef]
49. Wicaksono, P.; Danoedoro, P.; Hartono, H.; Nehren, U.; Ribbe, L. Preliminary work of mangrove ecosystem carbon stock mapping in small island using remote sensing: Above and below ground carbon stock mapping on medium resolution satellite image. *Remote Sens. Agric. Ecosyst. Hydrol. XIII* **2011**, *8174*, 81741B. [CrossRef]
50. Thapa, R.B.; Watanabe, M.; Motohka, T.; Shimada, M. Potential of high-resolution ALOS–PALSAR mosaic texture for aboveground forest carbon tracking in tropical region. *Remote Sens. Environ.* **2015**, *160*, 122–133. [CrossRef]
51. Nesha, M.K.; Hussin, Y.A.; van Leeuwen, L.M.; Sulistioadi, Y.B. Modeling and mapping aboveground biomass of the restored mangroves using ALOS-2 PALSAR-2 in East Kalimantan, Indonesia. *Int. J. Appl. Earth Obs. Geoinf.* **2020**, *91*, 102158. [CrossRef]
52. Pham, T.D.; Yoshino, K.; Le, N.N.; Bui, D.T. Estimating aboveground biomass of a mangrove plantation on the Northern coast of Vietnam using machine learning techniques with an integration of ALOS-2 PALSAR-2 and Sentinel-2A data. *Int. J. Remote Sens.* **2018**, *39*, 7761–7788. [CrossRef]
53. Stovall, A.E.L.; Fatoyinbo, T.; Thomas, N.M.; Armston, J.; Ebanega, M.O.; Simard, M.; Trettin, C.; Obiang Zogo, R.V.; Aken, I.A.; Debina, M.; et al. Comprehensive comparison of airborne and spaceborne SAR and LiDAR estimates of forest structure in the tallest mangrove forest on earth. *Sci. Remote Sens.* **2021**, *4*, 100034. [CrossRef]
54. Lucas, R.; Van De Kerchove, R.; Otero, V.; Lagomasino, D.; Fatoyinbo, L.; Omar, H.; Satyanarayana, B.; Dahdouh-Guebas, F. Structural characterisation of mangrove forests achieved through combining multiple sources of remote sensing data. *Remote Sens. Environ.* **2020**, *237*, 111543. [CrossRef]
55. Maeda, Y.; Fukushima, A.; Imai, Y.; Tanahashi, Y.; Nakama, E.; Ohta, S.; Kawazoe, K.; Akune, N. Estimating carbon stock changes of mangrove forests using satellite imagery and airborne LiDAR data in the South Sumatra state, Indonesia. *Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci.—ISPRS Arch.* **2016**, *41*, 705–709. [CrossRef]
56. Jin, Z.; Azzari, G.; You, C.; Di Tommaso, S.; Aston, S.; Burke, M.; Lobell, D.B. Smallholder maize area and yield mapping at national scales with Google Earth Engine. *Remote Sens. Environ.* **2019**, *228*, 115–128. [CrossRef]
57. Schulz, D.; Yin, H.; Tischbein, B.; Verleysdonk, S.; Adamou, R.; Kumar, N. Land use mapping using Sentinel-1 and Sentinel-2 time series in a heterogeneous landscape in Niger, Sahel. *ISPRS J. Photogramm. Remote Sens.* **2021**, *178*, 97–111. [CrossRef]
58. Hajduch, G.; Bourbigot, M.; Johnsen, H.; Piantanida, R. Sentinel-1 User Handbook. 2022. Available online: https://sentinel.esa.int/documents/247904/1877131/Sentinel-1-Product-Specification-18052021.pdf (accessed on 10 November 2022).
59. Simental, E.; Verner Guthrie, M.; Scientist Bruce Blundell, P.S. Polarimetry Band Ratios, Decompositions, and Statistics for Terrain Characterization. In *Global Priorities in Land Remote Sensing, Proceedings of the Pecora 16, Sioux Falls, South Dakota, 23–27 October 2005*; American Society for Photogrammetry and Remote Sensing: Bethesda, MD, USA, 2005.
60. Nasonova, S.; Scharien, R.; Geldsetzer, T.; Howell, S.; Power, D. Optimal Compact Polarimetric Parameters and Texture Features for Discriminating Sea Ice Types during Winter and Advanced Melt. *Can. J. Remote Sens.* **2019**, *44*, 390–411. [CrossRef]
61. Baronti, S.; Carla, R.; Sigismondi, S.; Alparone, L. Principal component analysis for change detection on polarimetric multitemporal SAR data. In Proceedings of the IGARSS'94—1994 IEEE International Geoscience and Remote Sensing Symposium, Pasadena, CA, USA, 8–12 August 1994; Volume 4, pp. 2152–2154. [CrossRef]
62. European Space Agency. Sentinel-2 User Handbook. 2015. Available online: https://sentinels.copernicus.eu/web/sentinel/user-guides/document-library/-/asset_publisher/xlslt4309D5h/content/sentinel-2-user-handbook (accessed on 15 November 2022).
63. Jordan, C.F. Derivation of Leaf-Area Index from Quality of Light on the Forest Floor. *Ecology* **1969**, *50*, 663–666. [CrossRef]
64. Tucker, C.J. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sens. Environ.* **1979**, *8*, 127–150. [CrossRef]
65. Candiago, S.; Remondino, F.; De Giglio, M.; Dubbini, M.; Gattelli, M. Evaluating Multispectral Images and Vegetation Indices for Precision Farming Applications from UAV Images. *Remote Sens.* **2015**, *7*, 4026–4047. [CrossRef]
66. Soria, J.; Ruiz, M.; Morales, S. Monitoring Subaquatic Vegetation Using Sentinel-2 Imagery in Gallocanta Lake (Aragón, Spain). *Earth* **2022**, *3*, 363–382. [CrossRef]
67. Huete, A.R. A soil-adjusted vegetation index (SAVI). *Remote Sens. Environ.* **1988**, *25*, 295–309. [CrossRef]
68. Gómez-Giráldez, P.J.; Pérez-Palazón, M.J.; Polo, M.J.; González-Dugo, M.P. Monitoring grass phenology and hydrological dynamics of an oak-grass savanna ecosystem using sentinel-2 and terrestrial photography. *Remote Sens.* **2020**, *12*, 600. [CrossRef]
69. Daughtry, C.S.T.; Walthall, C.L.; Kim, M.S.; de Colstoun, E.B.; McMurtrey, J.E. Estimating Corn Leaf Chlorophyll Concentration from Leaf and Canopy Reflectance. *Remote Sens. Environ.* **2000**, *74*, 229–239. [CrossRef]
70. Qi, J.; Chehbouni, A.; Huete, A.R.; Kerr, Y.H.; Sorooshian, S. A modified soil adjusted vegetation index. *Remote Sens. Environ.* **1994**, *48*, 119–126. [CrossRef]
71. Richardson, A.J.; Wiegand, C.L. Distinguishing vegetation from soil background information. *Photogramm. Eng. Remote Sensing* **1977**, *43*, 1541–1552.
72. Breiman, L. Random Forests. *Mach. Learn.* **2001**, *45*, 5–32. [CrossRef]
73. Vapnik, V.N. An overview of statistical learning theory. *IEEE Trans. Neural Networks* **1999**, *10*, 988–999. [CrossRef] [PubMed]
74. Pham, T.D.; Yoshino, K.; Bui, D.T. Biomass estimation of *Sonneratia caseolaris* (l.) Engler at a coastal area of Hai Phong city (Vietnam) using ALOS-2 PALSAR imagery and GIS-based multi-layer perceptron neural networks. *GIScience Remote Sens.* **2017**, *54*, 329–353. [CrossRef]

75. Chen, T.; Guestrin, C. XGBoost: A Scalable Tree Boosting System. In *KDD'16, Proceedings of the 22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining, San Francisco, CA, USA, 13–17 August 2016*; Association of Computing Machinery: New York, NY, USA, 2016.
76. Nielsen, D. Tree Boosting With XGBoost Why Does XGBoost Win "Every" Machine Learning Competition? Master's Thesis, NTNU: Norwegian University of Science and Trcnology, Trondheim, Norway, December 2016.
77. Pedregosa, F.; Grisel, O.; Weiss, R.; Passos, A.; Brucher, M.; Varoquax, G.; Gramfort, A.; Michel, V.; Thirion, B.; Grisel, O.; et al. Scikit-learn: Machine Learning in Python. *J. Mach. Learn. Res.* **2011**, *12*, 2825–2830.
78. Davis, L. *Handbook of Genetic Algorithms*; VNR Computer Library, Van Nostrand Reinhold: New York, NY, USA, 1991; ISBN 9780442001735.
79. Pham, T.D.; Yoshino, K. Aboveground biomass estimation of mangrove species using ALOS-2 PALSAR imagery in Hai Phong City, Vietnam. *J. Appl. Remote Sens.* **2017**, *11*, 026010. [CrossRef]
80. Rahmandhana, A.D.; Kamal, M.; Wicaksono, P. Spectral Reflectance-Based Mangrove Species Mapping from WorldView-2 Imagery of Karimunjawa and Kemujan Island, Central Java Province, Indonesia. *Remote Sens.* **2022**, *14*, 183. [CrossRef]
81. Wicaksono, P.; Danoedoro, P.; Hartono; Nehren, U. Mangrove biomass carbon stock mapping of the Karimunjawa Islands using multispectral remote sensing. *Int. J. Remote Sens.* **2016**, *37*, 26–52. [CrossRef]
82. Kamal, M.; Sidik, F.; Prananda, A.R.A.; Mahardhika, S.A. Mapping Leaf Area Index of restored mangroves using WorldView-2 imagery in Perancak Estuary, Bali, Indonesia. *Remote Sens. Appl. Soc. Environ.* **2021**, *23*, 100567. [CrossRef]
83. Kamal, M.; Hidayatullah, M.F.; Mahyatar, P.; Ridha, S.M. Estimation of aboveground mangrove carbon stocks from WorldView-2 imagery based on generic and species-specific allometric equations. *Remote Sens. Appl. Soc. Environ.* **2022**, *26*, 100748. [CrossRef]
84. Cerón-Souza, I.; Rivera-Ocasio, E.; Medina, E.; Jiménez, J.A.; McMillan, W.O.; Bermingham, E. Hybridization and introgression in New World red mangroves, Rhizophora (Rhizophoraceae). *Am. J. Bot.* **2010**, *97*, 945–957. [CrossRef] [PubMed]
85. Dharmawan, I.W.S.; Siregar, C.A. Karbon tanah dan pendugaan karbon tegakan. *Jurnal Penelitian Hutan Dan Konservasi Alam* **2008**, *5*, 317–328. [CrossRef]
86. Alimbon, J.A.; Manseguiao, M.R.S. Species composition, stand characteristics, aboveground biomass, and carbon stock of mangroves in panabo mangrove park, philippines. *Biodiversitas* **2021**, *22*, 3130–3137. [CrossRef]
87. Jachowski, N.R.A.; Quak, M.S.Y.; Friess, D.A.; Duangnamon, D.; Webb, E.L.; Ziegler, A.D. Mangrove biomass estimation in Southwest Thailand using machine learning. *Appl. Geogr.* **2013**, *45*, 311–321. [CrossRef]
88. Pham, T.D.; Yokoya, N.; Bui, D.T.; Yoshino, K.; Friess, D.A. Remote sensing approaches for monitoring mangrove species, structure, and biomass: Opportunities and challenges. *Remote Sens.* **2019**, *11*, 230. [CrossRef]
89. KLHK. *Rencana Operasional FOLU Net Sink 2030*; Kementerian LHK: Jakarta, Indonesia, 2022.
90. Simard, M.; Fatoyinbo, T.; Smetanka, C.; Rivera-Monroy, V.H.; Castaneda-Mova, E.; Thomas, N.; van der Stocken, T. *Global Mangrove Distribution, Aboveground Biomass, and Canopy Height*; ORNL DAAC: Oak Ridge, TN, USA, 2019. [CrossRef]
91. Ximenes, A.C.; Cavanaugh, K.C.; Arvor, D.; Murdiyarso, D.; Thomas, N.; Arcoverde, G.F.B.; da Conceição Bispo, P.; Van der Stocken, T. A comparison of global mangrove maps: Assessing spatial and bioclimatic discrepancies at poleward range limits. *Sci. Total Environ.* **2022**, *in press*. [CrossRef]
92. Nguyen, H.-H.; Nguyen, T.T.H. Above-ground biomass estimation models of mangrove forests based on remote sensing and field-surveyed data: Implications for C-PFES implementation in Quang Ninh Province, Vietnam. *Reg. Stud. Mar. Sci.* **2021**, *48*, 101985. [CrossRef]
93. Chrysafis, I.; Mallinis, G.; Siachalou, S.; Patias, P. Assessing the relationships between growing stock volume and Sentinel-2 imagery in a Mediterranean forest ecosystem. *Remote Sens. Lett.* **2017**, *8*, 508–517. [CrossRef]
94. Pham, L.T.H.; Brabyn, L. Monitoring mangrove biomass change in Vietnam using SPOT images and an object-based approach combined with machine learning algorithms. *ISPRS J. Photogramm. Remote Sens.* **2017**, *128*, 86–97. [CrossRef]
95. Pribadi, S.; Yatimantoro, T. *Peta Bahaya Tsunami Jawa Timur*; BMKG: Surabaya, Indonesia, 2021.
96. Denicko Roynaldi, A.; Maryono, M. Estimation of Waste Generation from Tidal Flood in North Semarang Sub-District. *E3S Web Conf.* **2019**, *125*, 07019. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.

Estuarine, Coastal and Shelf Science 205 (2018) 68–74

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Carbon isotope fractionation in the mangrove *Avicennia marina* has implications for food web and blue carbon research

Jeffrey J. Kelleway [a, *], Debashish Mazumder [a, b], Jeffrey A. Baldock [c], Neil Saintilan [a]

[a] Department of Environmental Sciences, Macquarie University, Sydney, NSW, Australia
[b] Australian Nuclear Science and Technology Organisation, Kirrawee DC, NSW, Australia
[c] CSIRO Agriculture and Food, Locked Bag 2, Glen Osmond, SA 5064, Australia

ARTICLE INFO

Article history:
Received 13 October 2017
Received in revised form
7 March 2018
Accepted 7 March 2018
Available online 13 March 2018

Keywords:
Biomarker
Blue carbon
Energy flow
Food web
Stable isotope
Trophic ecology

ABSTRACT

The ratio of stable isotopes of carbon ($\delta^{13}C$) is commonly used to track the flow of energy among individuals and ecosystems, including in mangrove forests. Effective use of this technique requires understanding of the spatial variability in $\delta^{13}C$ among primary producer(s) as well as quantification of the isotopic fractionations that occur as C moves within and among ecosystem components. In this experiment, we assessed $\delta^{13}C$ variation in the cosmopolitan mangrove *Avicennia marina* across four sites of varying physico-chemical conditions across two estuaries. We also compared the isotopic values of five distinct tissue types (leaves, woody stems, cable roots, pneumatophores and fine roots) in individual plants.

We found a significant site effect ($F_{3, 36} = 15.78$; $P < 0.001$) with mean leaf $\delta^{13}C$ values 2.0‰ more depleted at the lowest salinity site compared to the other locations. There was a larger within-plant fractionation effect, however, with leaf samples (mean ± SE = −29.1 ± 0.2) more depleted in ^{13}C than stem samples (−27.1 ± 0.1), while cable root (−25. 8 ± 0.1), pneumatophores (−25.7 ± 0.1) and fine roots (−26.0 ± 0.2) were more enriched in ^{13}C relative to both aboveground tissue types ($F_{4, 36} = 223.45$; $P < 0.001$).

The within-plant $\delta^{13}C$ fractionation we report for *A. marina* is greater than that reported in most other ecosystems. This has implications for studies of estuarine carbon cycling. The consistent and large size of the fractionation from leaf to woody stem (~2.0‰) and mostly consistent fractionation from leaf to root tissues (>3.0‰) means that it may now be possible to partition the individual contributions of various mangrove tissues to estuarine food webs. Similarly, the contributions of mangrove leaves, woody debris and belowground sources to blue carbon stocks might also be quantified. Above all, however, our results emphasize the importance of considering appropriate mangrove tissue types when using $\delta^{13}C$ to trace carbon cycling in estuarine systems.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

Understanding the flow of C in mangrove forests is of particular importance for a number of reasons. First, mangroves are highly productivity ecosystems, which can have broad influence upon coastal trophic dynamics and the primary industries reliant upon them. Previous studies have demonstrated the importance of mangrove primary production to food webs within mangrove forests themselves (Nagelkerken et al., 2008; Odum and Heald, 1975), but also to those in adjacent or connected habitats such as coral reefs, seagrass meadows, saltmarshes, estuarine waters and the coastal ocean (Abrantes et al., 2015; Alongi et al., 1989; Guest and Connolly, 2004; Hemminga et al., 1994). There remains uncertainty, however, as to what extent these food webs are supported by mangrove plant production (i.e. either direct herbivory of biomass or plant detrital pathways) versus benthic and/or pelagic algal production (Abrantes et al., 2015; Alderson et al., 2013; Fry and Ewel, 2003; Loneragan et al., 1997; Saintilan and Mazumder, 2010).

Understanding is also emerging on the role of mangrove forests in long-term carbon storage and sequestration (Atwood et al., 2017; Donato et al., 2011; Lovelock, 2008). Mangroves, along with saltmarshes and seagrasses, have been termed 'blue carbon'

* Corresponding author.
E-mail address: jeffrey.kelleway@mq.edu.au (J.J. Kelleway).

https://doi.org/10.1016/j.ecss.2018.03.011
0272-7714/© 2018 Elsevier Ltd. All rights reserved.

ecosystems, reflecting their capacity to naturally capture and store carbon more rapidly and more permanently than many terrestrial or freshwater ecosystems (McLeod et al., 2011). The carbon that accumulates in blue carbon ecosystems may derive from both aboveground and belowground plant biomass and detritus and in-situ algal production, as well as from external (allochthonous) sources including soil C, algae and organic detritus transported from catchments and tidal waters. Identifying and quantifying the contribution of the various sources of carbon that are ultimately stored in blue carbon soils informs our understanding of C transport and preservation in coastal environments (Kelleway et al., 2017; Kennedy et al., 2010). Accurate quantification of carbon source contribution to blue carbon soils will be important for carbon trading and offset projects as they become more broadly implemented.

One of the most common methods for investigating the transport and cycling of carbon in coastal ecosystems is through quantification of the relative proportions of the stable isotopes of C – ^{13}C:^{12}C or $\delta^{13}C$ (Abrantes et al., 2015; Bouillon et al., 2011; Guest et al., 2004; Kelleway et al., 2016). The utility of this approach lies in the fact that different primary sources of C may have distinct and identifiable $\delta^{13}C$ values. For example, $\delta^{13}C$ varies among photosynthetic pathway types, with terrestrial C3 (−24 to −34‰) and C4 (−6 to −19‰) plants showing distinct $\delta^{13}C$ distributions from one another (Smith and Epstein, 1971). Marine phytoplankton and benthic algae $\delta^{13}C$ typically lie between C3 and C4 plants, though there may be some overlap (France, 1995), while aquatic C3 plants (such as seagrasses), which take up dissolved inorganic carbon from the water column generally have a more enriched (i.e. less negative) $\delta^{13}C$ signature (Beer, 1989; Mazumder et al., 2011). Theoretically, such distinctions in $\delta^{13}C$ among primary producers may be used to follow C flow through an ecosystem. To do this effectively, however, the following information is required: 1) an understanding of the spatial variability in $\delta^{13}C$ among the primary producer(s) of interest; and 2) quantification of the isotopic changes (fractionations) that occur as C is transformed and transported within and among components of the ecosystem.

Attempts to identify the environmental and biological drivers of plant $\delta^{13}C$ have been a focus of plant isotope studies in recent decades (Cernusak et al., 2013). Such studies have proposed that photosynthetic water-use efficiency is one of the principal drivers of $\delta^{13}C$ fractionation as CO_2 is fixed within the photosynthetic organs of plants (Cernusak et al., 2013; Diefendorf et al., 2010; Farquhar and Richards, 1984). This is of consequence to mangroves, which use photosynthetic water-use efficiency as an adaptation for living in saline waters (Clough and Sim, 1989; Parida and Jha, 2010). Controlled studies have shown increases in water salinity around halophyte roots to make plant $\delta^{13}C$ less negative, most likely due to reduction in the ratio of intercellular and ambient partial pressures of CO_2 (Farquhar et al., 1982; Guy et al., 1980; McKee et al., 2002). Therefore, there are theoretical grounds to suspect that salinity may be a determinant of $\delta^{13}C$ variation among mangroves.

In addition to the variation in $\delta^{13}C$ among individual plants, the terrestrial plant literature also contains increasing evidence of post-photosynthetic fractionation within individuals. For example, it has been shown that leaves are isotopically lighter (i.e. more negative $\delta^{13}C$) than other plant organs, though the size of this effect appears to vary among settings and/or taxa (Badeck et al., 2005). Despite this, there appears to have been little investigation of this within-plant $\delta^{13}C$ fractionation among mangrove taxa, or for other halophytic or coastal plants. In one of the few studies to touch upon this phenomenon in mangroves (Saintilan et al., 2013), found that $\delta^{13}C$ variation among shoots and roots was site specific, postulating that this may be linked to the salinity of a site. More recently Weiss et al. (2016) demonstrated consistent carbon isotopic differentiation between leaves and roots in a single location for tropical mangrove species. Importantly, numerous studies have shown that there is little to no difference in $\delta^{13}C$ between fresh and decomposing mangrove leaves (Fry and Ewel, 2003; Saintilan et al., 2013; Zieman et al., 1984). Most studies exploring the provenance of carbon in mangrove soil stocks or ecosystems have considered only the isotope signature of leaves (see, for example, Gonneea et al., 2004; Meng et al., 2016; Tue et al., 2012; Xia et al., 2015), despite the far higher biomass of carbon within above-ground woody biomass and below-ground root systems (Donato et al., 2011; Saintilan, 1997).

A thorough understanding of mangrove $\delta^{13}C$ variability within and between individuals and sites is important to multiple fields of environmental research. In this study, we quantified the magnitude of $\delta^{13}C$ variability for a cosmopolitan species of mangrove, *Avicennia marina*. We tested the following hypotheses: 1) mangrove $\delta^{13}C$ will vary among locations with differing physico-chemical conditions; and 2) $\delta^{13}C$ varies among the different tissues of individual plants.

2. Materials and methods

2.1. Study sites

Two estuaries within the Sydney region of southeast Australia were chosen for this study – the Pittwater-Hawkesbury River estuary (33° 38′ S; 151° 18′ E) and the Botany Bay-Georges River estuary (33° 59′ S; 151° 10′ E). Both systems are drowned river valley estuaries with marine embayments located near the estuary mouth. In each system two study sites were chosen: one within the marine embayment ('Careel Bay' and 'Towra Point') and one located upstream ('Berowra Creek' and 'Georges River') (Fig. 1). Mean ± SD salinity of open water is 35.2 ± 0.4, 31.9 ± 2.8, 15.0 ± 8.3 and 11.6 ± 6.8, near the Careel Bay, Towra Point, Georges River and Berowra Creek sites, respectively (Geoscience Australia, 2015; Hornsby Shire Council, 2015; Pittwater Council, 1998). Rainfall in the region is spread throughout the year, with similar annual rainfall of 1084 mm y^{-1} at the coast (Sydney Airport weather station) and 1024 mm y^{-1} within the estuarine zone (Lucas Heights weather station).

2.2. Sample collection and analysis

At each site, ten mature *Avicennia marina* trees were randomly selected for tissue collection within central forest locations at each site (i.e. areas within ~15 m of the landward fringe and seaward fringe were avoided at all sites). The area of forest available was therefore a function of forest size and orientation at each location. For Berowra Creek trees were randomly selected among and area of ~300 m^2, 800 m^2 for Careel Bay and 320 m^2 for Georges River. For Towra Point, a representative sub-section of the forest was chosen (~800 m^2) due to the large mangrove area here (>470 ha).

Five living tissue types were collected from each tree. These were: 1) entire leaf samples (a collection of 10 mature leaves showing no sign of herbivory or damage selected from a single terminal branchlet); 2) a cross-section of woody branch (~15 mm diameter; taken from the same branch as the leaf collection); a cross-section of cable root (~15–30 mm diameter; taken from close to the junction with the tree trunk); a cross-section of pneumatophore (~15 mm diameter; taken aboveground); and entire, fine roots (collected from the surface 5 cm of substrate around the selected pneumatophore). This sampling strategy was used to maximize relatedness among neighboring tissue types – for example, the signature of the 10 leaves would be integrated into a single leaf value which is compared to the woody branch from which they were collected. All samples were transported in ice to

Fig. 1. Map of the study region in southeast Australia, encompassing the Hawkesbury-Pittwater and Georges-Botany estuaries. Study sites are marked with red stars. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the laboratory, where they were placed in a freezer prior to sample processing. All tissues were thawed and thoroughly rinsed under deionized water, with slight physical agitation by hand to remove any epiphytic and foreign materials, and to remove soil particles from fine root samples. All leaves from the same tree were combined into a single sample to provide enough material for chemical analyses. Samples were dried at 60 °C for 72 h and then pulverized to a fine, homogenous powder using a ball mill.

2.3. Isotopic analysis

Isotopic ($\delta^{13}C$) analyses were conducted at the Australian Nuclear Science and Technology Organisation (ANSTO) in Sydney, Australia. Powdered and homogenized plant samples were loaded into tin capsules and analysed with a continuous flow isotope ratio mass spectrometer (CF-IRMS), model Delta V Plus (Thermo Scientific Corporation, USA) interfaced with an elemental analyser (Thermo Fisher Flash, 2000 HT EA, Thermo Electron Corporation, USA). A two-point calibration was employed to normalise the isotope data, utilising standards that bracket the isotope ratios of the samples being analysed. Two quality control stable isotope references were included in each run, and for every tenth sample a replicate sub-sample was analysed. Results were precise (± 1 SD) to 0.3‰ for $\delta^{13}C$. Stable isotope values were reported in delta (δ) units in parts per thousand (‰) relative to the international standards (USGS 40, USGS41) that have been certified relative to VPDB and determined as follows:

$$\delta^{13}C\ (‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

where $R = {}^{13}C/{}^{12}C$.

2.4. Statistical analyses

A repeated measures analysis of variance (RM-ANOVA) design was employed for statistical analysis, whereby each of the five tissues collected from a single tree were treated as repeated measures on the same individual (tree). This was used to test differences among tissue types (i.e. the repeated measures), the four study sites, and interactions (tissue x site) between the two (Table S1). Data sphericity was tested using Mauchly's test of sphericity (Mauchly, 1940), and found to meet this assumption.

3. Results

Across the four study sites $\delta^{13}C$ values for *A. marina* ranged from −31.1 to −24.5‰ with an overall mean of −26.7‰ (SD = 1.5). There was a significant site effect ($F_{3,\ 36} = 15.78$; $P < 0.001$) with values more depleted in ^{13}C at Berowra Creek relative to the other three study sites, however, this site effect varied among tissue types (Fig. 2). There was a larger within-plant effect, with significant differences among plant tissue types ($F_{4,\ 36} = 223.45$; $P < 0.001$). That is, leaf samples (global mean ± SD = −29.1 ± 1.1‰) were significantly more depleted in ^{13}C than stem samples (−27.1 ± 0.6‰), while cable root (−25. 8 ± 0.5‰), pneumatophores (−25.7 ± 0.6‰) and fine roots (−26.0 ± 1.0‰) were significantly more enriched in ^{13}C relative to both aboveground tissue types (Table 1; Fig. 2). Overall, there were no significant differences in $\delta^{13}C$ among the three types of root tissue, except for in the Berowra Creek site. Here, mean $\delta^{13}C$ of fine roots was between 1.0‰ and 1.2‰ more depleted than mean values for cable roots and pneumatophores, respectively, and therefore within the range of values measured in stem tissues. Consequently, there was a significant site × tissue interaction ($F_{12,36} = 5.01$; $P < 0.001$).

4. Discussion

We measured substantial variability in $\delta^{13}C$ values - up to 6.6‰ - across 200 samples collected from a single species, in a single season, within a relatively confined spatial distribution. Within the confines of our sampling approach, we have identified that the greater source of variability in $\delta^{13}C$ for *Avicennia marina* in this region occurred at the individual plant level, where post-photosynthetic fractionation appeared to outweigh the limited differences observed among individual trees and among sites.

4.1. The role of physico-chemical parameters in site differences

The aboveground $\delta^{13}C$ values measured in this study are consistent with the broad range of values published previously for *A. marina* by multiple authors in SE Australia (Farquhar et al., 1982; Kelleway et al., 2016; Mazumder and Saintilan, 2010; Mazumder et al., 2011) and C3 mangrove species elsewhere (Farquhar et al., 1982; Fourqurean and Schrlau, 2003). Although data availability for belowground organs of mangroves is limited outside of our study region, our mean values for fresh belowground tissues were within <1.6‰ of mean values reported for both fresh and 1700y old preserved *A. marina* roots by Saintilan et al. (2013) in the

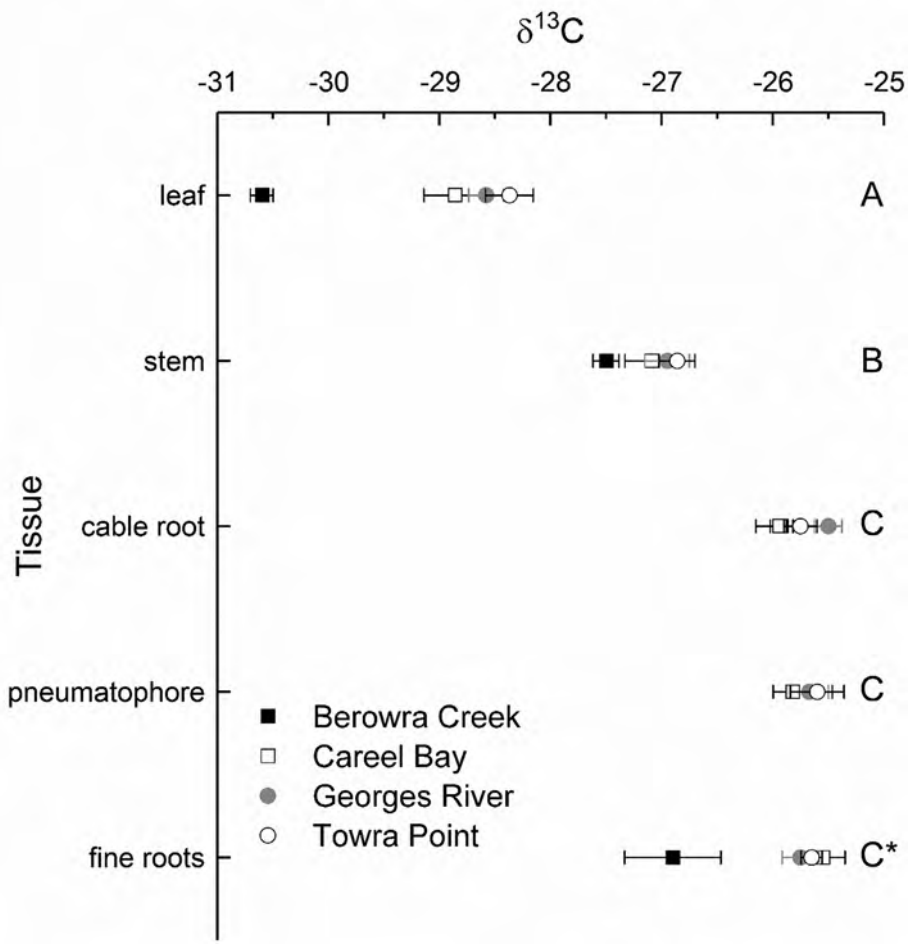


Fig. 2. Mean ± 1SE $\delta^{13}C$ values of *Avicennia marina* tissues, grouped by study site (10 trees per site). Different letters denote significant differences ($P < 0.05$) among tissue $\delta^{13}C$ values based upon repeated measures ANOVA (Bonferroni adjustment). *Inspection of estimated marginal means show that for Berowra Creek mean $\delta^{13}C$ of fine roots is not significantly different from the mean stem $\delta^{13}C$ for that site, but is significantly different from leaf and other belowground tissues (cable root, pneumatophores).

Hawkesbury estuary. We therefore suggest that the results presented in this study appear broadly representative of *A. marina* mangroves in this region, though further data are required to confirm this for belowground tissues.

Our first hypothesis stated that mangrove $\delta^{13}C$ would vary among study locations according to their physico-chemical conditions. Only one site to varied from the others in terms of $\delta^{13}C$ values, despite our experimental design incorporating two estuarine and two marine-influenced sites. The most substantial site difference was the 2‰ depletion in leaf values at the lowest salinity site (Berowra Creek; mean ± SD $\delta^{13}C = -30.6 \pm 0.3$‰), relative to the other three sites (-28.6 ± 0.7‰). This depletion in leaf $\delta^{13}C$ is consistent with results from two studies in southern China where broad trends of enrichment in $\delta^{13}C$ with increasing salinity for the mangrove species were reported for *A. marina* and *Kandelia obovata* (Huang et al., 2015; Wei et al., 2008). In the latter of the two studies, relationships between leaf $\delta^{13}C$ and stem $\delta^{18}O$ were used to infer a role of increased water use efficiency by mangroves under decreasing freshwater availability (Huang et al., 2015), though the authors did not explicitly test this phenomenon.

The sampling approach in the present study was weighted toward replication at the within-site scale. Nevertheless, the fact that only the lowest salinity site (Berowra Creek) showed a relative depletion in leaf $\delta^{13}C$ is an interesting result. It may represent a non-linear responses in leaf $\delta^{13}C$ in response to salinity, as demonstrated elsewhere with *Avicennia germinans* (Ish-Shalom-Gordon et al., 1992). Perhaps, however, other untested factors are driving the $\delta^{13}C$ variability among sites. Nutrient status of a site may be one such driver of $\delta^{13}C$ (Bowling et al., 2008; McKee et al., 2002) which, like salinity can vary across estuaries. Our preliminary data are a starting point for more targeted research on a range of potential physico-chemical drivers, and broader site replication. For salinity, this may include analyses of extreme settings (e.g. incorporating hypersaline through to oligohaline settings), characterization of within site salinity- $\delta^{13}C$ gradients, and delineating effects of porewater/groundwater versus surface water salinity.

4.2. Within plant $\delta^{13}C$ fractionation in Avicennia marina

Our second hypothesis stated that $\delta^{13}C$ varies among the different organs of an individual plant. Our analysis highlights a three-way differentiation in *A. marina* tissues, whereby there were significant depletions in the order leaf > stem > roots. The enrichment in $\delta^{13}C$ in non-leaf tissues relative to leaves of *A. marina* observed in our study was greater than the mean fractionation reported among (mostly terrestrial) plant taxa in the literature. For example, Badeck et al. (2005) reviewed 78 records where leaf and root $\delta^{13}C$ were reported for C3 plants and found a mean difference of 1.08‰ (ranging from depletion of 0.43‰ to enrichment of up to 3.5‰ enrichment). Across our four study sites, we report mean root

Table 1
Mean, minimum and maximum $\delta^{13}C$ fractionation values of *Avicennia marina* plant tissues relative to leaf $\delta^{13}C$.

Site	Within-plant $\delta^{13}C$ fractionation (‰)			
	leaf - stem	leaf - cable root	leaf - pneumatophore	leaf - fine root
Berowra Creek				
mean	3.1	4.7	4.9	3.7
min	2.4	3.9	3.7	1.1
max	3.8	5.2	5.8	5.7
Careel Bay				
mean	1.8	2.9	3.0	3.3
min	−0.4	1.5	1.2	1.2
max	4.9	4.1	4.5	4.3
Georges River				
mean	1.6	3.1	2.9	2.8
min	0.3	2.1	1.6	2.2
max	3.1	3.7	4.1	4.5
Towra Point				
mean	1.5	2.6	2.8	2.7
min	0.6	1.7	1.9	1.9
max	2.1	4.0	3.5	3.6
All sites				
mean	**2.0**	**3.3**	**3.4**	**3.1**
min	**−0.4**	**1.5**	**1.2**	**1.1**
max	**4.9**	**5.2**	**5.8**	**5.7**

– leaf $\delta^{13}C$ enrichments for *A. marina* of 3.3, 3.4 and 3.14‰ for cable, pneumatophore and fine roots, respectively, with within-tree maxima as high as 5.8‰ (Table 1). The enrichment in $\delta^{13}C$ of stems relative to nearby leaves was not as large as for root tissues, though mean enrichment averaged 2.0‰ across all trees studied, which is marginally higher than the average leaf-stem discrimination of 1.91‰ reported from measurement of 116 terrestrial plants Badeck et al. (2005).

A high degree of similarity in the direction and magnitude of within-plant $\delta^{13}C$ fractionation existed among the four study locations. One exception was $\delta^{13}C$ values of tissues collected from Berowra Creek. At this site, there was variability in fine root $\delta^{13}C$ with three of the ten samples having relatively depleted values between 27.5 and 29.7‰, therefore overlapping with stem tissue values. Most fine root samples at this site were more enriched, however, and fell within or near the range of values observed for fine roots at other sites. The cause of this variability in fine root samples at Berowra Creek is not easily explained, but could be related to spatial variability in fungal distributions (Adame et al., 2012; Alderson et al., 2013), or simply sample contamination (such as the unintended inclusion of dead fine roots, detritus or soil particles in the sample).

Notwithstanding the exceptions discussed above, our results show that within-plant fractionation appears to be the largest source of variability in *A. marina* $\delta^{13}C$ at the regional scale. At present, we have little information on what physiological (or other) processes might be driving within-plant differences in mangrove $\delta^{13}C$. It has been demonstrated for terrestrial plants that the molecular composition of a tissue may play a role, with lipids and lignin generally more depleted in $\delta^{13}C$ relative to bulk leaves, while sucrose and starch are isotopically enriched (Bowling et al., 2008). Terrestrial studies have also identified discrimination of ^{12}C relative to ^{13}C during transport of assimilates from leaves to other tissues and/or variation in the effect of respiratory processes on $\delta^{13}C$ in different plant organs (Badeck et al., 2005; Cernusak et al., 2013). As mangroves are semi-aquatic plants, assimilation of some dissolved inorganic carbon in non-leaf tissues might also be a cause of isotopic differences among tissues (as is the case for aquatic plants, including seagrass tissues). In this instance the diffusion of HCO_3^-/CO_2 through the plant water interface is a key factor controlling plant $\delta^{13}C$ values (Osmond et al., 1981). The accumulation of carbonate salts, which are enriched in ^{13}C relative to C3 and C4 plants (Hayes et al., 1999), might also explain enriched values of in longer-lived (i.e. woody) tissues, though would not explain the similarities between woody roots (low turnover) and fine roots (high turnover). We hypothesize that a combination of these plant physiological and marine-interface processes may be responsible for the large within-plant fractionation we report here for *A. marina*, relative to terrestrial studies.

4.3. Implications of results

Our results – if corroborated by findings in other geographic settings – will have implications for studies which utilize stable isotope methods to investigate estuarine carbon cycling, including research into blue carbon dynamics (e.g. carbon sequestration processes) and trophic structure (e.g. fisheries productivity). The consistent and large magnitude of ^{13}C fractionation between leaf and woody stem (2‰) and mostly consistent fractionation from leaf to root tissues (>3‰) means that it may be possible to partition the carbon sequestered within mangrove sediments to leaf litter versus woody debris and belowground (root production) sources. Similarly, the contribution of root carbon to estuarine food webs (e.g. through consumption by burrowing crabs) may now also be quantified. Our results also emphasize the importance of appropriate sampling and measurement of various plant tissues in studies which attempt to trace carbon cycling in estuarine systems.

4.3.1. Implications for food web studies

Our finding that $\delta^{13}C$ varies substantially among plant tissues of the same tree has significant implications for food web studies conducted in mangroves, or incorporating mangrove tissues as a potential endmember. Historically, it has been common practice in estuarine food web studies to sample only leaf tissues (fresh and/or decomposing litter), and perhaps epiphytes as the mangrove endmembers (e.g. Bouillon et al., 2002; Mazumder and Saintilan, 2010; Rodelli et al., 1984 among many others). Variations in consumer $\delta^{13}C$ from leaf $\delta^{13}C$ have then been attributed to contributions from other non-mangrove C sources which are more enriched in ^{13}C, such as seagrass, C4 saltmarsh species and macro- and microalgae (Mazumder et al., 2011). More recently, controlled-feeding experiments have shown mangrove crabs may selectively uptake certain

mangrove leaf compounds, resulting in leaf to animal tissue fractionation in the order of 5‰(Bui and Lee, 2014; Herbon and Nordhaus, 2013), though it is not known how applicable this is to other fauna. Our findings show it is also possible that enrichments of up to 5‰ or more may reflect uptake of C from other tissues of the same mangrove plant. This consumption could be through direct grazing of live or dead plant biomass, or possibly through detrital pathways, though the latter may be subject to diagenesis-related fractionation. One possibility that has not been well explored is whether burrowing fauna may graze on belowground plant tissues (especially fine roots which have a lower C:N value than the woody tissues (data not shown)). Based on our findings, such a phenomenon could (at least partly) explain the more ^{13}C enriched isotopic signature of many mangrove invertebrates relative to mangrove leaves (Bouillon et al., 2002; Mazumder and Saintilan, 2010).

4.3.2. Implications for blue carbon studies

Before coastal wetland conservation and restoration can be funded through carbon offset trading schemes (i.e. blue carbon), better information is required about the sources and fate of organic matter accumulating in mangrove and saltmarsh. Whilst stable isotope (C, N) methods have been used in these (and other) ecosystems to understand the movement of above-ground sources of organic matter through trophic pathways, little is currently known of the isotopic relationships between above and below ground tissues of coastal vegetation. An important implication is that the indiscriminate use of $\delta^{13}C$ of above-ground plant tissues (either through field sampling or literature values) to interpret sources of blue carbon accumulating below-ground may be invalid. Saintilan et al. (2013) previously identified that multiple studies in coastal wetlands have interpreted enriched $\delta^{13}C$ values in mangrove soil cores as either contributions from C4 plants or historic downcore shifts in vegetation type. The data we present in this paper suggests that such enrichment relative to C3 leaves may also be explained, at least partly, by within-plant fractionation.

There is a growing understanding of the magnitude of dissolved inorganic carbon (DIC) fluxes via groundwater and tidal pumping from mangrove forests (Alongi, 2014; Maher et al., 2017). Mangrove roots may be significant contributors to this flux, including through production of root exudates and the remineralisation of old mangrove root tissue. Our results highlight the importance of incorporating appropriate root tissue endmembers as $\delta^{13}C$ signatures are incorporated in studies of the quantity, source and/or transformations of this exported carbon. Although past studies have demonstrated enrichments in bulk soil $\delta^{13}C$ over time (or depth) in terrestrial soils associated with the processing/transformation carbon inputs (Rumpel and Kögel-Knabner, 2011), this has not been well quantified for mangrove soils (whose biochemistry may offer a higher level of protection), highlighting the need for further work to untangle the temporal drivers of $\delta^{13}C$ variation in in these systems.

If it can be demonstrated that immaterial or at least quantifiable levels of diagenesis-related fractionation take place within mangrove substrates, then it may be possible to estimate the relative contributions of leaf versus woody stem versus root C to soil C storage. For example, the consistent and large size of fractionation (>3‰) between leaf and (mostly consistent) fractionation in root tissues means that it may be possible to quantitatively partition the carbon sequestered within mangrove sediments to aboveground (leaf litter and woody debris) and belowground (root production) sources with the aid of mixing models. To achieve this, however, better understanding of the role of diagenesis on δ13C values of both aboveground and belowground mangrove tissues and bulk soil, plus appropriate endmember sampling will be required.

Acknowledgements

The authors thank three anonymous reviewers for their insightful comments which improved the manuscript. Ruth Mariel Bajo (Australian Catholic University) assisted with sample preparation for isotopic analysis. Barbora Neklapilova and Jennifer Vanholst (ANSTO) performed isotope analyses. This research was funded by the Australian Institute of Nuclear Science and Engineering (AINSE) award number ALNGRA 15534.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.ecss.2018.03.011.

References

Abrantes, K.G., Johnston, R., Connolly, R.M., Sheaves, M., 2015. Importance of mangrove carbon for aquatic food webs in wet–dry tropical estuaries. Estuaries and Coasts 38, 383–399.
Adame, M.F., Wright, S.F., Grinham, A., Lobb, K., Reymond, C.E., Lovelock, C.E., 2012. Terrestrail-marine connectivity: patterns of terrestrial soil carbon deposition in coastal sediments determined by analysis of glomalin related soil protein. Limnol. Oceanogr. 57, 1492.
Alderson, B., Mazumder, D., Saintilan, N., Zimmerman, K., Mulry, P., 2013. Application of isotope mixing models to discriminate dietary sources over small-scale patches in saltmarsh. MEPS 487, 113–122.
Alongi, D.M., 2014. Carbon cycling and storage in mangrove forests. Annu. Rev. Mar. Sci. 6, 195–219.
Alongi, D.M., Boto, K.G., Tirendi, F., 1989. Effect of exported mangrove litter on bacterial productivity and dissolved organic carbon fluxes in adjacent tropical nearshore sediments. Marine ecology progress series. Oldendorf 56, 133–144.
Atwood, T.B., Connolly, R.M., Almahasheer, H., Carnell, P.E., Duarte, C.M., Ewers Lewis, C.J., Irigoien, X., Kelleway, J.J., Lavery, P.S., Macreadie, P.I., Serrano, O., Sanders, C.J., Santos, I., Steven, A.D.L., Lovelock, C.E., 2017. Global patterns in mangrove soil carbon stocks and losses. Nat. Clim. Change 7, 523–528.
Badeck, F.W., Tcherkez, G., Nogues, S., Piel, C., Ghashghaie, J., 2005. Post-photosynthetic fractionation of stable carbon isotopes between plant organs—a widespread phenomenon. Rapid Commun. Mass Spectrom. 19, 1381–1391.
Beer, S., 1989. Photosynthesis and photorespiration of marine angiosperms. Aquat. Bot. 34, 153–166.
Bouillon, S., Connolly, R., Gillikin, D., 2011. Use of stable isotopes to understand food webs and ecosystem functioning in estuaries. In: Wolanski, E., McLusky, D.S. (Eds.), Treatise on Estuarine and Coastal Science. Academic Press, Waltham, pp. 143–173.
Bouillon, S., Raman, A.V., Dauby, P., Dehairs, F., 2002. Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). Estuarine. Coastal and Shelf Science 54, 901–913.
Bowling, D.R., Pataki, D.E., Randerson, J.T., 2008. Carbon isotopes in terrestrial ecosystem pools and CO2 fluxes. New Phytol. 178, 24–40.
Bui, T.H., Lee, S.Y., 2014. Does 'you are what you eat' apply to mangrove grapsid crabs? PLoS One 9, e89074.
Cernusak, L.A., Ubierna, N., Winter, K., Holtum, J.A., Marshall, J.D., Farquhar, G.D., 2013. Environmental and physiological determinants of carbon isotope discrimination in terrestrial plants. New Phytol. 200, 950–965.
Clough, B., Sim, R., 1989. Changes in gas exchange characteristics and water use efficiency of mangroves in response to salinity and vapour pressure deficit. Oecologia 79, 38–44.
Diefendorf, A.F., Mueller, K.E., Wing, S.L., Koch, P.L., Freeman, K.H., 2010. Global patterns in leaf 13C discrimination and implications for studies of past and future climate. Proc. Natl. Acad. Sci. Unit. States Am. 107, 5738–5743.
Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nat. Geosci. 4, 293–297.
Farquhar, G., Ball, M., Von Caemmerer, S., Roksandic, Z., 1982. Effect of salinity and humidity on δ13C value of halophytes—evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO2 under different environmental conditions. Oecologia 52, 121–124.
Farquhar, G., Richards, R., 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Funct. Plant Biol. 11, 539–552.
Fourqurean, J.W., Schrlau, J.E., 2003. Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay. USA. Chem. Ecol. 19, 373–390.
France, R., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar. Ecol. Prog. Ser. 124, 307–312.

Fry, B., Ewel, K.C., 2003. Using stable isotopes in mangrove fisheries research—a review and outlook. Isotopes Environ. Health Stud. 39, 191–196.
Geoscience Australia, 2015. Australian Online Coastal Information – Ozcoasts. www.ozcoasts.gov.au.
Gonneea, M.E., Paytan, A., Herrera-Silveira, J.A., 2004. Tracing organic matter sources and carbon burial in mangrove sediments over the past 160 years. Estuarine. Coastal Shelf Sci. 61, 211–227.
Guest, M.A., Connolly, R.M., 2004. Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. Aquat. Ecol. 38, 599–609.
Guest, M.A., Connolly, R.M., Loneragan, N.R., 2004. Carbon movement and assimilation by invertebrates in estuarine habitats at a scale of metres. Mar. Ecol. Prog. Ser. 278, 27–34.
Guy, R.D., Reid, D.M., Krouse, H.R., 1980. Shifts in carbon isotope ratios of two C3 halophytes under natural and artificial conditions. Oecologia 44, 241–247.
Hayes, J.M., Strauss, H., Kaufman, A.J., 1999. The abundance of 13C in marine organic matter and isotopic fractionation in the global biogeochemical cycle of carbon during the past 800 Ma. Chem. Geol. 161, 103–125.
Hemminga, M., Slim, F., Kazungu, J., Ganssen, G., Nieuwenhuize, J., Kruyt, N., 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). Mar. Ecol. Prog. Ser. 291–301.
Herbon, C.M., Nordhaus, I., 2013. Experimental determination of stable carbon and nitrogen isotope fractionation between mangrove leaves and crabs. Mar. Ecol. Prog. Ser. 490, 91–105.
Hornsby Shire Council, 2015. Water Quality Monitoring Program: 2015 Annual Report. Hornsby Shire Council, Sydney, NSW, p. 64 plus appendices.
Huang, M., Li, Q., Le, T., Tan, F., 2015. Foliar carbon isotope discrimination and water sources of mangrove forests along natural soil salinity gradients and implications for their distribution pattern. Nat. Environ. Pollut. Technol. 14, 957.
Ish-Shalom-Gordon, N., Lin, G., Sternberg, L.d.S.L., 1992. Isotopic fractionation during cellulose synthesis in two mangrove species: salinity effects. Phytochemistry 31, 2623–2626.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Baldock, J.A., Ralph, P.J., 2017. Sediment and carbon deposition vary among vegetation assemblages in a coastal salt marsh. Biogeosciences 14, 3763–3779.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Ralph, P.J., 2016. Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes. Ecosystems 19, 865–880.
Kennedy, H., Beggins, J., Duarte, C.M., Fourqurean, J.W., Holmer, M., Marbà, N., Middelburg, J.J., 2010. Seagrass sediments as a global carbon sink: isotopic constraints. Global Biogeochem. Cycles 24, 1–8.
Loneragan, N.R., Bunn, S.E., Kellaway, D.M., 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Mar. Biol. 130, 289–300.
Lovelock, C.E., 2008. Soil respiration and belowground carbon allocation in mangrove forests. Ecosystems 11, 342–354.
Maher, D.T., Santos, I.R., Schulz, K.G., Call, M., Jacobsen, G.E., Sanders, C.J., 2017. Blue carbon oxidation revealed by radiogenic and stable isotopes in a mangrove system. Geophys. Res. Lett. 44 (10), 4889–4896.
Mauchly, J.W., 1940. Significance test for sphericity of a normal n-variate distribution. Ann. Math. Stat. 11, 204–209.
Mazumder, D., Saintilan, N., 2010. Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. Wetlands 30, 375–380.
Mazumder, D., Saintilan, N., Williams, R.J., Szymczak, R., 2011. Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. Mar. Freshw. Res. 62, 11–19.
McKee, K.L., Feller, I.C., Popp, M., Wanek, W., 2002. Mangrove isotopic ($\delta^{15}N$ and $\delta^{13}C$) fractionation across a nitrogen vs. phosphorus limitation gradient. Ecology 83, 1065–1075.
McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Front. Ecol. Environ. 9, 552–560.
Meng, X., Xia, P., Li, Z., Meng, D., 2016. Mangrove degradation and response to anthropogenic disturbance in the Maowei Sea (SW China) since 1926 AD: mangrove-derived OM and pollen. Org. Geochem. 98, 166–175.
Nagelkerken, I., Blaber, S., Bouillon, S., Green, P., Haywood, M., Kirton, L., Meynecke, J.-O., Pawlik, J., Penrose, H., Sasekumar, A., 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. Aquat. Bot. 89, 155–185.
Odum, W.E., Heald, E.J., 1975. The detritus-based food web of an estuarine mangrove community. In: Cronin, L. (Ed.), Estuarine Research: Chemistry, Biology, and the Estuarine System. Elsevier, p. 265.
Osmond, C., Valaane, N., Haslam, S., Uotila, P., Roksandic, Z., 1981. Comparisons of δ 13 C values in leaves of aquatic macrophytes from different habitats in Britain and Finland; some implications for photosynthetic processes in aquatic plants. Oecologia 50, 117–124.
Parida, A.K., Jha, B., 2010. Salt tolerance mechanisms in mangroves: a review. Trees 24, 199–217.
Pittwater Council, 1998. Careel Bay Wetlands Plan of Management. Pittwater Council, Sydney, NSW, p. 74.
Rodelli, M., Gearing, J., Gearing, P., Marshall, N., Sasekumar, A., 1984. Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. Oecologia 61, 326–333.
Rumpel, C., Kögel-Knabner, I., 2011. Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. Plant Soil 338, 143–158.
Saintilan, N., 1997. Above-and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. Mar. Freshw. Res. 48, 147–152.
Saintilan, N., Mazumder, D., 2010. Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. Mar. Freshw. Res. 61, 615–620.
Saintilan, N., Rogers, K., Mazumder, D., Woodroffe, C., 2013. Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuarine. Coastal Shelf Sci. 128, 84–92.
Smith, B.N., Epstein, S., 1971. Two categories of 13C/12C ratios for higher plants. Plant Physiol. 47, 380–384.
Tue, N.T., Ngoc, N.T., Quy, T.D., Hamaoka, H., Nhuan, M.T., Omori, K., 2012. A cross-system analysis of sedimentary organic carbon in the mangrove ecosystems of Xuan Thuy National Park, Vietnam. J. Sea Res. 67, 69–76.
Wei, L., Yan, C., Ye, B., Guo, X., 2008. Effects of salinity on leaf δ13C in three dominant mangrove species along salinity gradients in an estuarine wetland, southeast China. J. Coast Res. 267–272.
Weiss, C., Weiss, J., Boy, J., Iskandar, I., Mikutta, R., Guggenberger, G., 2016. Soil organic carbon stocks in estuarine and marine mangrove ecosystems are driven by nutrient colimitation of P and N. Ecol. Evol. 6, 5043–5056.
Xia, P., Meng, X., Li, Z., Feng, A., Yin, P., Zhang, Y., 2015. Mangrove development and its response to environmental change in Yingluo Bay (SW China) during the last 150years: stable carbon isotopes and mangrove pollen. Org. Geochem. 85, 32–41.
Zieman, J., Macko, S., Mills, A., 1984. Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. Bull. Mar. Sci. 35, 380–392.

Wetlands (2019) 39:1145–1154
https://doi.org/10.1007/s13157-018-1016-7

WETLANDS AND CLIMATE CHANGE

Climate Change Impacts on the Coastal Wetlands of Australia

N. Saintilan[1] · K. Rogers[2] · J. J. Kelleway[1] · E. Ens[1] · D. R. Sloane[1]

Received: 30 May 2017 / Accepted: 6 February 2018 / Published online: 23 February 2018
© Society of Wetland Scientists 2018

Abstract
The Australian continent spans coastal wetland settings ranging from extensive mangrove forest and sabkha plains occupying in the tropical north, to the southern half of the continent, where high wave energy constrains wetlands within numerous barrier-fronted estuaries, drowned river valleys and coastal embayments. Only on the island of Tasmania are mangroves absent; elsewhere mangroves, *Casuarina, Melaleuca* and saltmarsh interact in ways illustrative of the effects of ongoing climate, tidal and sea-level change. Observations over several decades have suggested that recent anthropogenic climate change may already be impacting Australian coastal wetlands in important ways. A period of accelerating sea-level rise has been associated with saline intrusion, mangrove encroachment and *Melaleuca* dieback in the tropical north, punctuated by widespread mangrove mortality in drought periods. The consistent trend of mangrove encroachment and replacement of saltmarsh in the south, is associated with an "accretion deficit" in saltmarsh during contemporary sea-level rise. We review the ecological and cultural implications of these changes, including impacts on habitat provision for migratory birds, fisheries values, carbon sequestration and Indigenous cultural values. Current legislative and policy protections may not be sufficient to meet the increasingly dynamic impacts of climate change in altering wetland boundaries, composition and function.

Keywords Mangrove · Saltmarsh · Melaleuca · Dieback · Salinisation · Australia

Extent and Composition of Australian Intertidal Wetlands

At the taxonomic levels of family and genus, Australian mangroves, saltmarshes, *Casuarina* spp. and the "paperbark" *Melaleuca* spp. have strong affinities with species on other continents. Australian mangroves belong to the broader biogeographic association of Old World mangroves, finding greatest diversity immediately to the north of the continent in Indonesia. Few species are endemic to Australia and there is a notable decrease in mangrove floristic diversity away from the tropics on both eastern and western Australian coastlines. Aridity is an important constraint on mangrove diversity and extent on the west coast (Duke et al. 1998). By contrast, saltmarsh floristic affinities are primarily Gondwanan, with strong similarities at family level with the saltmarsh flora of New Zealand, South Africa and temperate South America (Adam 1990; Boon et al. 2011). Saltmarsh diversity decreases towards the tropics, and the northern and southern halves of the continent, separated by 23 degrees latitude, form distinctive biogeographic provinces (Saintilan 2009). Often a feature of the landward intertidal zone, some coastal *Melaleuca* and *Casuarina* species are found across Australia and Malesia (e.g. *Melaleuca cajuputi* and *Casuarina equisetifolia*) (ABARES 2013) as well as some in New Caledonia, Papua New Guinea and Lord Howe Island (Boland et al. 2006; Brophy et al. 2013).

Intertidal areas are far larger in the tropical north due to high tidal ranges and the presence of large rivers depositing deltas and building floodplains into shallow continental shelves. *Melaleuca* or *Casuarina*-marsh-mangrove dynamics characterise the intertidal-supratidal zone which also commonly encounters hypersaline conditions during the dry season. Grassy flats, sedges and cyanobacterial "sabkha" flats are more commonly encountered than saltmarshes (Cowie et al. 2000). In the southern biogeographic provinces, coastlines are subject to high wave energy with intertidal environments

✉ N. Saintilan
neil.saintilan@mq.edu.au

[1] Department of Environmental Sciences, Macquarie University, Sydney, Australia

[2] School of Earth and Environmental Sciences, University of Wollongong, Wollongong, Australia

constrained within estuaries behind sand barriers. The intertidal gradient here is largely characterised by saltmarsh-mangrove complexes with a transition from saltmarsh to *Melaleuca* or *Casuarina* near the supratidal zone (Rogers et al. 2017). Mean minimum daily temperature explains nearly 80% of variation in diversity of saltmarsh between the 36 coastal bioregions, with the smaller pockets of saltmarshes in southern estuaries supporting most of the 140 species recorded for the continent (Saintilan 2009; Boon et al. 2011).

This unusual sympatric distribution of mangrove, saltmarsh and *Melaleuca* or *Casuarina* across the continent, and their contrasting climatic and hydrological requirements, makes them an interesting example of climate change impacts. The contrasting latitudinal clines in diversity strongly related to temperature thresholds suggests that warming may affect species distribution and competitive advantage. For much of the continent, mangroves, saltmarsh/sabkha and *Melaleuca/Casuarina* form shore-normal zonation, with *Melaleuca/Casuarina* confined to areas above the mean high water and mangrove largely confined to areas below mean high water to approximate mean sea-level, diurnally inundated, in all but exceptionally wet climates (Bucher and Saenger 1994), though a landward mangrove fringe is common in tropical settings. The influence of sea-level rise on coastal wetlands, and the interaction of mangrove, saltmarsh and *Melaleuca* in particular, are best observed in wide coastal plains of gentle gradient, where vegetation communities are tightly controlled by tidal hydroperiod.

In this review, after a consideration of ecosystem services provided by Australian coastal wetlands, we present evidence that coastal wetlands in Australia are already showing the impacts of human-induced climate change. The distribution of mangrove, saltmarsh and *Melaleuca/Casuarina* along the Australian coastline is changing rapidly, often in ways contrary to longer-term trends through the Holocene and consistent with changes in atmospheric CO_2, temperature and sea-level. These changes have implications for ecosystem services. For components of the natural environment, changes to the structure of coastal wetland communities have implications for available habitat that may already compromised by historic reclamation. The cultural dimensions of these changes are also profound, and we review recent work exploring Indigenous perspectives on the impacts of recent landscape change on biocultural values.

Ecosystem Services Associated with Australian Coastal Wetlands

Coastal wetlands perform a number of important ecosystem services in Australia, many in common with wetlands across the globe. These include shoreline protection from waves, and storms, nutrient and carbon cycling and storage, habitat provision for invertebrates, nekton, shorebirds and mammals, and cultural and recreational uses (Kelleway et al. 2017a). Here, we focus on the ecosystem services which are most important in Australia.

Migratory shorebirds utilise southern hemisphere summer feeding habitat in Australia prior to northern migration in the East-Asian Australasian flyway (Zharikov and Milton 2009; Spencer et al. 2009). Coastal wetlands form important roosting habitat for several species, and coastal saltmarsh in particular provides high tide and night-time roosting and secondary feeding habitat. Species preferentially selecting coastal saltmarsh for this purpose include the Sharp-Tailed Sandpiper (*Calidris acuminata*), the Eastern Curlew (*Numenius madagascariensis*), the Pacific Golden Plover (*Pluvialis fulva*) and the Red-necked Stint (*Calidris ruficollis*) (Spencer et al. 2009). Saltmarsh is an important feeding and breeding habitat for rare endemic species including the White Fronted Chat (*Epthianura albifrons*) and the critically endangered orange-bellied parrot (*Neophema chrysogaster*), which is confined to a small number of saltmarshes in Victoria (Mondon et al. 2009). Insectivorous microbats have also been observed feeding preferentially in saltmarshes (Gonsalves et al. 2013).

Fish, including several species of commercial importance, utilise mangrove and saltmarsh environments during high tides. During spring tide periods when the saltmarsh is inundated, fish actively feed on crab larvae released in high densities into the shallow inundating tidal water. These larvae form a particularly important component of the diet of the Ambassids (*Ambassis jacksoniensis*), the most numerous fish in the estuary. Stable isotope analysis has demonstrated a bottom-up trophic cascade from the saltmarsh crabs, through zooplanktivorous fishes, to commercially important species (Mazumder et al. 2011; Saintilan and Mazumder 2017). The importance of coastal mangrove and saltmarsh has also been highlighted in analysis of fisheries landing data, with the relative proportions of mangrove, saltmarsh and seagrass predicting the composition of fishing yields in multi-estuary comparisons (Saintilan 2004; Meynecke et al. 2008). For much of the tropical and subtropical north prawn harvest is associated with mangrove area (Loneragan et al. 1997; Vance et al. 2002).

Australia has the third largest extent of mangroves in the world, covering 11,500 km^2, an estimated 13,825 km^2 of saltmarsh/saltpan and 63,020 km^2 of *Melaleuca* (Saintilan 2009; ABARES 2013). This represents an important store of "blue carbon" in contemporary and relict wetland soils. Estimates of coastal wetland carbon stores are heavily weighted towards more heavily populated areas, such as temperate southeast Australia where mangroves typically store 200–300 t of carbon belowground per hectare (Saintilan et al. 2013; Kelleway et al. 2016b); high by terrestrial forest standards but lower than equatorial mangrove systems (Donato

et al. 2011). Further research is required to characterise and explain global variation in below-ground carbon stores in mangrove. Belowground carbon stocks in southern Australian saltmarshes are typically lower than adjacent mangroves, though stocks vary among geomorphic settings (Kelleway et al. 2016a; Macreadie et al. 2017). Carbon stores may be high beneath saltpan (sabkha) coastal plains in the tropical north, given the widespread occurrence of mangrove facies representing a prior "big swamp" phase in the early to mid-Holocene (Woodroffe et al. 1985). There is currently a paucity of information on coastal *Melaleuca* and *Casuarina* carbon stores. One published study on the range of carbon stored by all Australian *Melaleuca*s lumped together (coastal and inland) suggested ecosystems stocks between 158 Mg C ha^{-1} and 286 Mg C ha^{-1} (Tran et al. 2013), though this was limited to the upper 30 cm of the soil profile and excludes belowground biomass. Subsequent work in Queensland *Melaleuca* woodland, open forest and closed forest has suggested that permanently inundated *Melaleuca* ecosystems from this region store 381 Mg C ha^{-1} on average, compared with non-inundated *Melaleuca* areas which store 278 Mg C ha^{-1} on average (Tran and Dargusch 2016).

Trends in Extent

Palaeo-stratigraphic work in both tropical and temperate SE Australia has suggested more extensive mangroves stands across the intertidal zone earlier in the Holocene than is evident today. During the latter phases of the postglacial marine transgression, mangroves colonised the flooded valleys of the Fitzroy, Ord, Daly and Alligator Rivers in tropical northern Australia (Thom et al. 1975; Woodroffe et al. 1985; Clark and Guppy 1988). Progressive infilling following high-stand led to the retreat of mangroves to channel fringes, and the development of expansive hypersaline flats and freshwater wetlands (Clark and Guppy 1988). At a smaller scale, mangrove peats are commonly encountered beneath saltmarsh in the estuaries of SE Australia, dating on the Hawkesbury River to 1200–1700 y BP, in Jervis Bay to 1300–1900 y BP (Saintilan and Hashimoto 1999; Saintilan and Wilton 2001) and Port Stephens to 750–1800 y BP (Kelleway et al. 2017b).

The upslope and head-ward expansion of mangroves and decline in *Melaleuca* fringes observed in recent decades in these same environments is therefore an interesting reversal of longer-term trends. Comparisons of earliest aerial photographic records with contemporary distributions document a consistent trend of saltmarsh being progressively replaced by mangrove from subtropical Queensland to the southernmost estuaries of the continent in Victoria and South Australia (Saintilan and Williams 1999; Rogers et al. 2005; Jupiter et al. 2007). Mangrove encroachment associated with an extension of tidal channel networks over successive decades has been observed in the coastal plains of Kakadu, the Gulf of Carpentaria, often co-incident with extensive dieback of floodplain fringe *Melaleuca* forest (Winn et al. 2006; Knighton et al. 1991; Mulrennan and Woodroffe 1998). Through both historical aerial photography analyses (Williams 1984; Bowman et al. 2011) and recent field based studies (Ens et al. 2017; Sloane 2017; Sloane et al., in review) the retreat of *Melaleuca* forests has largely been attributed to combinations of saltwater intrusion and the effects of feral buffalo. Williams (1984) found a 38% decline in *Melaleuca* forest from 1950 to 1975 in the Magela catchment while Bowman et al. (2011) found an overall 5% decline in Kakadu National Park from 1964 to 2004 noting spatial variability and greater declines at *Melaleuca* edges, on low-lying sites and where past buffalo activity was highest.

Conversely, mangroves expanded their range in the Kakadu region by 17% (Williamson et al. 2011). Similarly, across the Gulf of Carpentaria concurrent seaward and landward mangrove encroachment was observed for the period 1987–2014 (Asbridge et al. 2016) during a period of increased tidal inundation, higher freshwater flows and seasonal inundation of rivers during the monsoonal period. It is these same landward mangroves, primarily *Avicennia marina*, that were subject to widespread mortality during the 2015–16 summer, when lower than average rainfall coincided with regional declines in sea-level (Fig. 1). Indigenous Traditional Owners in north east Arnhem Land also suggested that feral ungulates (buffalo and pig), rising sea levels, king tides and cyclones are likely to becontributing factors of observed intertidal *Melaleuca* dieback (Fig. 1) (Sloane 2017; Sloane et al., in review).

Climate Change Impacts

Sea-Level and Rainfall

Climate and sea-level in Australia are subject to inter-annual and inter-decadal oscillations in oceanic and atmospheric circulation operating at hemispheric scales. Phases of the El Niño Southern Oscillation (Allen 1988; Verdon et al. 2004) and the Indian Ocean Dipole (Ummenhofer et al. 2009) exert strong influences on the timing and duration of periods of drought and flood across the continent. This modularity in prevailing conditions of atmospheric pressure and rainfall exerts a strong influence on inter-annual trends in sea-level. While the trajectory of sea-level rise across the continent has been rising at a rate comparable to global eustatic trends (White et al. 2014), there is a notable regional variability in the amplitude of sea-level trends and oscillations at annual and decadal time-scales. For example, the El Niño droughts of 2000–2008 dampened the rate of sea-level rise across the southern parts of the

Fig. 1 Dieback of *Melaleuca* (top panel) and mangrove (lower panel) in north east Arnhem Land, Northern Territory, Australia. Photo: Emilie Ens, May 2016

continent, but not in the tropical north where higher rainfall conditions prevailed.

Our understanding of the response of coastal wetlands to sea-level rise has been improved through use of the Surface Elevation Table-Marker Horizon technique (SET-MH). The elevation of coastal wetland surfaces responds dynamically to sea-level change, being influenced by the rate of sediment delivery and settlement, autotrophic plant productivity, and soil water volume. The SET-MH combines an elevation benchmark rod from which repeated measures of marsh surface elevation are taken, with a feldspar marker horizon recording surface sediment accretion. Together, the technique allows an assessment of the vertical response of a wetland to sea-level rise and the extent to which this response is a result of surface sediment accretion (Cahoon et al. 2002; Webb et al. 2013). The rapidly expanding network of sites globally has facilitated regional and international comparisons of wetland responses to sea-level rise and clarified processes controlling wetland elevation trajectory (e.g. Lovelock et al. 2015).

Within Australia several institutions have contributed to a network of SET-MH stations spanning temperate SE Australia, subtropical Queensland, and the tropical north and northwest of the continent (Fig. 2). In SE Australia, the SET-MH technique was deployed in 2000–2001 to help interpret the regional trend of mangrove encroachment into saltmarsh, and is amongst the longest-running SET networks in the world. Along some coastlines, phases of mangrove encroachment were associated with periods of higher rainfall and the freshening of the upper intertidal has been invoked as a driver of mangrove encroachment in SE Queensland (Eslami-Andargoli et al. 2009). However, as previously mentioned, rainfall and sea-level trends are tightly associated at timescales relevant to broad vegetation transitions, and are likely to have similar effects on mangrove propagule dispersal, survival and growth. The SET-MH installations in paired mangrove and saltmarsh environments have demonstrated a consistently lower rate of vertical elevation gain in saltmarsh compared to mangrove, and consistent elevation deficits in saltmarsh relative to local sea-level trends (Rogers et al. 2005, 2013, 2014a, b). Sea-level rise across the region is translating into a net competitive advantage of mangrove in saltmarsh environments regardless of rainfall trends. Patterns of encroachment into saltmarsh largely follow tidal drainage networks suggesting alterations to tidal hydro-period as an active mechanism promoting mangrove encroachment into saltmarsh.

The widespread use of the SET-MH method has also facilitated assessments of carbon sequestration associated with wetland responses to sea-level rise. The technique is conservative when used in this context, as new root growth below the feldspar horizon is not captured. Even so, estimates of below-ground carbon accumulation above feldspar horizons in mangroves in SE Australia in the range of 2–3 t per hectare per annum (Saintilan et al. 2013). Saltmarsh carbon accumulation is generally lower, especially in *Sarcocornia-Sporobolus* marshes (Kelleway et al. 2017b) though is consistently in the range of 2 t ha yr.$^{-1}$ beneath *Juncus kraussii*-dominated marshes on fluvial deltas (Saintilan et al. 2013). Sedimentary methods have also emphasised the importance of geomorphic setting, and sediment grain size in particular, in predicting carbon store and accumulation in these wetlands (Kelleway et al. 2016a; Macreadie et al. 2017).

Temperature

Mangrove species distribution and diversity finds greatest expression in the tropics, with diversity decreasing steadily towards the poles on all coastlines. At the broadest scale, minimum sea-surface temperature of 20°C corresponds to poleward limits on most continents (Duke et al. 1998), though air temperatures and the occurrence of frost may regulate distributions on some coastlines. The effect of climate change on poleward range expansion of mangroves is a topic receiving considerable attention globally (Saintilan et al. 2014; Cavanaugh et al. 2015; Gabler et al. 2017).

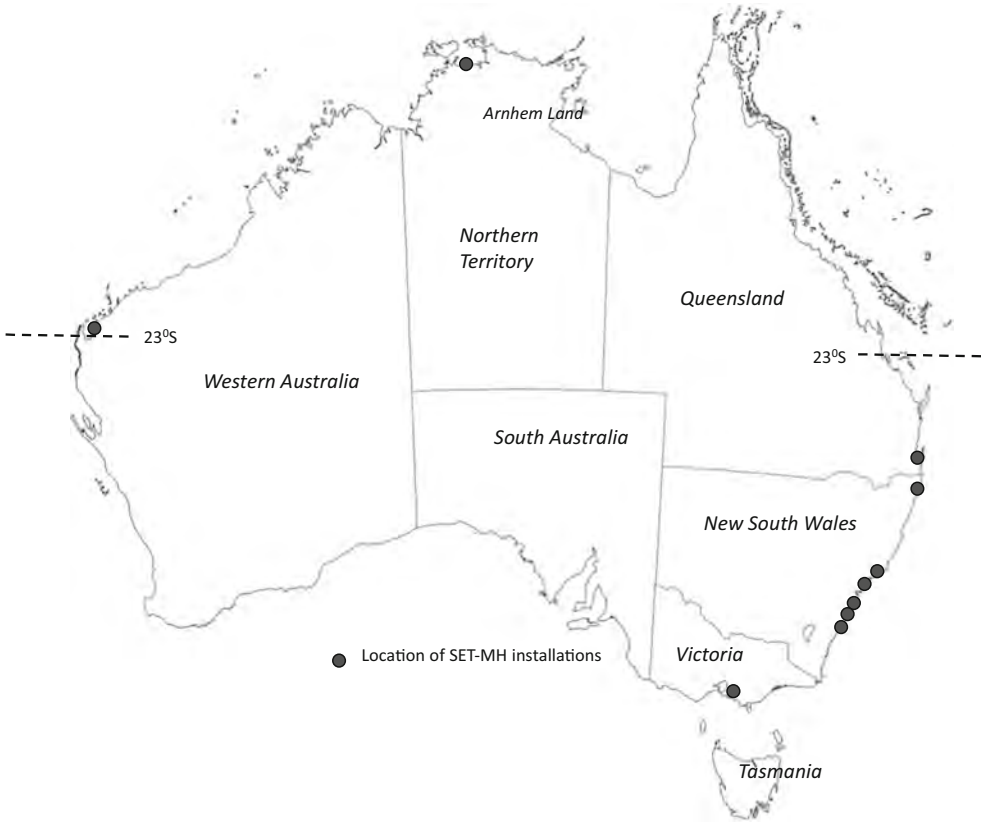


Fig. 2 Location of SET-MH installations in Australia, and the 23rd latitude separating northern and southern saltmarsh biogeographic provinces

There is little evidence in Australia for thermal tolerances playing an important role in defining the poleward limit of mangrove species. Mangroves, represented by *Avicennia marina*, are found south to Corner Inlet, Victoria (38.9°S), less than 30 km from Wilsons Promontory, the southernmost tip of the Australian continent. While mangroves are absent from Tasmania, this is thought to be due to dispersal constraints imposed by currents within Bass Strait, as *A. marina* seedlings have been observed to survive and grow in at least short-term plantings (~2 years) in locations along Tasmania's east coast (Woodroffe and Grindrod 1991). The relatively benign thermal conditions at the southern limits of mangrove growth in Australia forms a stark contrast with the poleward limits of mangrove growth in the United States. Here, northward expanding populations are periodically checked by deep frosts causing widespread mortality (Stevens et al. 2006). Populations are recovering from freezing events, the most notable being 1989 when extensive mortality of mangroves occurred in Texas, Louisiana and Florida (Armitage et al. 2015; Giri and Long 2016).

Barriers to dispersal may also be important in defining the southern limit of individual species. Of the Rhizophoraceae, *Rhizophora stylosa* has the most poleward range, forming small but expanding clusters of individuals in many east coast estuaries as far south as South-West Rocks Creek in NSW (−30.88°S). Within these estuaries, the timing of leaf emergence and senescence, and the timing of propagule development and maturation are broadly comparable to tropical populations of the species (Wilson 2009; Wilson and Saintilan 2012). This contrasts to the growth characteristics of *R. mangle* on the US Atlantic coast, where rapidly expanding populations at the leading edge of the species range exhibit "precocious reproduction", producing propagules on younger saplings than is observed within more established communities (Dangremond and Feller 2016).

These differences between controls on poleward range in North America and Australia can be understood in the context of continental-scale controls on extreme temperature fluctuation. Extreme cold conditions on the US Gulf Coast occur as a result of polar vortexes generated over the northern arctic tracking south across the North American land mass. In the southern hemisphere, the Southern Ocean provides a thermal buffer between extreme cold in Antarctica and the southern tips of the South American, New Zealand and Australian land masses. The southern limits of mangrove growth in Australia occur at higher latitudes than the northernmost mangroves in the US, in climates characterised by more frequent frost than the US Gulf coast but far less intense. Within Australia, *Avicennia marina* has evolved a higher degree of frost tolerance than has been possible for *A. germinans* or *R. mangle* in the US, where frost is less frequent but more intense (Stuart et al. 2007). *A. marina* and *Aegiceras corniculatum*, the two most poleward species in Australia, have smaller vessel diameters than *A. germinans* and *R. mangle* in the USA, with a

consequent higher tolerance of mild freezing commonly encountered in temperate Australia (Stuart et al. 2007).

Mangrove populations in the Gulf and Florida coasts of the US therefore possess a latent capacity for rapid expansion in response to temperature change. Climate models project a decrease in the frequency and intensity of frost in the coming decades, removing the barrier to mangrove expansion into contiguous saltmarsh along sheltered, subtropical coastlines. The situation is different in Australia in several important respects. Mangrove species largely occupy discrete estuaries, and while long-shore currents flow predominantly southward on the east coast, threading the needle of estuarine entrances has proven to be an impediment to rapid response to climatic warming. Instead, populations appear to be expanding within their range, infilling saltmarsh within estuaries and, in the case of Rhizophora, backfilling into estuaries that may have previously been uninhabited (Wilson and Saintilan 2012). Observations of mangrove range expansion from Australia generally support the findings of range conservatism with respect to thermal limits noted elsewhere (Quisthoudt et al. 2012).

Unlike mangrove, saltmarsh diversity in Australia increases poleward, strongly correlating with monthly minimum temperatures (Saintilan 2009). The effect of cold temperatures on saltmarsh germination deserves further study, given the possibility that warming may inhibit germination and survival of some species (Greenwood and MacFarlane 2006). On the Australian east coast, a 2-degree warming would, on the basis of current mangrove and saltmarsh distribution, lead to the loss of several species finding their northern limit in Sydney region (e.g. *Rhagodia baccata; Distichlis distichophylla, Austrastipa stipoides, Wilsonia backhausii:* Fig. 3) and the expansion of Rhizophoraceae south to occupy the shorelines of estuaries. This modelling assumes unrestricted dispersal which we have indicated is unlikely to be the case, though human agents have facilitated poleward range expansion in other settings (e.g. south to the Nahoon estuary in South Africa: Hoppe-Speer et al. 2015).

Distributional shifts in coastal *Melaleuca* and *Casuarina* have not been well studied and require further investigation. However, the biogeography of *Melaleuca* at the species level, at least in northern Australia, reflects a distinct pattern of local flooding and salinity tolerance (Cowie et al. 2000). For example, *Melaleuca acacioides,* occurs at the limit of *Melaleuca* spp. salinity tolerance in this region on the landward side of mangroves (Levitt 1981). Such is the link between *Melaleuca* and salinity, that the limits to salinity tolerance of *Melaleuca* spp. have been exploited in the Alligator Rivers Region of northern Australia, in which *Melaleuca* spp. dieback was utilised as a bioindicator of saltwater intrusion into previously predominantly freshwater wetlands (Bell et al. 2001). More recently, field-based assessment in north east Arnhem Land has correlated ~70% of *Melaleuca* dieback (across three species: *M. cajuputi, M. viridiflora* and *M. acacioides*) with soil salinity, feral pig (*Sus scrofa*) and feral buffalo (*Bubalus bubalis*) impacts; which was in strong alignment with explanations by local Aboriginal people (Sloane 2017; Sloane et al., in review).

Biophysical and Cultural Implications

The encroachment of mangrove into saltmarsh and *Melaleuca* forest has several important implications for the provision of habitat (Kelleway et al. 2017a). Species of migratory shorebirds occupying coastal saltmarsh prefer open roosting habitat, in particular shallow open pools useful for secondary foraging opportunities and thermal regulation (Spencer et al. 2009). Trees provide ambush hides for predatory birds (Dekker and Ydenberg 2004), which may be one reason Lawler (1998) noted a preference for saltmarsh habitat more than 30 m from tree-form vegetation. Mangrove encroachment therefore compromises the habitat value of saltmarsh for shorebirds (Guo et al. 2017).

Several species are known to inhabit coastal *Melaleuca* forest such as colonies of flying foxes (*Pteropus scapulatus* and *Pteropus alecto*) and the Northern Blossom Bat (*Macroglossus minimus*) (Tidemann et al. 1999; Finlayson et al. 2006); however again, more research is needed to document that habitat values of *Melaleuca* as well *Casuarina*,

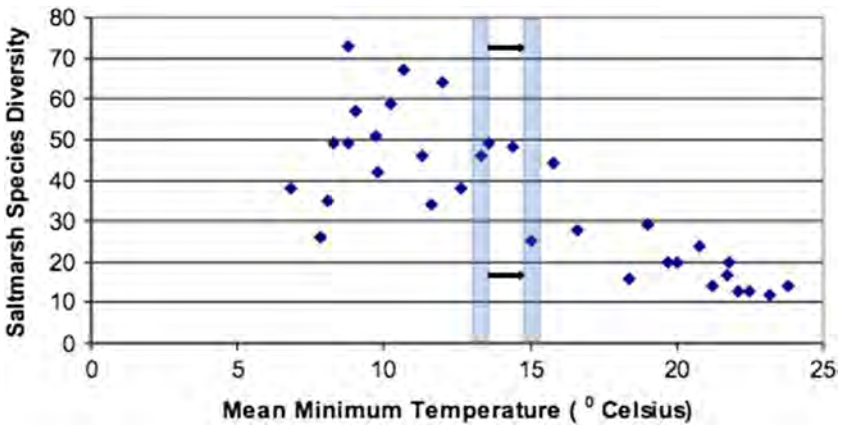


Fig. 3 Changes in the diversity of saltmarsh species with mean minimum temperate for bioregions on the Australian east coast. Blue lines represent the shift in mean minimum temperature from current to 2040 (an increase of 2 °C, averaged for winter months: Olson et al. 2016)

even in high profile locations such as the World Heritage Area Kakadu National Park (Finlayson et al. 2006). In northern Australia, the salinisation of *Melaleuca* forests is likely to have profound impacts on flora and fauna that inhabit these areas including Magpie Goose (*Anseranus semipalmata)* and the water chestnut *Eleocharis* spp. which also have great Indigenous cultural significance.

Relationships to plants and animals are important for emotional, social and physical wellbeing of Australian Indigenous people (Kingsley et al. 2010). *Melaleuca* species exemplify this relationship as they are valued by Indigenous people for a range of ethnobotanical reasons. One such important use is as bush medicine. Crushed leaves of many species can be placed in hot water and the resulting steam is inhaled to treat coughs, colds and nasal congestion. Alternatively, a wash made from the leaves and water can be applied to relieve skin irritation. Water from swellings in the trunk of some species can be utilised as a freshwater source. Bark can be used as blankets, for shelter or for carrying things. Wood of some of the larger species can be used to make canoes. Leaves of *M. acacioides* can flavour food or function as mosquito repellent when burned. Flowering of *M. viridiflora* can indicate good turtle hunting (Levitt 1981; Wrigley and Fagg 1993; Yunupiŋu et al. 1995; Winn 2001; Ens et al. 2017).

Recent research by (Sloane 2017; Sloane et al. in review) showed that Yolngu Traditional Owners of north east Arnhem land were very concerned about the loss of coastal swamps and patches of culturally significant coastal *Melaleuca*. For recent observations of decline, a Senior Traditional Owner and Senior Cultural Advisor for The Yirralka Rangers, Jimmy Wunungmurra said that people are hurting because the land (notably *Melaleuca* spp. and *Eleocharis* spp.) are being damaged by feral pigs, feral buffalo and saltwater intrusion. He had observed these feral animals creating erosion channels and trampling which facilitated intrusion of saltwater and movement of mangrove propagules further toward the landward side of the floodplain than he had observed in the past. He was wondering how to bring the land "back to life". Therefore, the potential cultural impacts of the conversion of *Melaleuca* to mangrove forest warrants further study.

The cultural and commercial implications of mangrove encroachment in saltmarshes is also not clear. The production of crab zoea also occurs in the mangrove, and so may not be compromised by mangrove encroachment (Saintilan and Mazumder 2017). Indeed, Moussalli and Connolly (1998) found that fish diversity was higher in mangrove than in saltmarsh at comparable hydroperiod in SE Queensland. There is some evidence that saltmarsh area may be important in providing habitat for the commercially important mud crab *Scylla serrata*, though predictive models suggest both mangrove and saltmarsh are important (Saintilan 2004). This latter point highlights the potential significance of habitat connectivity and diversity in meeting species habitat requirements, rather than saltmarsh or mangrove alone. Fish within the estuary utilise multiple habitats at different stages of the tidal cycle (Saintilan et al. 2007), and microbat utilisation of saltmarsh habitat may depend on the mangrove-saltmarsh boundary, against which insects are concentrated (Gonsalves et al. 2012). Bats appear to use echo-location in the open habitat to identify insects in front of the mangroves.

Given the general trend of higher carbon storage and accumulation rates in Australian mangrove relative to saltmarsh, we expect encroachment by mangrove may have a beneficial carbon sequestration outcome. To date, only one study has directly quantified this in SE Australia, showing significant increases in both aboveground biomass and belowground (roots, rhizomes and soil) carbon pools with mangrove encroachment (Kelleway et al. 2016b). Importantly, these changes were not apparent until after >30 years of encroachment, and were larger belowground, than aboveground. That is, annual increases in belowground carbon storage of up to 2.30 Mg C ha^{-1} y^{-1} were reported over the entire 70-year study sequence, compared to increases equating to 0.58 Mg C ha^{-1} y^{-1} in aboveground carbon pools (Kelleway et al. 2016b). The recent dieback of *Melaleuca* and encroachment of mangroves, especially in northern Australia, warrants further investigation.

Policy Directions and Conclusions

By global standards Australian coastal wetlands enjoy strong legislative protection in most states and territories (Rogers et al. 2016). At a National level, the Environment Protection and Biodiversity Conservation Act 1999 affords protection of Ramsar sites (19 of which contain mangrove and/or saltmarsh in Australia), and the coastal salt marsh ecological community south of 23 degrees latitude. Most Australian states protect coastal wetland vegetation under legislation targeting fish habitat (e.g. Fisheries Management Act NSW 1994; Fisheries Act Qld 1994; Fisheries Management Act South Australia 2007; Fisheries Resource Management Act Western Australia 1994), or special area protection (State Environmental Planning Policy (SEPP) 14 NSW, Marine Estate Management Act NSW 1974; Marine Parks Act Qld 2004; Flora and Fauna Guarantee Act Vic 1988; Nature Conservation Act (Tas.) 2002 etc.). The cultural significance of the intertidal zone is also starting to be recognised through Native Title legislation and Australia's Indigenous Protected Area system, although much more work needs to be done to fully acknowledge Indigenous rights and values in these ecosystems. These legislative and policy initiatives were implemented to arrest the widespread clearance and reclamation of coastal wetlands primarily in eastern states in the twentieth Century. Flood control works on large east coast rivers in NSW and Queensland led to substantial losses of coastal

wetlands in the 1950's and 1960's. Though the extent of historic losses is difficult to quantify, as many as 4200 structures have been identified impeding tidal flow in NSW alone (Williams and Watford 1997).

While this legislative and policy framework has been effective in preventing further net decline in coastal wetlands in eastern Australia, they may not be sufficient to address the emerging threat of climate change across the nation. A suite of climate change drivers, potentially including elevated CO_2, temperature and sea-level, are altering the composition of coastal wetlands in important ways, and while coastal wetland area has stabilised in eastern Australia, the decline of coastal saltmarsh has continued unabated. Modelling of coastal wetland responses to projected sea-level rise has demonstrated the importance of migration pathways to facilitate mangrove and saltmarsh colonisation of coastal lowlands, even factoring in vertical elevation gains documented by the SET network (Rogers et al. 2014a; b). Many of the policy instruments identify wetlands as discrete mapped locations, an approach that while providing unequivocal identification of the protected asset, has the disadvantage of growing obsolescence in dynamically evolving landscapes. In particular, "coastal squeeze", where by landward encroaching wetlands meet hard human infrastructure barriers, is not currently addressed within the delineation approach of Ramsar or local planning controls such as SEPP14 in NSW (Rogers et al. 2014b; Rogers et al. 2016).

While coastal wetland protection in Australia has focussed on the fisheries and biodiversity values of wetlands, consideration is currently being given to carbon sequestration (blue carbon) and cultural values as a tool for promoting wetland preservation and climate change mitigation in Australia. Wetland conservation and restoration activities are relevant to National Greenhouse Gas inventory reporting (now possible under the IPCC wetlands supplement guidelines; Hiraishi et al. 2014), as well as investment through carbon mitigation activities. Australia has in recent years moved away from emissions trading towards direct investment by government through the Emissions Reduction Fund and Direct Action programs. While these have largely focussed on terrestrial carbon sequestration and emission reductions in agricultural and industrial sectors, blue carbon opportunities are being actively scoped. Until blue carbon methodologies are included under national carbon mitigation policies, voluntary carbon market opportunities will offer the best prospect of economic incentive for wetland preservation, restoration and creation.

One of the attractive features of blue carbon is the potential economic incentive provided to tidal wetland reinstatement and wetland encroachment in private and Indigenous landholdings. Further research is required to quantify these benefits and possible hydrological challenges (see Rodríguez et al. 2017) and further policy work required to facilitate market-based approaches to carbon trading in Australia. However, it is likely that the true value of coastal wetlands, encompassing carbon sequestration, fisheries value, biodiversity conservation, cultural values and shoreline protection will need to be recognised to allow their preservation in coastal lowlands facing the challenge of retreat. Ongoing preservation will therefore require public-private partnerships, incorporating the perspectives and values of Indigenous communities, agriculturalists, local communities and fisheries.

References

ABARES (2013) Australia's state of the forests report 2013. Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra

Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge

Allen RJ (1988) El Nino southern oscillation influences in the Australasian region. Prog Phys Geogr 12:313–348

Armitage AR, Highfield WE, Brody SD, Louchouarn P (2015) The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. PLoS One 10(5):e0125404

Asbridge E, Lucas R, Ticehurst C, Bunting P (2016) Mangrove response to environmental change in Australia's gulf of Carpentaria. Ecology and Evolution 6(11):3523–3539

Bell D, Menges CH, Bartolo RE (2001) Assessing the extent of saltwater intrusion in a tropical coastal environment using radar and optical remote sensing. Geocarto International 16:45–52

Boland DJ, Brooker MIH, Chippendale GM, Hall N, Hyland BPM, Johnston RD, Kleinig DA, McDonald MW, Turner JD (2006) Forest trees of Australia. CSIRO publishing, Melbourne

Boon PI, Allen T, Brook J, Carr G, Frood D, Harty C, Hoye J, McMahon A, Mathews S, Rosengren N, Sinclair S, White M, Yugovic J (2011) Mangroves and coastal saltmarsh of Victoria: distribution, condition, threats and management. Institute for Sustainability and Innovation, Victoria University, Melbourne

Bowman DMJS, Prior LD, De Little SC (2011) Retreating melaleuca swamp forests in Kakadu National Park: evidence of synergistic effects of climate change and past feral buffalo impacts. Austral Ecology 35:898–905

Brophy JJ, Craven, LA Doran JC (2013) Melaleucas: their botany, essential oils and uses. ACIAR, Canberra

Bucher D, Saenger P (1994) A classification of tropical and subtropical Australian estuaries. Aquat Conserv Mar Freshwat Ecosyst 4(1):1–19

Cahoon DR, Lynch JC, Perez BC, Segura B, Holland RD, Stelly C et al (2002) High-precision measurements of wetland sediment elevation: II. The rod surface elevation table. J Sediment Res 72(5): 734–739

Cavanaugh KC, Parker JD, Cook-Patton SC, Feller IC, Williams AP, Kellner JR (2015) Integrating physiological threshold experiments with climate modeling to project mangrove species' range expansion. Glob Chang Biol 21(5):1928–1938

Clark RL, Guppy JC (1988) A transition from mangrove forest to freshwater wetland in the monsoon tropics of Australia. J Biogeogr 15: 665–684

Cowie ID, Short PS, Ostercamp Madsen M (2000) Floodplain Flora: a flora of the coastal floodplains of the northern territory. Australia, ABRS, Canberra/PWCNT, Darwin

Dangremond EM, Feller IC (2016) Precocious reproduction increases at the leading edge of a mangrove range expansion. Ecology and Evolution 6(14):5087–5092

Dekker D, Ydenberg R (2004) Raptor predation on wintering dunlins in relation to the tidal cycle. Condor 106:415–419

Donato DC, Kauffman JB, Murdiyarso D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. Nat Geosci 4(5):293–297

Duke NC, Ball MC, Ellison JC (1998) Factors influencing biodiversity and distributional gradients in mangroves. Glob Ecol Biogeogr Lett 7:27–47

Ens EJ, Bentley-Toon S, Campion F, Campion S, Kelly J, Towler G (2017) Rapid appraisal links feral buffalo with kunkod (melaleuca spp.) decline in freshwater billabongs of tropical northern Australia. Mar Freshw Res 68:1642–1652

Eslami-Andargoli L, Dale PER, Sipe N, Chaseling J (2009) Mangrove expansion and rainfall patterns in Moreton Bay, southeast Queensland, Australia. Estuar Coast Shelf Sci 85(2):292–298

Finlayson C, Lowry J, Bellio M, Nou S, Pidgeon R, Walden D, Humphrey C, Fox G (2006) Biodiversity of the wetlands of the Kakadu region, northern Australia. Aquatic Sciences - Research Across Boundaries 68:374–399

Gabler CA, Osland MJ, Grace JB, Stagg CL, Day RH, Hartley SB, Enwright NM, From AS, McCoy ML, McLeod JL (2017) Macroclimatic change expected to transform coastal wetland ecosystems this century. Nat Clim Chang 7:142–147

Giri C, Long J (2016) Is the geographic range of mangrove forests in the conterminous United States really expanding? Sensors 16(12):2010

Gonsalves L, Law B, Webb C, Monamy V (2012) Are vegetation interfaces important to foraging insectivorous bats in endangered coastal saltmarsh on the central coast of new South Wales? Pac Conserv Biol 18(4):282–292

Gonsalves L, Law B, Webb C, Monamy V (2013) Foraging ranges of insectivorous bats shift relative to changes in mosquito abundance. PLoS One 8(5):e64081

Greenwood ME, MacFarlane GR (2006) Effects of salinity and temperature on the germination of Phragmites Australis, Juncus Kraussii, and Juncus Acutus: implications for estuarine restoration initiatives. Wetlands 26:854–861

Guo H, Weaver C, Charles S, Whitt A, Dastidar S, D'Odorico P, Fuentes JD, Kominoski JE, Armitage AR, Pennings SC (2017) Coastal regime shifts: rapid responses of coastal wetlands to changes in mangrove cover. Ecology 98:762–772

Hiraishi T, Krug T, Tanabe K, Srivastava N, Baasansuren J, Fukuda M, Troxler TG (2014) 2013 supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: wetlands. IPCC, Switzerland

Hoppe-Speer SC, Adams JB, Rajkaran A (2015) Mangrove expansion and population structure at a planted site, East London, South Africa. Southern Forests: a Journal of Forest Science 77(2):131–139

Jupiter SD, Potts DC, Phinn SR, Duke NC (2007) Natural and anthropogenic changes to mangrove distributions in the Pioneer River estuary (QLD, Australia). Wetl Ecol Manag 15(1):51–62

Kelleway JJ, Saintilan N, Macreadie PI, Ralph PJ (2016a) Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes. Ecosystems 19:865–880

Kelleway JJ, Saintilan N, Macreadie PI, Skilbeck CG, Zawadzki A, Ralph PJ (2016b) Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. Glob Chang Biol 22:1097–1109

Kelleway JJ, Cavanaugh K, Rogers K, Feller IC, Ens E, Doughty C, Saintilan N (2017a) Review of the ecosystem service implications of mangrove encroachment into salt marshes. Glob Chang Biol 23: 3967–3983

Kelleway JJ, Saintilan N, Macreadie P, Baldock J, Heijnis H, Zawadzki A, Gadd P, Jacobsen G, Ralph PJ (2017b) Importance of environmental history to blue carbon stocks revealed by geochemical analyses. J Geophys Res Biogeosci 122:1789–1805

Kingsley JY, Phillips R, Townsend M, Henderson-Wilson C (2010) Using a qualitative approach to research to build trust between a non-aboriginal researcher and aboriginal participants (Australia). Qual Res J 10:2–12

Knighton AD, Mills K, Woodroffe CD (1991) Tidal-creek extension and saltwater intrusion in northern Australia. Geology 19:831–834

Lawler W (1998) Guidelines for management of migratory shorebird habitat in southern east coast estuaries, Australia. University of New England

Levitt DL (1981) Plants and people: aboriginal uses of plants on Groote Eyelandt. Canberra, Australian Institute of Aboriginal Studies

Loneragan NR, Bunn SE, Kellaway DM (1997) Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Mar Biol 130: 289–300

Lovelock CE, Cahoon DR, Friess DA, Guntenspergen GR, Krauss KW, Reef R et al (2015) The vulnerability of indo-Pacific mangrove forests to sea-level rise. Nature 526:559–563

Macreadie PI, Ollivier QR, Kelleway JJ, Serrano O, Carnell PE, Ewers Lewis CJ, Atwood TB, Sanderman J, Baldock J, Connolly RM, Duarte CM, Lavery PS, Steven A, Lovelock CE (2017) Carbon sequestration by Australian tidal marshes. Sci Rep 7:44071

Mazumder D, Saintilan N, Williams RJ, Szymczak R (2011) Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses. Mar Freshw Res 62:11–19

Meynecke JO, Lee SY, Duke NC (2008) Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. Biol Conserv 141(4):981–996. https://doi.org/10.1016/j.biocon.2008.01.018

Mondon J, Morrison K, Wallis R (2009) Impact of saltmarsh disturbance on seed quality of sarcocornia (Sarcocornia Quinqueflora), a food plant of an endangered Australian parrot. Ecological management & restoration 10(1):58–60

Moussalli A, Connolly RM (1998) Fish use of the inundated waters of a subtropical saltmarsh-mangrove complex in Southeast Queensland, Australia. Short communication In: Tibbetts, IR., Hall, NJ. & Dennison, WD (eds) Moreton Bay and Catchment. School of Marine Science, The University of Queensland, Brisbane, 471-472

Mulrennan ME, Woodroffe CD (1998) Saltwater intrusion into the coastal plains of the lower Mary River, northern territory, Australia. J Environ Manag 54:169–188

Olson R, Evans JP, Di Luca A, Argüeso D (2016) The NARCliM project: model agreement and significance of climate projections. Clim Res 69(3):209–227

Quisthoudt K, Schmitz N, Randin CF, Dahdouh-Guebas F, Robert EM, Koedam N (2012) Temperature variation among mangrove latitudinal range limits worldwide. Trees 26(6):1919–1931

Rodríguez JF, Saco PM, Sandi S, Saintilan N, Riccardi G (2017) Potential increase in coastal wetland vulnerability to sea-level rise suggested by considering hydrodynamic attenuation effects. Nat Commun 8: 16094

Rogers K, Saintilan N, Heijnis H (2005) Monitoring of mangrove and saltmarsh resources in Westernport Bay, Australia. Estuaries 28: 551–559

Rogers K, Saintilan N, Howe AJ, Rodríguez JF (2013) Sedimentation, elevation and marsh evolution in a southeastern Australian estuary during changing climatic conditions. Estuar Coast Shelf Sci 133: 172–181

Rogers K, Saintilan N, Woodroffe CD (2014a) Surface elevation change and vegetation distribution dynamics in a subtropical coastal wetland: implications for coastal wetland response to climate change. Estuar Coast Shelf Sci 149:46–56

Rogers K, Saintilan N, Copeland C (2014b) Managed retreat of saline coastal wetlands: challenges and opportunities identified from the Hunter River estuary, Australia. Estuar Coasts 37(1):67–78

Rogers K, Boon PI, Branigan S, Duke NC, Field CD, Fitzsimons JA, Kirkman H, Mackenzie JR, Saintilan N (2016) The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. Mar Policy 72:139–155

Rogers K, Boon P, Lovelock C, Saintilan N (2017) Coastal halophytic vegetation. In: Vegetation A (ed) D. A. Keith. Cambridge University Press, New York

Saintilan N (2004) Relationships between estuarine geomorphology, wetland extent and fish landings in new South Wales estuaries. Estuar Coast Shelf Sci 61(4):591–601. https://doi.org/10.1016/j.ecss.2004.07.002

Saintilan N (2009) Biogeography of Australian saltmarsh plants. Austral Ecology 34:929–937

Saintilan N, Hashimoto R (1999) Mangrove-saltmarsh dynamics on a prograding bayhead delta in the Hawkesbury River estuary, new South Wales, Australia. Hydrobiologia 413:95–102

Saintilan N, Mazumder D (2017) Mass spawning of crabs: ecological implications in subtropical Australia. Hydrobiologia 803(1):239–250

Saintilan N, Williams RJ (1999) Mangrove transgression into saltmarsh environments in south-east Australia. Glob Ecol Biogeogr Lett 8:117–124

Saintilan N, Wilton K (2001) Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetl Ecol Manag 9:409–420

Saintilan N, Hossain K, Mazumder D (2007) Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, new South Wales. Wetl Ecol Manag 15:277–286

Saintilan N, Rogers K, Mazumder D, Woodroffe C (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuar Coast Shelf Sci 128:84–92

Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW (2014) Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob Chang Biol 20:147–157

Sloane DR (2017) An eco-cultural investigation of melaleuca spp. dieback in north-east Arnhem land, Australia. Master of Research, Macquarie University

Spencer J, Monamy V, Breitfuss M (2009) Saltmarsh as habitat for birds and other vertebrates. In: Saintilan N (ed) Australian saltmarsh ecology. CSIRO Publishing, Collingwood, pp 149–165

Stevens PW, Fox SL, Montague CL (2006) The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. Wetl Ecol Manag 14:435–444

Stuart SA, Choat B, Martin KC, Holbrook NM, Ball MC (2007) The role of freezing in setting the latitudinal limits of mangrove forests. New Phytol 173:576–583

Thom BG, Wright LD, Coleman JM (1975) Mangrove ecology and deltaic-estuarine geomorphology, Cambridge gulf-Ord River, Western Australia. J Ecol 63:203–222

Tidemann CR, Vardon MJ, Loughland RA, Brocklehurst PJ (1999) Dry season camps of flying-foxes (Pteropus spp.) in Kakadu world heritage area, north Australia. J Zool 247:155–163

Tran DB, Dargusch P (2016) Melaleuca forests in Australia have globally significant carbon stocks. For Ecol Manag 375:230–237

Tran DB, Dargusch P, Herbohn J, Moss P (2013) Interventions to better manage the carbon stocks in Australian melaleuca forests. Land Use Policy 35:417–420

Ummenhofer CC, England MH, McIntosh PC, Meyers GA, Pook MJ, Risbey JS, Gupta AS, Taschetto AS (2009) What causes southeast Australia's worst droughts? Geophys Res Lett 36:L04706

Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragan NR, Pendrey RC (2002) Distribution of juvenile penaeid prawns in mangrove forests in a tropical Australian estuary, with particular reference to Penaeus Merguiensis. Mar Ecol Prog Ser 228:165–177

Verdon DC, Wyatt AM, Kiem AS, Franks SW (2004) Multidecadal variability of rainfall and streamflow: eastern Australia. Water Resources Research 40:1–8

Webb EL, Friess DA, Krauss KW, Cahoon DR, Guntenspergen GR, Phelps J (2013) A global standard for monitoring coastal wetland vulnerability to accelerated sea-level rise. Nat Clim Chang 3(5):458–465

White NJ, Haigh ID, Church JA, Koen T, Watson CS, Pritchard TR et al (2014) Australian sea levels—trends, regional variability and influencing factors. Earth Sci Rev 136:155–174

Williams AR (1984) Changes in melaleuca forest density on the Magela floodplain, northern territory, between 1950 and 1975. Aust J Ecol 9:199–202

Williams RJ, Watford FA (1997) Identification of structures restricting tidal flow in new South Wales, Australia. Wetl Ecol Manag 5(1):87–97

Williamson GJ, Boggs GS, Bowman DM (2011) Late 20th century mangrove encroachment in the coastal Australian monsoon tropics parallels the regional increase in woody biomass. Reg Environ Chang 11(1):19–27

Wilson NC (2009) The distribution, growth and population genetics of a mangrove species Rhizophora stylosa in NSW, Australia. PhD Thesis, School of Arts and Sciences, Australian Catholic University

Wilson NC, Saintilan N (2012) Growth of the mangrove species Rhizophora Stylosa Griff. At its southern latitudinal limit in eastern Australia. Aquat Bot 101:8–17

Winn KO (2001) Saltwater intrusion and morphological change at Point Farewell, Alligator Rivers region. BSc (Hons) Honours Thesis, The University of Western Australia

Winn KO, Saynor MJ, Eliot MJ, Eliot I (2006) Saltwater intrusion and morphologicvla change at the mouth of the east Alligator River, northern territory. J Coast Res 22:137–149

Woodroffe CD, Grindrod J (1991) Mangrove biogeography: the role of quaternary environmental and sea-level change. J Biogeogr 18:479–492

Woodroffe CD, Thom BG, Chappell J (1985) Development of widespread mangrove swamps in mid-Holocene times in northern Australia. Nature 317(6039):711–713

Wrigley JW, Fagg M (1993) Bottlebrushes, paperbarks & tea trees: and other plants in the leptospermum alliance. Angus & Robertson, Sydney

Yunupiŋu B, Yunupiŋu-Marika L, Marika D, Marika B, Marika B, Marika R, Wightman G (1995) Rirratjiiŋu ethnobotany: aboriginal plant use from Yirrkala, Arnhem land, Australia. Parks and Wildlife Commission of the Northern Territory, Palmerston

Zharikov Y, Milton DA (2009) Valuing coastal habitats: predicting high-tide roosts of non- breeding migratory shorebirds from landscape composition. Emu 109:107–120

Marine Policy 72 (2016) 139–155

Contents lists available at ScienceDirect

Marine Policy

journal homepage: www.elsevier.com/locate/marpol

The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services

Kerrylee Rogers [a,*], Paul I. Boon [b], Simon Branigan [c], Norman C. Duke [d], Colin D. Field [e], James A. Fitzsimons [c,f], Hugh Kirkman [g], Jock R. Mackenzie [d], Neil Saintilan [h]

[a] School of Earth and Environmental Science, University of Wollongong, Wollongong, NSW 2522, Australia
[b] Victoria University (Footscray Park Campus), PO Box 14428, MCMC Melbourne, VIC 8001, Australia
[c] The Nature Conservancy, Suite 2-01, 60 Leicester Street, Carlton, VIC 3053, Australia
[d] James Cook University, Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER), PO Box 1250, Elanora, Queensland 4221, Australia
[e] University of Technology Sydney, PO Box 123, Broadway, NSW 2007, Australia
[f] School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, VIC 3125, Australia
[g] Private Consultant, 5A Garden Grove, Seaholme, VIC 3018, Australia
[h] Department of Environmental Science, Macquarie University, NSW 2109, Australia

ARTICLE INFO

Article history:
Received 11 January 2016
Received in revised form
27 June 2016
Accepted 27 June 2016

Keywords:
Mangrove
Salt marsh
Coastal wetland
Climate change
Ecosystem services
Sea-level rise

ABSTRACT

Saline coastal wetlands, such as mangrove and coastal salt marsh, provide many ecosystem services. In Australia, large areas have been lost since European colonization, particularly as a result of drainage, infilling and flood-mitigation works, often starting in the mid-19th century and aimed primarily towards converting land to agricultural, urban or industrial uses. These threats remain ongoing, and will be exacerbated by rapid population growth and climate change in the 21st century. Establishing the effect of wetland loss on the delivery of ecosystem services is confounded by the absence of a nationally consistent approach to mapping wetlands and defining the boundaries of different types of coastal wetland. In addition, climate change and its projected effect on mangrove and salt marsh distribution and ecosystem services is poorly, if at all, acknowledged in existing legislation and policy. Intensifying climate change means that there is little time to be complacent; indeed, there is an urgent need for proper valuation of ecosystem services and explicit recognition of ecosystem services within policy and legislation. Seven actions are identified that could improve protection of coastal wetlands and the ecosystem services they provide, including benchmarking and improving coastal wetland extent and health, reducing complexity and inconsistency in governance arrangements, and facilitating wetland adaptation and ecosystem service delivery using a range of relevant mechanisms. Actions that build upon the momentum to mitigate climate change by sequestering carbon – 'blue carbon' – could achieve multiple desirable objectives, including climate-change mitigation and adaptation, floodplain rehabilitation and habitat protection.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Mainland Australia has a coast 35,900 km long; islands add another 23,900 km, giving Australia a total coastline of 59,736 km [1]. Few countries – Canada and the Russian Federation, for example – have a longer coast. Not only is the coast long but the Australian mainland extends over 20° of latitude, from 22°S at Cape York in northern Queensland to nearly 44°S at South East Cape in southern Tasmania. It covers all the Köppen climate zones [2], spanning equatorial climates in the extreme north, through tropical and then subtropical climates, desert and grasslands on the western coast in particular, and to temperate zones in the south [3]. With such a long coast covering such a wide range of latitudes and an extreme of climates, it is not surprising that the marine embayments, estuaries, riverine floodplains, drowned river valleys and deltas of the Australian coast support wetlands that are simultaneously abundant and diverse, variously degraded or in good ecological condition, and protected by legislation to various degrees in different jurisdictions [4].

Mangroves are particularly extensive along northern shorelines, but stunted forms extend to the southernmost parts of the mainland. They are relatively easy to distinguish from other vegetation fringing the coast and are usually defined on the basis of

* Corresponding author.
E-mail address: kerrylee@uow.edu.au (K. Rogers).

http://dx.doi.org/10.1016/j.marpol.2016.06.025
0308-597X/© 2016 Elsevier Ltd. All rights reserved.

their structure and unique position in the landscape: trees, shrubs or palms located within the upper intertidal zone and therefore subject to regular tidal inundation [5,6]. Australia has among the floristically most diverse of the Earth's mangrove systems, with 47 species, or 59% of total mangrove species [5,7,8]. Australia also has the third-largest area of mangroves in the world, after Indonesia and Brazil. They line about 18% of the coast [5].

Coastal salt marshes are more difficult to delineate, as definitions vary across jurisdictions. It is also highly variable, their vegetation including a wide range of monocots and dicots, grasses, herbs, rushes, sedges, and shrubs typically located in the upper intertidal zone, where they are subject to episodic, but recurrent, tidal inundation. Salt marshes tend to occur in the upper intertidal zone, between mean sea level (MSL) and the level of the highest astronomic tide (HAT), although plant species typical of salt marshes may occur beyond these limits, often in splash zones or in stranded and relict palaeo-wetlands. Floristically and structurally coastal salt marshes are most complex in the temperate and southern parts of the country, and northern salt marshes, while extensive, are often floristically poor [Fig. 1] [9–13]. The coastal salt marshes of southern Australia are perhaps the most diverse, on structural and floristic criteria, of any on the planet. Carr [14], for example, collated information on the floristic diversity of saline coastal wetlands in south-eastern Australia and identified 130 indigenous taxa (along with 121 exotic taxa) of vascular plants [14]. Boon et al. [13] showed there were at least seven structurally distinctive forms of coastal salt marshes in south-eastern Australia, including different types dominated by herbs, grasses, forbs and shrubs.

At higher elevations, rarely subject to tidal inundation but influenced strongly by freshwater seepage, are diverse types of freshwater or brackish water coastal wetlands, often dominated by rushes, sedges or reeds, or by trees and shrubs such as paperbarks (*Melaleuca* spp.), tea trees (*Leptospermum* spp.) and swamp oaks (*Casuarina* spp.). The very highest elevations of coastal floodplains are influenced only by freshwater flows and, in these areas, forested wetlands dominated by tall eucalypt species inter-grade with the terrestrial vegetation of the hinterland [12].

Mangroves, salt marshes and these other types of saline coastal wetlands provide a range of ecosystems services, or benefits, for which the economic value can be assessed [15,16]. Descriptions of ecosystems services typically build upon the framework developed for describing ecosystems services within the Millennium Ecosystem Assessment [17] and include provisioning, supporting, regulating and cultural services. The value of ecosystem services is increasingly quantified by resource economists and acknowledged by many policy makers [18], although the merit of ecosystem valuation is debated by some ecologists and conservationists [19]. The ecosystem services provided by tidal marshes/mangroves globally was estimated in 2011 to be in the order of US $194,000 per hectare per year [15]. This estimation constituted an increase of $180,000 per hectare per year from an earlier estimate made by Costanza et al. in 1997 [20]; the large difference was attributed by the authors to new information about mangrove and salt marsh ecosystem services and their valuation, such as storm protection, erosion control and waste treatment [15]. The rationale for the large increase in ecosystem service value has been rejected by others on the basis that cited data does not indicate better valuation methods, some components of Costanza et al. estimates are mutually exclusive, and analysis techniques do not adequately account for variation in ecosystem service values [21]. Barbier et al. [16] reviewed the published literature on the way ecosystems provide raw materials and food, coastal protection, erosion control, water purification, maintenance of fisheries, carbon sequestration, and tourism, recreation, education and research. This review demonstrated these services have been poorly valued, in large part because of spatial and temporal variability in the ecological processes that underpin their provision. Links between carbon sequestration and other ecosystems services are yet to be fully incorporated in the valuation of ecosystem services for coastal ecosystems such as mangroves and salt marshes. This is a critical omission as carbon is the building block of food webs and sustains fisheries and wildlife within coastal wetlands and in nearshore areas [22,23]. Biomass of coastal wetland vegetation constitutes approximately 50% carbon [24,25] and contributes to the vegetation complexity that acts to stabilize shorelines, buffer wave action, increase coastal protection, and create nursery grounds for fisheries.

The amount of carbon stored and the carbon-fixing process in saline coastal wetlands makes a measurable and significant contribution to global carbon flux between the atmosphere and the land/water surface. Managed properly, mangroves and coastal salt marshes could therefore play an important role in the mitigation of atmospheric climate forcing [26]. At present, however, the widespread conversion of coastal wetlands to other uses (e.g. aquaculture) contributes up to 19% of all emissions from deforestation globally [26,27]. These contributions are not accounted in any current regulatory or market mechanism [28,29]. Nor are these losses fully acknowledged in terms of the other ecosystem services foregone when coastal wetlands are cleared for agriculture or for aquaculture [30]. The increasing need to attempt to mitigate the effects of climate change has focussed research attention on carbon sequestration benefits in Australia [31–35], yet these benefits are yet to be adequately evaluated. Similarly, assessments of the economic benefit of ecosystem services provided by mangrove and salt marsh are very few and cover only a small range of wetlands, limited in terms of geographic spread, of wetland diversity, and of the range of inferred benefits.

In contrast to the case with carbon sequestration, habitat-supporting services have received some attention by Australian ecologists and policy makers, with northern-Australian mangroves estimated to generate $14,000 AUD per hectare each year to commercial fisheries [36]. Furthermore, Creighton et al. [37] have shown that returns to commercial and recreational fishing alone of rehabilitating estuaries and their associated fringing wetlands is one of the most effective investments that can be made by natural resource managers in Australia, far outweighing the returns that accrue from investment into inland wetlands. This is consistent with the economic value of ecosystem services quantified in the United Kingdom's 2011 *National Ecosystem Assessment* [38], which showed that coastal wetlands in the UK provided ecosystem services worth £1534 million each year in terms of flood control and the protection of shorelines against erosion, £1275 million annually in biodiversity value, £1245 million in water-quality improvement, £514 million in the provision of clean water, and £1081 million in amenity value. On a per-area basis, coastal wetlands were estimated to be worth £3700 per hectare per year merely for the protection they offered to coasts against flooding and erosion.

Although society is yet to fully understand – let alone value or quantify – the ecosystem services provided by saline coastal wetlands, there is little time to wait for full economic appraisals. Global increases in urbanization and industrialization, coupled with the effects of climate change on coastal wetland distribution and function, are a continuing threat and are only likely to become worse with time. A new approach to coastal management is required that adequately recognizes the dynamic nature of the fringing saline coastal wetlands and values the ecosystem services they provide, without which these systems will be subject to further decline. The deficiencies of current arrangements are particularly pertinent in Australia, where 85% of Australians live within 50 km of the coast [39], which, as noted earlier, supports extensive areas of saline coastal wetland of exceptionally high

biodiversity and ecosystem value.

In this paper Australia is used as a case study – and ecosystem services as a focus – with the aim of assessing the capacity of existing legislation and policy to maintain or improve the status of saline coastal wetlands. Mangroves and salt marshes are the focus because across the globe these habitats are particularly sensitive to population growth and are threatened by coastal development. As coastal ecosystems, they are highly susceptible to climate change and in particular to sea-level rise. Initially a brief overview of the status of mangrove and salt marsh communities in different jurisdictions across Australia is provided, and follow this an assessment of the major threats they face to the delivery of ecosystem services is discussed. In doing so the effectiveness (or ineffectiveness) of existing policy and legislation at slowing the rate of decline in coastal wetland extent and ecological condition in the 20th century is demonstrated. Finally, a range of actions are identified, with varying ease of implementation, which will improve ecosystem services provided by mangrove and salt marsh.

2. Status of Australian saline coastal wetlands

Despite mounting evidence of the services provided by coastal wetlands and the economic benefits that accrue from maintaining them in good ecological condition, saline coastal wetlands continue to be degraded, or worse, lost completely, across the globe [40]. In Australia, 40% of New South Wales estuaries were found to be 'extensively modified' and less than 10% were in 'near pristine'

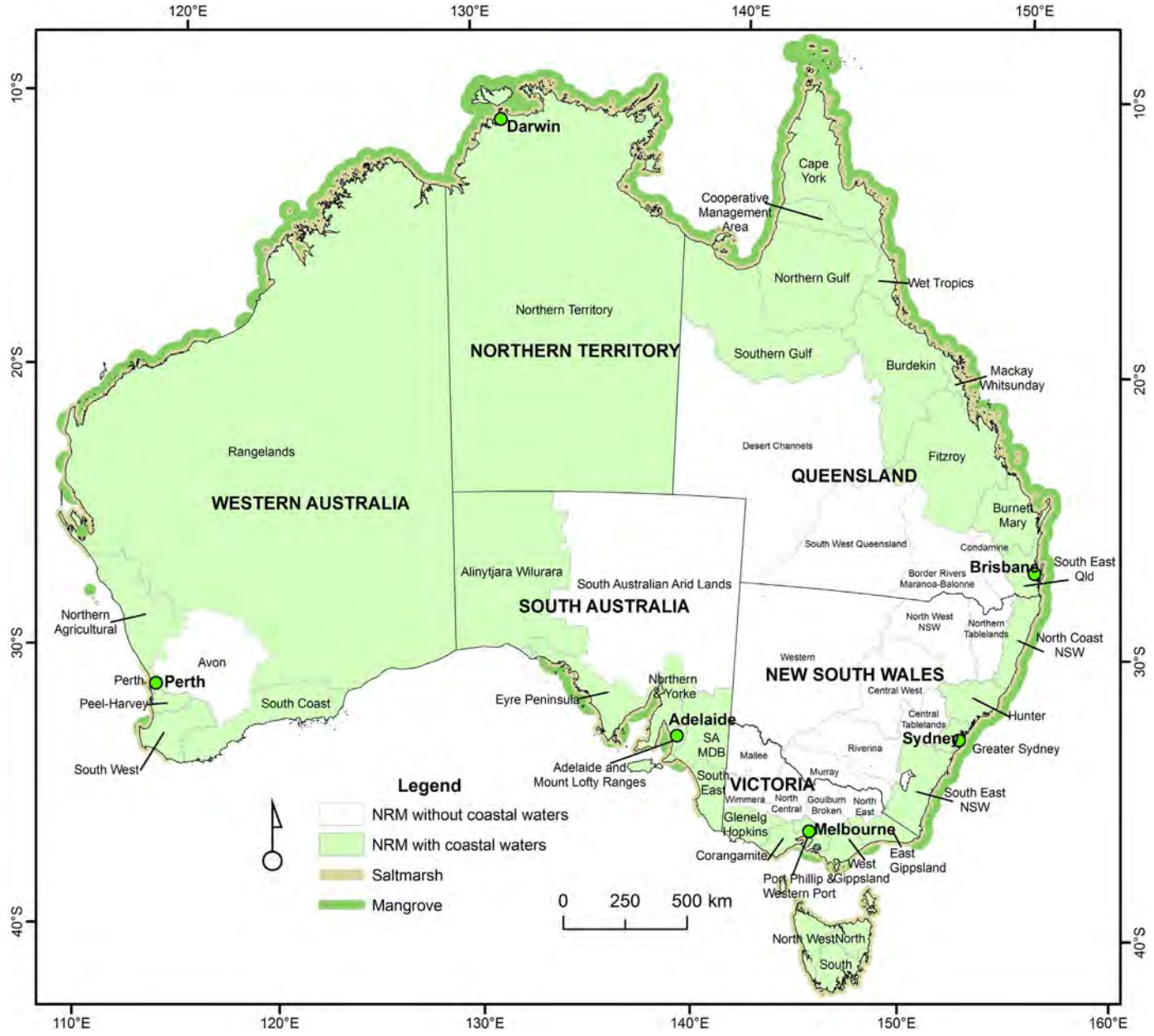


Fig. 1. Map of Australian management jurisdictions for saline coastal wetlands, showing mangrove distributions (dark green, shaded shoreline) and coastal salt marsh distributions (light brown, shaded shoreline) around the entire coast. Management is undertaken at multiple levels, including: the shoreline under the jurisdiction of the Australian Government (limited to for example parts of the Great Barrier Reef Marine Park); for state shorelines by seven state/territory governments (Western Australia, Northern Territory, Queensland, New South Wales, Victoria, South Australia and Tasmania); for regional areas by 34 Natural Resource Management (NRM) organizations with coastal fringes in their jurisdiction (light green shaded areas; 18 NRM organizations do not have coastal waters), and for a greater number of coast-bordering local government areas, rural and aboriginal councils (not indicated on map). Figure adapted from Duke [5], mangrove and salt marsh shorelines adapted from [53], NRM organizations at 2015 accessed from [54].

condition in the national audit of ecosystem condition undertaken in 2001 [41]. Saintilan & Williams [42,43] reviewed the records of salt marsh loss in eastern Australia and, based on 28 surveys employing historical aerial photographs, showed that there had been a widespread loss since the 1940–1950s. Losses were as high as 100% for Weeney Bay (part of Botany Bay, New South Wales, from 1950 to 1994) and 67% for the Hunter River estuary (excluding Hexham) from 1954 to 1994. Sinclair and Boon [44] surveyed the loss of mangroves and coastal salt marsh in Victoria since European colonization in the 1840s, and showed that in some areas over 50% of all pre-European saline coastal wetlands had been lost to coastal development since the mid-19th century. On The Great Barrier Reef floodplains of northern Queensland, more than 80% of fresh-to-brackish water wetlands have been cleared and drained, with serious adverse/negative impacts on recreational and commercial fisheries [37].

Recent Australian regulation, particularly across the eastern states (Queensland, NSW and Victoria), has stemmed the demise within Australia, but it has yet to fully prevent the loss or degradation of coastal wetlands on a national scale. Quantifying the demise of coastal wetlands is difficult for a number of reasons. First, accurate benchmark estimates of the pre-European distribution of coastal wetlands are rare, though there have been some studies quantifying changes in mangrove and salt marsh distribution following European occupation using historic records [44–46], or geomorphic characteristics of coastal landscapes [47,48]. Second, the delineation of mangrove and salt marsh communities is often difficult, especially where they merge into other types of coastal wetland [13]. Third, mangrove and salt marsh zones are often intricately shaped and their area measurement varies greatly depending on how closely and accurately the boundaries are delimited. Finally, the methods for determining the area has varied across studies and jurisdictions (Fig. 1), and in particular the scale at which the mapping and associated inventory has been prepared. For the purpose of quantifying ecosystem services, these issues are exacerbated as ecosystem service provision varies on the basis of floristic composition; establishing floristic composition benchmarks and changes over time is typically beyond the scope of assessments as it is difficult to quantify. In addition, ecosystem services vary both spatially and temporally as environmental conditions change over time, however this variation may be at a scale not captured in mapping assessments (e.g. younger mangrove forests do not have the same carbon storage as older forests, but mapping rarely distinguishes forest age). These difficulties are not limited to Australia; Friess and Webb [49] demonstrated considerable variability in mangrove extent trends globally and in Australia they found trends in mangrove decline ranged between 2.5 and 65 square kilometers per year.

Despite these limitations, there have been numerous efforts to quantify the extent of coastal wetlands nationally and within various Australian States (Table 1, Fig. 1). Even so, there is no nationally consistent approach to determine the area of mangrove or salt marsh, and because of this it is difficult to compare current area or historical losses across different jurisdictions. In addition, descriptions of salt marsh extent only provide a limited description of Australian salt marshes. This is because the very extensive coastal salt marshes in the northern parts of Australia are floristically poor, and it is the southern, temperate-zone salt marshes that are floristically and structurally the most rich [9,13,50–52]. This difference, and the significance of the more southerly examples, has been recognized in the recent listing of subtropical and temperate coastal salt marsh under the Commonwealth of Australia *Environment Protection and Biodiversity Conservation Act 1999*.

These estimates do not provide a benchmark from which to assess human impacts on mangroves and salt marshes in Australia as they are largely based on estimates of wetland extent that occurred after the large-scale losses that were associated with structural flood-mitigation works and the infilling of coastal land [55]. It is only in two states – New South Wales and Victoria – that such an activity was possible, and it may be no coincidence that these two states are the most populous and the longest settled of the various jurisdictions in Australia. The best 'benchmark' of the extent of coastal wetland habitats in NSW prior to large-scale degradation is provided by Goodrick [48] who estimated that the original extent of 'medium value waterfowl habitat', which included salt meadows, reed swamps, salt flats and mangrove swamps was 33,670 ha prior to drainage works commencing. This area declined by 12% by 1969, prior to the most extensive drainage works in the region occurring in the 1970s. The largest decline in extent occurred on the NSW mid-North Coast between Coffs Harbour and Tuncurry, where approximately 27% of saline coastal wetland extent had been lost to drainage by 1969. For Victoria, Sinclair and Boon [44] estimate a pre-European extent of coastal marshes (constituting mangroves and salt marshes) of 346–421 square kilometers, with declines ranging from 5–100% in different coastal areas after the mid-19th century. (Note that in some cases, for example around the Ramsar-listed Gippsland Lakes in eastern

Table 1
Previous estimates of the extent of mangrove and coastal salt marsh (km^2) in various jurisdictions in Australia. Differences are primarily due to different mapping techniques and classifications rather than changes over time (see text).

Jurisdiction	Mangrove extent			Coastal salt marsh extent		
	Year	Area (km^2)	Source	Year	Area (km^2)	Source
National	1982	11,500	[56,57]	1991	13,595	[63]
	1997	9695	[58]	2009	13,029	[64]
	2000	9550	[59]			
	2007	14,809	[60]			
	2010	9910	[61]			
	2013	9130	[62]			
New South Wales	1981	99	[56,57]	1991	57	[63]
	1991	107	[63]	2006	72	[65]
	2006	124	[65]	2009	68.5	[64]
	2008	50	[66]			
	2009	110	[64]			
	2013	160	[62]			
Northern Territory	1981	4120	[56,57]	1991	5005	[63]
	2008	3590	[66]			
	2013	3340	[62]			
Queensland	1981	4602	[56,57]	1991	5322	[63]
	2008	4360	[66]			
	2013	4410	[62]			
South Australia	1981	201	[56,57]	1991	84	[63]
	1991	111	[63]	2011	215[a]	[67][a]
	2008	140	[66]			
	2013	130	[62]			
Tasmania				1991	37	[63]
Victoria	1981	12	[56,57]	1979	< 60	[68]
	1991	41	[63]	1991	125	[63]
	2008	20	[66]	2012	132	[69]
	2013	20	[62]	2014	192	[13]
	2014	52	[13]			
Western Australia	2008	1640	[66]	1991	2965	[63]
	2012	2501	[70]			
	2013	1070	[62]			

[a] Fairweather [67] noted the existence of 150 km^2 of coastal salt marsh in the Northern and Yorke Natural Resource Management Areas and 65 km^2 in the Eyre Natural Resource Management Area.

Victoria, there is evidence for an expansion in the area of mangroves and salt marshes, consequent to the man-made conversion of formerly freshwater to estuarine lagoonal systems, however the ecosystem services provided by these new areas is likely to differ from well-established mangrove and salt marsh).

3. Threats and risks to mangrove and salt marsh and saline coastal wetlands in australia

A wide range of threatening processes has contributed to the loss of saline coastal wetlands in Australia (Table 2). The most significant anthropogenic process contributing to the loss of saline coastal wetlands has been land reclamation and drainage [13,71,72]. Efforts to mitigate flooding and reclaim land accelerated from the early 20th century, and was facilitated by landfilling and structures preventing or impeding tidal flow. In NSW alone, 4200 structures are estimated to impede flows in coastal rivers and streams [73], many of which were established as flood-control measures in major coastal waterways following substantial flooding and inundation of coastal floodplains in the 1950s. Because of the alienation of the formerly saline floodplain, the saline wetlands on land behind these levees and dykes have slowly converted into freshwater wetlands (principally vegetated with *Phragmites australis*) and/or been sown with introduced pasture grass to facilitate their conversion to fully agricultural landscapes. Rogers et al. [47] calculated the loss of potential fish habitat (primarily mangrove and salt marsh) by drainage in the same region assessed by Goodrick [48] and estimated that 62,258 ha were drained since European settlement, constituting over 70% of the pre-European extent of 87,008 ha. Similarly, in coastal Victoria much of the reduction in the pre-European extent of coastal marsh (mangroves and salt marshes) was a result of extensive drainage works to convert the land for pasture or cropping, infilling for agriculture, or conversion to evaporative salt ponds for salt extraction [44]. Often drainage works consisted of straightening formerly meandering coastal rivers with the intention of allowing them to discharge floodwaters more quickly [74]. This not only degraded the rivers, their floodplains and associated wetlands, but allowed heavy loads of nutrient and sediment to enter coastal waterways from the increasingly disturbed catchments. It is likely that destruction and impacts to mangroves and salt marshes will be ongoing due to industrial and port developments. Receiving considerable attention more recently has been proposed conversion of mangroves and salt marshes to other land uses, and changes in sedimentation and hydrological patterns, associated with liquid natural gas developments in northern Australia, such as at Port Curtis [75] and in Darwin Harbour [76].

Table 2
Processes responsible for the potential degradation or loss of mangroves or coastal salt marshes in Australia, adapted from [86].

Threat type	Potentially degrading activity
Resource exploration and production	– Exploration within or nearby, including geological/geophysical sampling and surveys, drilling, trenching, and bulk sampling – Gas storage within or nearby for carbon sequestration facilities – Production/extraction for salt extraction, underground mining, pipelines, pit extraction, dredging and pipelines – Processing for mineral, petrol or geothermal facilities
Recreation and education	– Access by trailbikes, four wheel drives, recreational vehicles and pedestrians – Grazing by sheep/cattle/goats – Destructive research – Commercial photography/film making – Competitions/organized sporting events (non-fishing) – Tourism operations – Animal feeding/baiting/burleying
Fishing and collecting	– Bait digging/pumping – Burleying for fishing – Line fishing (including long lining) – Pot and trap fishing (including drop/hoop nets) – Raking (crab) – Competitions/organized events (fishing) – Boat propellers and anchors – Collecting naturally occurring materials such as wood, mulch or other dead vegetation or seagrass/algae (including beach cast)
Harbour, navigating and transport activities	– Permanent vessel moorings and consequent clearing to allow for vessels – Dredging – Depositing dredged materials
Coastal developments and infrastructure	– Infrastructure (including marinas, jetties, pontoons, breakwalls, walkways) – Drainage and reclamation for other developments – Outfall and pipelines – Renewable energy infrastructure (wind, tidal)
Aquaculture	– Farming of bivalve molluscs – Farming of aquatic animals with regular feeding – Farming of algae – Pilot leases for aquaculture trials
Wastewater disposal/ discharges	– Discharge of wastewater – Vessel discharge of wastewater

Land use conversion and drainage modification, aside from the direct and complete loss of existing wetlands, have contributed to the development of pollution hot-spots, which are associated with the conversion of greenhouse gas sinks into likely sources [77], acid sulfate discharge into estuarine waters [78], and eutrophication [79]. Elevated nutrient loads associated with catchment development and discharges of sewage and stormwater influence the success of opportunistic algae in coastal settings and may result in the smothering of mangrove seedlings and/or pneumatophores [80]. Nutrient enrichment may also increase the primary productivity of mangrove [81] and salt marsh [82] communities and cause shifts across different types of primary producers (e.g., from woody plants to algae), thereby altering the fundamental basis of their ecosystem structure and function. Increases in nutrient content may also lead to increased rates of herbivory and thus – paradoxically – to decreases in above-ground biomass. In general, however, plant dieback and loss of vigor is associated with severe nutrient enrichment [83,84]. Loss of soil structure and subsidence is associated with drainage of mangroves and salt marshes [85] and increases exposure of land to rainfall/run-off and the effects of sea-level rise. As mangroves and salt marshes are at the terminal end of coastal rivers, they are also highly susceptible to pollution with heavy metals, pesticides and hydrocarbons [13].

With greater governance and community awareness of the value of mangroves and salt marshes, attempts have been made to limit the impact of threatening processes on the provision of ecosystem services. Even so, elevated concentrations of atmospheric carbon dioxide and their effects on eustatic sea level, storm surges, temperature, and rainfall patterns remain an ongoing and poorly managed threat. Changes in the distribution of mangroves and salt marshes have been linked to sea-level rise [87], altered rainfall patterns [88,89] and elevated atmospheric carbon dioxide concentrations [90]. The effect of sea-level rise has received the most attention to date, probably because of the urgent need to plan for possible coastal retreat and for mangrove and salt marsh adaptation to sea-level rise.

Coastal retreat, however, is only one of the possible responses for saline coastal wetlands. Under conditions of higher eustatic sea levels, mangroves and salt marshes can, in principle, adapt by two mechanisms. The first is horizontal migration to more elevated

land behind their current position. This is the response recognized by most wetland ecologists and acknowledged in most current policies regarding management of the coastal zone in Australia. The second is not as well recognized: saline coastal wetlands can also maintain themselves in response to higher sea levels by increasing their vertical position through processes of sediment accretion, expansion of below-ground plant material, and the accumulation of dead organic matter such as peat [91]. Due in large part to the long history of reclamation and the network of structures limiting tidal exchange, there is in many places only limited opportunity for horizontal migration of coastal wetlands. Commonly called 'coastal squeeze' [92], this process will lead to significant changes in the ecosystem services provided by coastal wetlands as wetlands are confronted with rising sea levels and are forced to move to higher land. This dichotomy is addressed more fully in Section 4.3. Research has indicated that where adaptation is facilitated and not limited by barriers to migration, ecosystem services provided by coastal wetlands may increase when exposed to low to moderate rates of sea-level rise; in contrast, high rates of sea-level rise will generally exceed resilience thresholds of coastal wetlands, causing ecosystem services to be reduced or lost completely [93]. However, there are also considerable equity and cross-sectoral issues that need to be balanced, particularly in urban areas, to ensure that the benefits of coastal ecosystems exceed the negative effects of facilitating adaptation [94].

4. Existing policy and legislative protection

4.1. The Australian approach

Australia is a federation of six states and two territories. Australia's constitutional arrangements enable the states to retain broad residual power, including for land and sea management (but to 3 nautical miles, exceptions do occur such as in the case of defense). The Australian Government has few powers in this regard, and it relies on powers in relation to external affairs to legislate for the protection, conservation and rehabilitation of coastal ecosystems. As a consequence there is a disparate system of conservation approaches across the nation. The location of coastal wetlands between the land and the sea has resulted in them being included in both terrestrial and marine protected areas but boundaries make management and prosecution at times unclear.

4.2. Coastal wetland delimitation and inventory

The primary legislative and policy instruments used to protect wetlands by Australian states (Table 3) apply to designated wetlands defined geographically, or according to a tidal benchmark and are usually mapped as polygons or lines on maps or by larger protected areas. For example, wetlands listed as internationally significant under the International Convention on Wetlands (Ramsar Treaty) are defined in spatial extent by geographic coordinates. This may apply to individual wetlands (e.g. Towra Point, Ramsar site no. 286), or much larger landscapes containing mosaics of wetlands (e.g. Moreton Bay Marine Park, Ramsar site no. 631). In NSW, the State Environmental Planning Policy 14 (Coastal Wetlands), a mechanism that operates under the NSW *Environmental Planning and Assessment Act (1979)*, applies only to those coastal wetlands mapped as such at the time of gazettal, and while updates are possible within the planning framework, few have been attempted. Similarly, wetlands protected under the reserve system are protected insofar as their boundaries lie within the reserve boundaries. In Victoria, the state-wide system for vegetation mapping includes a Bioregional Conservation Status (BCS) assessment for each vegetation type. Current BCS ratings for coastal salt marsh and mangroves vary across the State's bioregions, but for those containing the majority of coastal salt marsh and mangrove vegetation the status is the lowest possible, of 'least concern' [13]. However, these ratings are typically based on extent of past clearing and threats of future degradation (such as clearing or grazing) which may not be appropriate given the likely changes in ecosystem processes in the future [95].

The protection of wetlands through geographic designation is an approach with certain strengths and other weaknesses. There can be little argument as to the status of wetlands so defined, a factor that provides for a higher degree of planning certainty than definitions based, for example, on plant community composition. The wetland is afforded a greater degree of public attention if identified as a geographic entity. Wetlands are, however, dynamic systems, responding to changing hydrological and geomorphic conditions by moving in the landscape. Static planning instruments have struggled to adapt to the migrating boundaries of wetlands [93,96]. Revision of static boundaries at designated time periods, for example every 10 years, may allow for realignment of management boundaries with ecosystem boundaries. However there is a risk of significant loss of new wetland areas in the intervening period between revisions, particularly where the rate of change in the geographic position of wetland boundaries is high; this has been observed as coastal wetlands retreat landward across coastal floodplains of low slope [97]. In addition, there is considerable inter-annual and inter-decadal variation in wetland extent that may be driven by shorter-term perturbations (e.g. changing hydrodynamic conditions or rainfall patterns, see for example Asbridge et al. [98]). Such changes are likely to accelerate in a changing climate [99], making the delimitation of wetland boundaries even more fraught. As part of the NSW Coastal Reform process being implemented in 2016, SEPP14 wetlands are proposed to include a 100 m perimeter buffer area that will allow for natural fluctuations in wetland extent and provide protection from the effects of developments in close proximity [100]. This constitutes the first major revision in more than 30 years since boundaries were initially delineated; and while the buffer area does afford some protection it does not adequately account for the variable response of coastal wetlands to changing environmental conditions over the previous 30 years or the ensuing changes that are projected to occur in response to sea-level rise. Should geographic approaches persist, protocols for realignment of management and ecosystem boundaries that appropriately accounts for changing hydrodynamic conditions associated with sea-level rise, coastal geomorphology, and inter-annual and inter-decadal variation in environmental conditions are essential.

The listing in 2004 of coastal salt marsh as an Endangered Ecological Community under the NSW *Threatened Species Conservation Act 1995*, and, south of latitude 23 degrees, as a Threatened Ecological Community under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* in 2013 provides important protective measures for salt marsh, requiring higher level (Ministerial) referral for proposals deleteriously altering the community or its hydrology. Under these listings, the plant community is defined in terms of floristic composition and hydro-geomorphic setting, but not specific location, which potentially provides greater flexibility in protecting the community as it responds to sea-level rise. If the community can adapt, it continues to be protected, in contrast to a wetland moving beyond its presently-defined protection boundaries. As the sea rises, the tidal frame becomes a perambulatory boundary within which the ecosystem can reposition in the landscape. Similar floristically-based definitions appear in relation to marine vegetation (including mangroves and salt marshes) under the NSW *Fisheries Management Act 1994* and in the definition of 'Marine Plants' under the Queensland *Fisheries Act 1994*. In some cases, protection is

Table 3
Some important legislation that relates to the protection and/or restoration of mangrove and coastal salt marsh in Australia. Protection within legislation may be defined geographically (G), floristically on the basis of species present or species assemblages (F), or with reference to a tidal benchmark (B). In many states, broad native vegetation protection legislation, planning and development control legislation or coastal management policies may be implemented to achieve mangrove and salt marsh protection outcomes; these instruments have not been listed here.

Jurisdiction	Legislation	Relevant ecosystems, boundaries or inclusions	Scope	Additional comments
International	Intergovernmental conventions and agreements of which Australia is a signatory and which have largely been incorporated under the Federal *Environment Protection and Biodiversity Conservation Act 1999*. This includes the following conventions and agreements: • Convention on Wetlands of International Importance (Ramsar Convention) • Bilateral migratory shorebird agreements Australia and China (CAMBA), Japan (JAMBA) and Republic of Korea (ROKAMBA) • Convention concerning the protection of the World Cultural and Natural Heritage (World Heritage Convention) • Convention on Biological Diversity (Bonn Convention)			
National	*Environment Protection and Biodiversity Conservation Act 1999*	Designated wetlands of international importance (Ramsar wetlands). Applies to a range of wetlands types.	G	19 Ramsar wetlands in Australia include mangrove or salt marsh wetland types. Protection largely based on function as waterbird and fish habitat.
		Migratory species included in the appendices of the Bonn Convention, annexes of JAMBA and CAMBA, or listed under ROKAMBA	n/a	Commitment to protect listed species, habitats and ecosystems. Largely applies to designated priority sites
		Designated World, National and Commonwealth Heritage sites.	G	Some listed sites contain mangrove and salt marsh: Kakadu, Wet Tropics of Queensland
		Commonwealth protected areas	G	Kakadu National Park, Booderee National Park, Christmas Island National Park
		Listed nationally threatened species or ecological communities.	F	Applies broadly to subtropical and temperate coastal salt marsh ecological community; and some separately listed threatened species within sal tmarsh (e.g. *Halosarcia flabelliformis*) relying on salt marsh (e.g. Orange-bellied Parrot)
	Great Barrier Reef Marine Park Act 1975	Ecosystems, including mangroves and saltmarsh, within the Great Barrier Reef Marine Park	G	Low water mark of most of coastal Queensland from Bundaberg to tip of Cape York; zoned for different levels of use and protection
NSW	*Threatened Species Conservation Act 1995*	Threatened ecological community: Coastal Salt marsh in the New South Wales North Coast, Sydney Basin and South East Corner bioregions.	F	The salt marsh community is listed as 'vulnerable'
	Fisheries Management Act 1994	Marine vegetation: including mangrove and saltmarsh	F	Any development or activity that may harm mangroves or salt marshes must be referred to NSW Department of Primary Industries for approval
	State Environmental Planning Policy No. 14, *Environmental Planning and Protection Act 1979*	Applies to a range of wetland types and largely limited in size to the optical factors of interpretation. Wetland boundaries mapped by Adam et al. [87]	G	Does not apply to wetlands outside mapped boundaries
	Marine Estate Management Act 2014	Marine Parks limited to low-water mark and typically include mangrove, not salt marsh.	B	Provides for management of the NSW marine estate, the coordination of the public authorities involved in the marine estate, and 'declaration and management of a comprehensive system of marine parks and aquatic reserves'
	National Parks and Wildlife Act 1974	Based on mapped NSW estate boundaries that are designated as part of the mainly terrestrial national parks and reserves of NSW. Some mangrove and salt marsh may occur within coastal parks and reserves.	G	Mangrove and salt marsh may be reserved where their distribution coincides with primarily terrestrial reserves
Queensland	*Sustainable Planning Act 2009* and associated State Planning Policy	High Ecological Significance Wetlands, as defined in the State Planning Policy (SPP)	G	Designates that local government planning schemes must identify and manage potential significant adverse environmental impacts on matters of environmental significance, including wetlands
	Environmental Protection (Water) Policy 2009	All wetlands and waterways in declared High Ecological Value Waters, mapped spatially in SPP interactive mapping.	G	Designates that activities are required to avoid, minimize and offset any significant impacts on wetland environmental values
	Fisheries Act 1994	Fish habitat areas mapped geographically	G	Designates the protection of marine plants (tidal) in declared fish habitat areas. Coastal wetlands outside declared fish habitat areas (e.g. on pasture land) is precluded.
	Marine Parks Act 2004	Designates marine parks, of which significant areas of these communities occur in the Great Barrier Reef Coast Marine Park	G	Mangrove and salt marsh may be reserved where their distribution coincides with marine park reserves
	Nature Conservation Act 1992	Designates national parks and other terrestrial reserves, and threatened species and ecological communities	G	Mangrove and salt marsh may be reserved where their distribution coincides with primarily terrestrial reserves
	Vegetation Management Act 1999	Identified spatially on vegetation management maps	G	Regulates clearing of woody vegetation within and near watercourses and wetlands.
Victoria	*Coastal Management Act 1995* and associated Victorian Coastal Strategy (2014)	Private and Crown land in the intertidal zone and within 200 m of the high-water mark	B	Aims to plan for and manage coastal resources sustainably, protect coastal areas of environmental significance, facilitate recreation and tourism facilities, and provide public education on coastal matters.

Table 3 (*continued*)

Jurisdiction	Legislation	Relevant ecosystems, boundaries or inclusions	Scope	Additional comments
	National Parks Act 1975	National, State and other parks within Victoria, including marine national parks and marine sanctuaries.	G	A framework to establish and manage National, State and other parks within Victoria. A number of these areas include mangrove and coastal salt marsh (e.g. Wilsons Promontory National Park; Yaringa, French Island and Churchill Island Marine National Parks).
	Flora and Fauna Guarantee Act 1988	All native vegetation; listed threatened species that may occur within salt marsh (e.g. *Halosarcia flabelliformis*) or rely on salt marsh for habitat (e.g. Orange-bellied Parrot)	F	As native indigenous vegetation, mangroves and coastal salt marsh are, in principle, given a fundamental level of protection. Advisory Lists of Rare or Threatened Plant, Vertebrate Fauna and Invertebrate Fauna address the deficiencies in the Act not being explicit about vegetation. *Avicennia marina* and 16 salt marsh species listed as rare in Victoria on the Advisory List.
Tasmania	*Nature Conservation Act 2002*	Nature conservation areas including game reserves and designated protection areas	G	Designates nature conservation areas, including to Ramsar listed game reserves. Designates the protection of 'Saline Aquatic Herblands' and 'Wetland Undifferentiated', but excludes other specific wetland vegetation units identified in Tasmanian Vegetation Monitoring and Mapping Program, including 'Succulent Saline Herbland', 'Saline Sedgeland/Rushland' and 'Saltmarsh (undifferentiated)'
South Australia	*Fisheries Management Act 2007*	Mangrove explicitly identified	F	Objective is to protect and conserve aquatic habitats, and aquatic reserves, but does not refer to salt marsh.
	National Parks and Wildlife Act 1972	Endangered, vulnerable and rare species identified floristically Conservation areas (national parks, game reserves, conservation parks, recreation parks) identified geographically	F and G	Seeks the protection of endangered and vulnerable plants and animals, including some salt marsh species. Also designates national parks and other reserves, some of which support mangrove and saltmarsh, identified geographically
	Marine Parks Act 2007	Marine Parks to median high water mark and typically includes mangroves and salt marsh in a number of parks.	B	Various zones within South Australian Marine Parks allow different uses from Sanctuary to Habitat Protection to General Managed Use Zones
Western Australia	*Wildlife Conservation Act 1950*	Sub-tropical and temperate coastal salt marsh listed as a threatened ecological community	F	Minister can designate threatened and priority ecological communities for protection
	Conservation and Land Management Act 1984	Designates terrestrial reserves, marine nature reserves, marine parks and marine management areas for conservation and protection	G	Some mangrove and salt marsh protected within reserves under the provisions of this act.
	Fish Resources Management Act 1994	Designates areas as fish habitat protection areas	G	Some mangrove and salt marsh protected within reserves under the provisions of this act.
Northern Territory	*Territory Parks and Wildlife Conservation Act 2006*	Designates sanctuaries for protection	G	Portion of mangrove protected within reserve system [111]

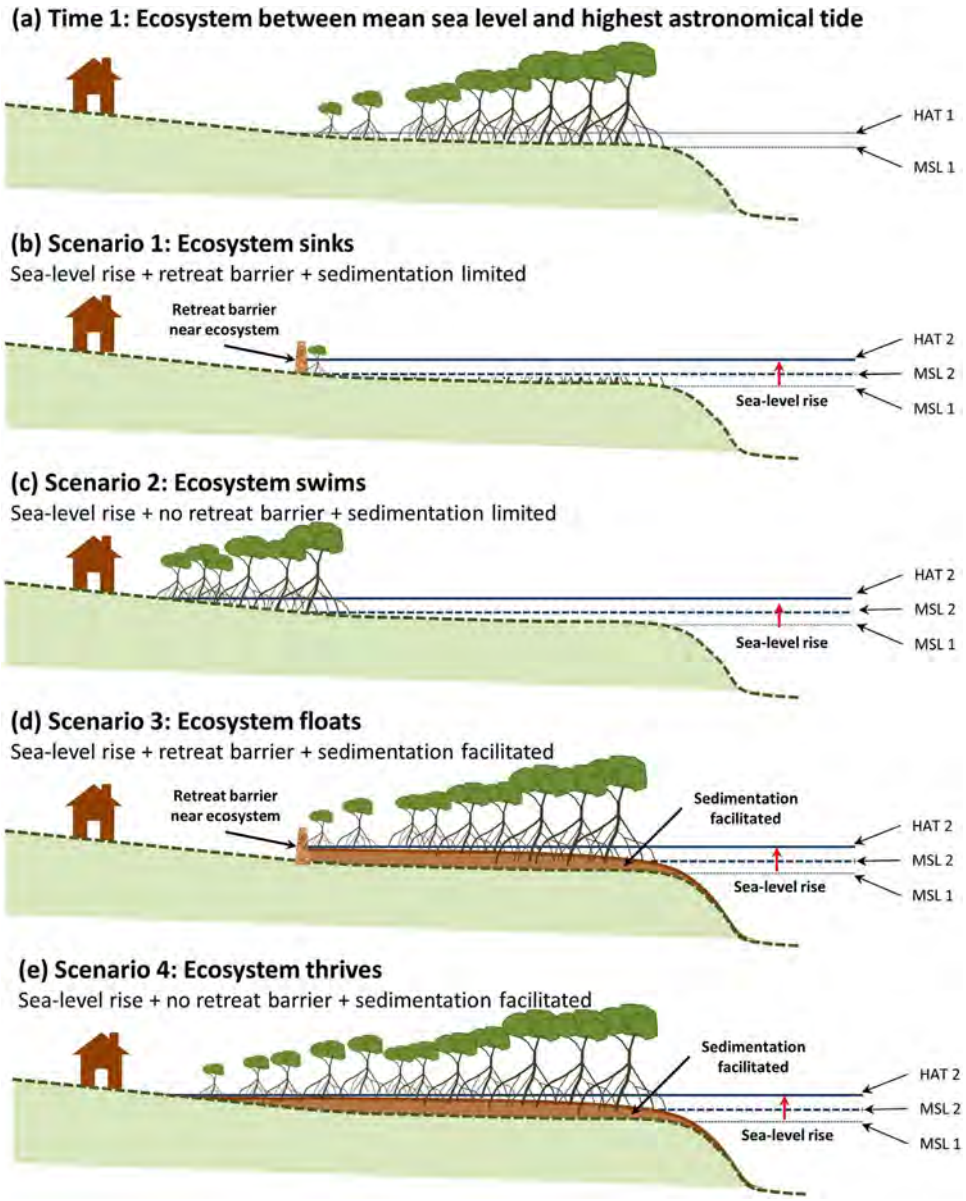


Fig. 2. (a) Coastal wetlands are distributed within the tidal frame approximately between mean sea level (MSL) and highest astronomical tide (HAT). As the sea rises they respond by (b) becoming submerged when sedimentation is limited and barriers limit the retreat of ecosystems to the new elevation within the tidal frame, here described as 'sinking'; (c) retreating to the new elevation within the tidal frame when sedimentation is limited and there are no barriers to limit retreat, here described as 'swimming'; (d) building elevation by increasing the soil volume with sediment and organic material, which can occur in the presence of barriers to retreat when sediment availability is sufficient, here described a 'floating'; or (e) increasing extent across the floodplain as the combination of sedimentation at the seaward edge and an elevated tidal frame increases the accommodation space for coastal wetlands.

defined on the basis of a benchmark with respect to water levels; for example in NSW protection is only provided to the position of mean high water (MHW), thereby excluding most coastal salt marsh, which grows between MHW and HAT.

4.3. Coastal wetland sea-level rise adaptation pathways

The perambulatory nature of coastal wetland boundaries will ensure that sea-level rise will confound protection and management of coastal wetlands [101]. The adaptation response of coastal wetlands to sea-level rise and any associated alterations to ecosystem services are dependent upon the availability of upland space to accommodate the retreat of coastal wetlands, and/or the deposition of sediment to facilitate elevation building to maintain their position within the tidal frame (Fig. 2a). The provision of these factors is not only dependent upon a suite of biophysical and socio-economic factors. The least significant of these is development of coastal floodplains for urban, industrial and agricultural purposes, which has resulted in the creation of barriers to retreat, such as buildings, roads, ports, levees and ring drains. Adaptation is also hindered by impacts on ecosystem health and productivity associated with coastal developments, such as eutrophication, and activities in catchments that limit delivery of sediments from catchments for deposition within coastal wetlands [102], such as dams in upper catchments or coastal wetland drainage using ring drains and levees. In combination, the occurrence of barriers to retreat, low sediment availability and poor ecosystem health will result in progressive loss of coastal wetland extent to permanent inundation or erosion at the seaward boundary causing the ecosystem to 'sink' beneath the tidal waters or becoming increasingly eroded at the seaward boundary resulting in coastal squeeze [92,103] (Fig. 2b).

Timely and appropriate planning of developments on coastal floodplains may limit alterations to potential adaptation pathways and the establishment barriers to retreat (Fig. 2c). Sea-level rise planning benchmarks have been used by some state governments to prevent development within coastal wetland retreat pathways (Table 4). For many state governments the intent of these benchmarks was to reduce climate risks to new developments from erosion and inundation hazards associated with sea-level rise and provide guidance on protective actions for existing developments, with only NSW, Victoria and Tasmania referring to the accommodation of coastal ecosystems and retreat pathways. Independent of whether sea-level rise planning policy specifically refers to coastal ecosystem retreat pathways, these planning benchmarks may effectively prevent the development of large barriers to ecosystems within retreat pathways. However small barriers such as pavements, fences and mowing, that may not require development approval will continue to limit retreat. Unfortunately, many of these benchmarks have been repealed in Australian jurisdictions for various political reasons [104], despite their basis on reliable, and possibly underestimated, projections of sea-level rise by the Intergovernmental Panel on Climate Change (IPCC) [105,106]. Flexible approaches to development control are now increasingly advocated with consideration given to accommodating natural coastal processes, though relatively little guidance is provided on how to implement this accommodation (See for example the NSW sea-level rise planning guideline [107]).

While sea-level rise planning benchmarks may effectively limit the establishment of new barriers to coastal wetland retreat, they are limited in application to locations where development of land within coastal wetland retreat pathways has not occurred, and do not provide for the restoration of adaptation pathways in catchments where development for urban and industrial purposes is extensive and retreat barriers, including geomorphic features such as adjoining steep slopes, are well established. In these circumstances sediment delivery from catchments to coastal wetlands and provision of environmental conditions that support healthy and productive coastal ecosystems become even more important. These conditions enable coastal wetlands to increase elevation by the addition of mineral sediments and organic material from in situ and nearby vegetation, effectively enabling them to maintain their position within the new tidal frame by 'floating' as sea levels rise (Fig. 2d). In particularly sensitive locations, planning approaches that have primarily been developed for eroding coastlines exposed to sea-level rise, such as 'rolling easements' [108] and land swaps – coastal for inland [109,110], have been advocated and may be effectively applied to provide for the retreat of coastal ecosystems.

The biophysical and socio-economic conditions required for effective coastal wetland adaptation to sea-level rise are substantial and complex, particularly along the highly developed coastline of eastern Australia, as was demonstrated by Abel et al. [109] who explored implementing actions for retreat of shorelines and coastal ecosystems in southeast Queensland. Despite the complexity, there is little doubt that the ensuing gain in ecosystem services provided by facilitating ecosystem adaptation may be substantial, particularly on broad, low-relief coastal floodplains where there are few barriers to coastal inundation (Fig. 2e).

5. Existing and emerging opportunities for protecting ecosystem services in australian policy and legislation

There are several opportunities to include ecosystem services in existing regulatory and market-based conservation instruments in Australia. These opportunities are discussed, without prejudice regarding the orthodoxy of these opportunities or ethical considerations. Recent discussions indicate that there is no consensus regarding the efficacy or integrity of these approaches [see for example 19,124,125,126].

5.1. International treaties and mechanisms

International treaties developed under the auspices of the United Nations Framework Convention on Climate Change (UNFCCC), including the Kyoto Protocol, require signatory nations to report on their greenhouse gas emissions, with targets set for reductions over a fixed time period. In Australia, National Greenhouse Accounts include not only the quantification of emissions from industrial and domestic fossil fuel consumption, but emissions and savings resulting from other 'activities', including the sequestration of carbon dioxide, and changes to land management. The IPCC provides guidance to nations on how changes to carbon emissions from these processes can be quantified. Recently, the IPCC produced a 'wetlands supplement' to the 2006 Guidelines for National Greenhouse Gas Inventories that for the first time provided specific advice on how carbon stocks in coastal wetlands can be estimated, and carbon emissions resulting from land-use change can be estimated [127]. Currently, Australia does not report on changes in land-use influencing carbon storage in saline coastal wetlands such as mangrove and salt marsh, although the frameworks exist to allow this.

5.2. Compensatory habitat

As a component of environmental impact assessments, several articles of legislation require that compensatory habitat be established in lieu of wetland destruction or modification. For example, compensatory habitat can be conditional with a Part 7 Fisheries Permit issued by NSW Fisheries (see Dwyer [128] for a case study). The need to incorporate ecosystem services within the decision-making process for compensatory habitat is increasingly recognized, especially in the USA [129,130]. The US Army Corps of Engineers guidance states that 'In general, compensatory mitigation should be located within the same watershed (i.e., catchment) as the impact site, and should be located where it is most likely to successfully replace lost functions and services' [131]. Sutton-Grier et al. [28] argue that the restoration of carbon services can and should be considered in determining the nature of compensatory wetland habitats being created under the provisions of the *Clean Waters Act* in the USA. In contrast to the USA experience, ecosystem services concepts are yet to be recognized amongst Australian states with regards to compensatory habitat [132]. Market-based mechanisms for off-setting habitat loss, such as the NSW Biobanking Scheme, which is underpinned by the NSW *Threatened Species Conservation Amendment (Biodiversity Banking) Bill 2006*, primarily focus on threatened species and communities with no link to maintaining ecosystem services [133]. A robust approach to identifying compensatory habitat would incorporate not only the full range of ecosystem services being lost, but the likelihood that the constructed wetland would survive projected rates of sea-level rise. But critically, such an approach would also better incorporate the strict application of the 'mitigation hierarchy', which views the role of biodiversity offsets as a 'last resort', after all reasonable measures have been taken first to avoid and minimize the impact of a development project and then to restore biodiversity on-site. Offset schemes inherently assume a knowledge-based perception of coastal wetlands, whereas there are compelling arguments for adopting instead an ignorance-based and precautionary approach to the management of coastal waters [125].

Table 4
Status of sea-level rise planning benchmarks in Australia, at October 2015.

Jurisdiction	Relevant policy	SLR benchmark status and relevant statements	Recognition of wetland retreat pathways	Notes
National	Currently lies outside jurisdictional capacity to develop nationally applied benchmarks. Adopted a sea-level rise benchmark of 1.1 m at 2100 for the National First Pass Assessment [112]			
NSW	NSW Coastal Planning Guideline: Adapting to SLR [107]	Councils are encouraged to give local sea-level rise projections due and proper consideration.	Strategic planning to accommodate the effects of sea-level rise on landward migration of wetlands, and recognition of wetland migration in development applications.	Rescinded NSW Sea Level Rise Policy Statement [113] identified a planning benchmark of 0.4 m by 2050 (above 1990 mean sea levels) and 0.9 m by 2100. Policy currently under review.
Northern Territory	NT Climate Change Policy [114]	No benchmarks identified.	No direct planning to address sea-level rise.	Refers to coastal wetlands being at risk from rising sea levels.
Queensland	Coastal Management Plan [115]	Impacts of climate variability, including sea-level rise, are considered in managing the coast.	No specific guidance regarding accommodation of wetland retreat.	Draft Coastal Management Plan [116] identified a planning benchmark of 0.3 m by 2050 (above 1990 mean sea levels) and 0.8 m by 2100.
Tasmania	Coastal Policy Statement [117]	Areas subject to significant risk from coastal processes and hazards, including sea-level rise, will be identified and managed to minimize the need for engineering or remediation works to protect land, property and human life.	Retreat pathways for natural ecosystems prioritized when planning new infrastructure.	No benchmarks identified. Draft Tasmanian Coastal Policy Statement [118] does not identify planning benchmarks.
South Australia	Coastal Protection Board Policy Document [119]	0.3 m by 2050 (above 1990 mean sea levels) and 1.0 m by 2100.	No recognition of coastal ecosystem retreat	Policy Document revised in May 2012 [119]
Victoria	Victorian Coastal Strategy 2014 [120]	0.8 m by 2100. Suggested allowances of 0.2 m at 2040, 0.4 m at 2070 and 0.8–0.9 m at 2099.	Actions proposed that facilitate retreat of coastal ecosystems	Supported by document: Derivation of Victorian Sea Level Planning Allowances: IPCC AR5 Update [121]
Western Australia	State Coastal Planning Policy 2.6 [122]	0.9 m over 100 year timeframe (2010–2110). 0.01 m/year added to 0.9 m for every year beyond 2110.	No specific guidance regarding accommodation of wetland retreat.	Supporting document Bicknell [123] Sea level change in Western Australia: Application to coastal planning.

5.3. Climate-change adaptation

Coastal ecosystems are increasingly promoted as a key defense against the impact of climate change and coastal hazards; for example by buffering wave action, trapping sediments and mitigating flood waters [26,134]. A recent review of Australian insurance law identified that the legal principles underlying the insurance industry in Australia can legitimately be applied to insure mangrove rehabilitation following storm damage [135]. An essential foundation to insuring ecosystem services is valuation of an asset to ensure that an insurance settlement covers costs of repair or replacement of the asset; and a standard methodology for doing so would be required for this to occur. Despite the feasibility, marketing and selling remain ongoing barriers in a voluntary insurance market; and success is unlikely to be achieved without government intervention. However, restoring vegetated shorelines with mangroves and salt marshes, commonly referred to as 'living shorelines', represents a means for mitigating storm effects, improving shoreline resilience [136,137] and providing a range of ecosystem services including carbon sequestration.

Market-based instruments may also be used to encourage landholders, both public and private, to protect wetlands and their ecosystem services, and improve resilience. In Victoria, the Corangamite Catchment Management Authority (CMA) and the West Gippsland CMA have both used single-bid auctions to determine the cost for landholders to manage salt marsh according to a pre-existing management plan. Winning bids were selected on the basis of the cost to achieve the benefits designated in the management plan, and landholders were invited to enter into a five year contract to undertake works to protect coastal saltmarsh. Currently 17 land managers (public and private) in the Corangamite region have committed to the project at 18 sites covering some 660 ha of native vegetation with management objectives including woody weed control, stock exclusion and pest animal control [138]. In the Gippsland region, 700 ha of salt marsh has been enhanced since 2009 using a similar approach [139].

These climate change adaptation actions could also contribute to national and regional priorities in wetland conservation and restoration. Additions to the National Reserve System (NRS), such as coastal national parks or the Ramsar estate, must contribute to the NRS objectives of comprehensiveness, adequacy and representativeness [140]; and are currently prioritized against a range of values including ecological values, representativeness, condition and opportunity. While the contribution of the NRS to Australia's above-ground biological carbon stock is substantial (approximately 20 million hectares of Kyoto forest, equivalent to 1.5 billion tonnes of carbon [141]), carbon sequestration is not a value against which additions are made to the NRS. The likely contribution of coastal lowlands to wetland migration and carbon storage are additional values that could be incorporated in NRS objectives and may complement conservation efforts. Indeed, land acquisition [142], upgrading of coastal public land and declaration of marine protected areas fringing the coast [143], and the establishment of Indigenous protected areas (particularly in northern Australia) [144] has seen significant additions of mangroves and salt marshes to the protected area estate.

5.4. Climate-change mitigation

Governments play a role in 'operationalizing' blue carbon as an ecosystem service, and increasingly through the introduction of market mechanisms for the inclusion of blue carbon in economic decisions [145]. In many places, coastal wetlands are lost because of the overriding imperative of economic development. If the value of carbon storage and sequestration potential is included in these decisions, along with other ecosystem services such as the provision of fish habitat and coastal protection, more informed decisions could be made [146]. However, inclusion of carbon value in decisions about the fate of wetlands presupposes three preconditions: first, the existence of a penalty for carbon pollution, in which the economic costs of carbon pollution are 'internalized' in the costs of producing the pollution; second, the existence of a carbon market, whereby pollution could be offset by, for example, the purchase of carbon sequestration values in natural or restored wetlands; and third that the valuations are realistic and accurate, which cannot be assured.

Australia has in recent years moved away from the development of market-based incentives for carbon preservation and enhancement. The six Acts that formed the basis of the previous carbon pricing mechanism were repealed in July 2014, which also halted new research initiatives under the Carbon Farming Initiative [121]. The scheme was replaced with an Emissions Reduction Fund (ERF) and a Direct Action (DA) program, the latter based largely on the modification of agricultural practices to minimize emissions. The ERF and DA have received criticism that neither will be effective in reducing Australia's greenhouse gas emissions [see for example 147]. Moreover, both the Carbon Farming Initiative and the DA policy largely focussed on terrestrial carbon sources, and management actions that promote carbon storage; blue carbon was not recognized within either scheme, despite high rates of carbon sequestration in saline coastal wetlands [148], and significant opportunities for restoration on public, private and indigenous owned land.

In the absence of an integrated global carbon market, emissions offset trading for coastal wetlands is largely limited to a fragmented voluntary market [149]. Many businesses see the value in lowering net emissions through targeted investment in programs with conservation outcomes, though to date the voluntary market has only realized relatively low carbon prices due to limited demand and low certainty [150]. The Australian Government implemented the National Carbon Offset Standard (NCOS) in July 2010 to provide consumer confidence and national consistency to the voluntary carbon market. NCOS provides guidance [151] on what is a legitimate voluntary carbon emissions offset and sets minimum requirements for determining the carbon footprint of an activity. While still in its infancy, NCOS is yet to provide guidance on the inclusion of mangrove and salt marsh soil carbon in voluntary carbon markets. The mechanisms exist in Australia for private investment in coastal wetland restoration as a voluntary emissions offset, though policy settings still frustrate the growth of these markets.

5.5. Changes to flood-mitigation approaches

Alteration to the hydrological conditions of saline coastal wetlands can lead to the rapid remineralization and loss of carbon from the upper meter of soil. Granek and Ruttenberg [152] estimated losses of Panamanian mangrove soil carbon to be approximately 50% over eight years following deforestation. Short-term carbon dioxide loss from a cleared mangrove has been measured at 29 Mg per hectare per year [153]. Estimates of carbon loss from wetlands behind protective levees throughout Australia, that were primarily established before the 1980s, are not available; though pronounced differences in elevation in relation to adjacent intertidal wetlands suggests that this might be substantial, and an as yet unquantified contribution to greenhouse gas flux.

Most of the flood control levees constructed in the estuaries of NSW have been built and maintained at public expense. The unintended consequences of isolating coastal lowlands from tidal inundation has been the creation of acid sulfate conditions [78,154], the loss of salt marsh habitat known to provide significant carbon flux to estuarine food-chains [23], and subsidence

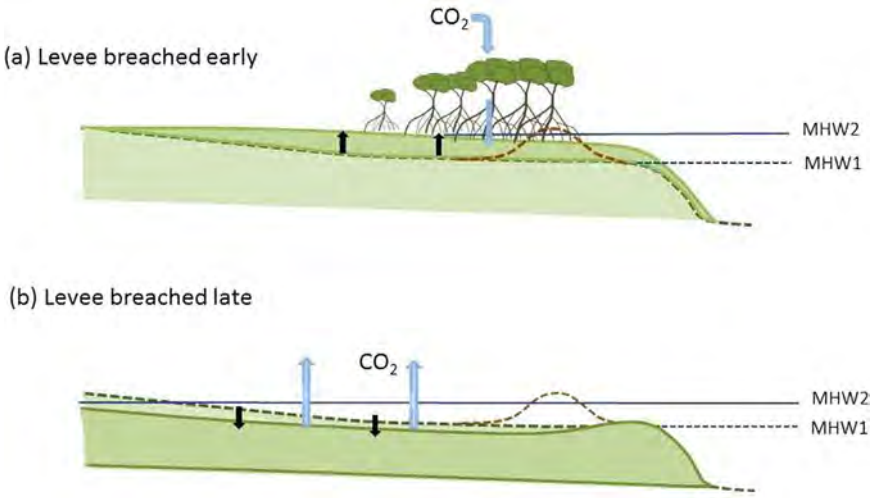


Fig. 3. Different outcomes associated with breaching protective levees early and late with the onset of sea-level rise. Early levee breach (a) encourages vertical accretion, including a carbon sequestration component. Late levee breach (b) follows subsidence of the floodplain, including carbon remineralisation and loss. Subsequent flooding is widespread, with associated third party impacts.

of floodplains [155,156]. Decisions made now about maintenance or opening of levees have long-term consequences, both biophysical and legal. The starvation of sediment supply to coastal lowlands and remineralization of carbon may lead to an elevation deficit beyond what might be recolonized by intertidal vegetation. Early intervention in opening lowlands to tidal exchange promotes positive feedbacks between inundation and elevation gain that facilitates adaptation to sea-level rise (Fig. 3), and will have a flow on effect to other ecosystem services. Delaying the opening of levees may place governments with a degree of culpability in relation to any subsequent third-party flooding impacts. The cost of levee maintenance and potential legal suits following levee failure or opening builds over time under this scenario (Fig. 3).

As the sea rises, and tidal impediments are removed, coastal ecosystems may retreat to adjacent land that now supports freshwater ecosystems that also provide valuable ecosystem services. Current research largely focuses on the recovery of ecosystem services as coastal wetlands are restored or created, as demonstrated by Osland et al. [157] regarding the return of carbon services approximately 20 years after mangrove restoration, and by Eong [158] regarding the functional equivalence of mangrove productivity after approximately 15 years of growth; or accounts solely for the gain in ecosystem services provided by coastal wetlands as they adapt to projected sea-level rise, as demonstrated by Rogers et al. [93] and discussed in Section 3, and Runting et al. [159] for southeast Queensland who demonstrate that high costs associated with preserving coastal wetlands under high rates of sea-level rise can be alleviated using payments for ecosystem services. Information on the loss of ecosystem services provided by the prior ecosystem or land use is yet to be explored in an Australian context and needs to be adequately accounted for, particularly when management actions are intended to promote a net gain in ecosystem services over time.

However, across many coastal floodplains incursion of saline water may facilitate the restoration of floodplains to a prior state, having flow-on effects to fish passage, acid sulfate soil remediation, mosquito management, and habitat provision [160], and a profound effect on ecosystem service provision. On the Hunter River, where a network of levees and floodgates has drained coastal floodplains, staged management of the floodgates to restore coastal wetlands across the floodplain is now occurring [161] and is projected to restore and increase ecosystem services [93].

6. New directions for mangrove and salt marsh policy and legislation

The immediate problem for mangrove and salt marsh in Australia is that even a conservative assessment of likely climate change impacts on coastal wetlands would caution against complacency, or of maintenance of the status quo. By focussing on the capacity of existing legislation and policy to maintain or improve the status of saline coastal wetlands in Australia the deficiencies that limit ecosystem service provision in the 21st century are highlighted. To this end seven key actions are proposed that will improve the fate of coastal ecosystems in Australia and the services they provide.

6.1. Establish nationally consistent and scientifically based approach to wetland delineation

Conservation on the basis of ecosystem boundaries delineated geographically provides a degree of certainty for planning in the coastal zone, but does not adequately account for changing wetland extent associated with climatic variability and sea-level rise (see Section 4.2). Approaches that define coastal ecosystems on the basis of floristic and geomorphic properties provide greater capacity for conservation in a landscape exposed to changing environmental conditions; though require greater knowledge of mangrove and salt marsh geomorphology and floristics. National guidance on the identification of coastal wetlands using geomorphic and floristic indicators will improve the capacity for identifying sensitive coastal ecosystems. This guidance should also extend to the provision of a scientifically robust methodology for identifying sea-level rise pathways, which will provide the certainty needed for planning for coastal developments and coastal ecosystem services.

6.2. Benchmark coastal wetland extent and health

The absence of reliable benchmarks, even at the most basic level of coastal wetland extent, prevents accurate assessment of future losses in coastal wetland ecosystem services due to coastal developments and sea-level rise. Indeed, Section 2 demonstrated the limited knowledge of the losses that have occurred since European occupation, or even the current extent of coastal wetlands. Geomorphic approaches for quantifying pre-European extents have been applied at regional scales [13,47], but have yet to be

undertaken using a consistent approach or at a national scale. Remote sensing techniques, while limited by their spatial resolution (e.g. Landsat has a 30 m × 30 m cell resolution), the information provided (e.g. ecosystem condition is largely derived from indices such as normalized difference vegetation index, NDVI) and cost (i.e. higher resolution imagery is costly and not available nationally), currently provide the best approach to national scale assessments of extent and health. The Geoscience Australia Earth Observation Data Cube [162] is a computationally powerful resource that can be used for quantifying temporal changes in coastal wetland extent and condition (indicated by NDVI) using all available Landsat 5–8 imagery of Australia from 1987. Establishment of a nationally consistent mapping protocol, using nationally available datasets such as that provided by the Data Cube, and investment in the application of mapping protocols at a national scale is essential for quantifying changes in ecosystem services. Assessments of condition and health at smaller spatial scales are also needed to bridge the gap between remote sensing and field-based surveys. New approaches, such as the shoreline video assessment method (S-VAM) [163] may assist with identifying links between vegetation, shoreline condition and drivers of change.

6.3. Reduce complexity and inconsistency in governance arrangements

Because of the suite of existing legislation and associated policy tools and frameworks across different jurisdictions, there is complexity in legislative arrangements and how they are administered across diverse government agencies [164]. Management arrangements for mangroves and coastal salt marsh are made even more complex because of the occurrence of these vegetation types within estuaries and the coastal zone, an area covered by multiple terrestrial and marine policies, statutes and by-laws and with diverse international, national, state and local influences [see for example 165]. That complexity is further complicated by the number of government agencies and non-government organizations that play a role in the planning and management of the coastal zone, as shown in Table 3. Reducing complexity in legislative arrangements within jurisdictions and harmonizing legislation between jurisdictions will provide the framework for a nationally consistent approach to coastal wetland conservation and management.

6.4. Improve coastal wetland extent and health

Reliance solely on sea level benchmarks for coastal wetland adaptation will limit adaptation of coastal ecosystems in highly developed catchments where barriers limit retreat from sea-level rise. In these circumstances, maintenance or improvement of ecosystem health and productivity is essential. This requires knowledge of the linkages between catchments – the source of sediments and toxicants, and coastal wetlands – the sinks. Importantly, management actions within catchments that currently have minimal impact on coastal wetlands now, such as increasing levee heights to reduce tidal incursions, may have long-term biophysical and legal consequences for coastal wetlands and adjoining land (see Section 5.5). Catchment management to maintain tidal exchange, sediment delivery and limit delivery of toxicants is essential for improving the health of coastal wetland ecosystems. Monitoring against the benchmark of ecosystem extent and condition will establish whether management actions are effective.

6.5. Facilitate improvement of ecosystem services using a range of relevant mechanisms

There exists a range of opportunities for protecting and improving coastal wetland ecosystem services that are embedded within Australian policy and legislation (See Section 5). However, there is not one solution that can be readily applied at a national scale. Additions to the national reserve system (see Section 5.3) on the basis of ecosystem service provision would improve protection of coastal wetlands. Payment for ecosystem services using market based instruments (see Section 5.4) may be favorable on agricultural land, particularly as sea-level rise or subsidence landward of levees decreases the agricultural value of land (see Section 5.5). Land-swaps, buy-backs and rolling easements may facilitate adaptation to sea-level rise in built-up landscapes where coastal wetlands are at risk of coastal squeeze (see Section 4.3). Preventing development of coastal wetland adaptation pathways using relevant legislative and policy mechanisms (e.g. sea-level rise planning benchmarks) will facilitate adaptation where development of adjoining landscape is low (see Section 4.3). Many of these are dependent upon quantification and valuation of ecosystem services, such as carbon sequestration, and emphasize the need for improved scientific information on coastal wetland extent, condition and adaptation pathways, to assist with selection of the most appropriate mechanism.

6.6. Prioritize landscapes for restoration and protection of ecosystem services

The biodiversity value of the Australian coastal zone is diverse and spatially variable, so too is catchment development and pressures on coastal wetlands. As current spending on climate change remains low relative to the projected future costs [166], there is a need to prioritize coastal landscapes for restoration and protection. Restoration prioritization of landscapes is particularly important for the coastal wetlands of temperate Australia where species diversity is high, but spatial extent is restricted by widespread coastal development and geomorphic conditions (e.g. smaller catchments, see Section 2). With increasing emphasis placed on the value of ecosystem services provided by coastal ecosystems, and in particular carbon-related services, a serviced based approach to conservation would favor the protection of coastal wetlands where ecosystem service delivery is high; this is particularly relevant for mangrove and salt marsh of northern Australia where the most recent estimates of extent indicate that 85% of mangrove extent is located in Queensland and the Northern Territory (See Section 2). Conservation on the basis of carbon related services should focus on tropical Australia where carbon sequestration and storage by mangrove is high, spatial extent is large, and where catchment development is low, thus reducing pressures on ecosystem extent and condition. Identifying biodiversity and ecosystem service values is essential.

6.7. Implement adaptation actions as soon as possible

Sea-level rise and increasing pressures within coastal catchments provides a degree of urgency to implement the actions detailed above. The cost of delaying actions to protect and improve coastal wetland ecosystem services compounds over time (see Fig. 3). Biophysical and economic modeling of costs associated with preserving coastal wetlands in southeast Queensland demonstrate exponential increasing impacts on coastal wetland extent, service provision and costs associated with preservation under increasing rates of sea-level rise in the 21st century [159]. This would indicate that delays in implementing strategies for adaptation would incur greater costs and/or provide reduced benefits as sea-level rise impacts increase, investment now will reap the greatest benefit.

Acknowledgments

KR receives financial support from the Australian Research Council (FT130100532). This paper was the result of a workshop following the 1st Australian Mangrove and Saltmarsh Network Conference, held in February 2016 at Wollongong, Australia. We kindly thank The Nature Conservancy (Australia) and the University of Wollongong Global Challenges Program for financial and logistical support for the workshop.

References

[1] Geosciences Australia, Border Lengths – States and Territories, accessed at ⟨http://www.ga.gov.au/scientific-topics/national-location-information/dimensions/border-lengths⟩, 2016 (accessed 04.01.16).
[2] M. Kottek, J. Grieser, C. Beck, B. Rudolf, F. Rubel, World map of the Köppen-Geiger climate classification updated, Meteorol. Z. 15 (2006) 259–263.
[3] Bureau of Meteorology, Climate classification maps, accessed at ⟨http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications/index.jsp?maptype=kpngrp⟩, 2016 (accessed 05.01.16).
[4] A.D. Heap, S.M. Bryce, D.A. Ryan, L. Radke, C. Smith, R. Smith, et al., Australian Estuaries and Coastal Waterways: A Geoscience Perspective for Improved and Integrated Resource Management. A Report to the National Land and Water Resources Audit Theme 7: Ecosystem Health, Australian Geological Survey Organisation, Canberra, 2001.
[5] N.C. Duke, Australia's Mangroves, University Of Queensland, Brisbane, 2006.
[6] C.D. Woodroffe, G. Davies, The morphology and development of tropical coastal wetlands, in: G. Perillo, E. Wolanski, D. Cahoon, M. Brinson (Eds.), Coastal Wetlands: An Integrated Ecosystem Approach, Elsevier, Amsterdam, The Netherland and Oxford, United Kingdom, 2009, pp. 65–88.
[7] N.C. Duke, World Mangrove iD: expert information at your fingertips - e-book, Mangrovewatch Publication, Australia, 2014.
[8] W.E. Cooper, H. Kudo, N.C. Duke, Bruguiera hainesii C.G.Rogers (Rhizophoraceae) a critically endangered species recently discovered in Australia, Austrobaileya, (in press).
[9] N. Saintilan, Biogeography of Australian saltmarsh plants, Austral Ecol. 34 (2009) 929–937.
[10] P. Adam, Australian saltmarshes in global context, in: N. Saintilan (Ed.), Australian Saltmarsh Ecology, CSIRO Publishing, Collingwood, Victoria, 2009, pp. 1–22.
[11] N. Saintilan, Distribution of Australian saltmarsh plants, in: N. Saintilan (Ed.), Australian Saltmarsh Ecology, CSIRO Publishing, Collingwood, Victoria, Australia, 2009, pp. 23–52.
[12] P.I. Boon, D. Keith, E. Raulings, Vegetation of coastal floodplains and wetlands in south-eastern Australia, in: S. Capon, C. James, M. Reid (Eds.), Vegetation of Australia's Riverine Landscapes, CSIRO Publishing, Collingwood, VIC, pp. 145–176.
[13] P.I. Boon, T. Allen, G. Carr, D. Frood, C. Harty, A. McMahon, et al., Coastal wetlands of Victoria, south-eastern Australia: providing the inventory and condition information needed for their effective management and conservation, Aquat. Conserv.: Mar. Freshw. Ecosyst. 25 (2015) 454–479.
[14] G.W. Carr, Inventory of Victorian marine, estuarine and saltmarsh vascular plant species, in: G.R. Sainty, J. Hosking, G.W. Carr, P. Adam (Eds.), Estuary Plants and What's Happening to Them in South-East Australia, Sainty and Associates, Potts Point, 2012, pp. 379–421.
[15] R. Costanza, R. de Groot, P. Sutton, S. van der Ploeg, S.J. Anderson, I. Kubiszewski, et al., Changes in the global value of ecosystem services, Glob. Environ. Change 26 (2014) 152–158.
[16] E.B. Barbier, S.D. Hacker, C. Kennedy, E.W. Koch, A.C. Stier, B.R. Silliman, The value of estuarine and coastal ecosystem services, Ecol. Monogr. 81 (2011) 169–193.
[17] Millennium Ecosystem Assessment, Ecosystems and Human Well-being, Island Press, Washington, DC, 2005.
[18] P. Figgis, B. Mackey, J. Fitzsimons, J. Irving, P. Clarke, Valuing Nature: Protected Areas and Ecosystem Services, Australian Committee For IUCN, Sydney, 2015.
[19] D.J. McCauley, Selling out on nature, Nature 443 (2006) 27–28.
[20] R. Costanza, R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, et al., The value of the world's ecosystem services and natural capital, Nature 387 (1997) 253–260.
[21] L.H. Pendleton, O. Thébaud, R.C. Mongruel, H. Levrel, Has the value of global marine and coastal ecosystem services changed? Mar. Policy 64 (2016) 156–158.
[22] K. Abrantes, R. Johnston, R. Connolly, M. Sheaves, Importance of mangrove carbon for aquatic food webs in wet–dry tropical estuaries, Estuaries Coasts 38 (2015) 383–399.
[23] D. Mazumder, N. Saintilan, J.R. Williams, R. Szymczak, Trophic importance of a temperate intertidal wetland to resident and itinerant taxa: evidence from multiple stable isotope analyses, Mar. Freshw. Res. 62 (2011) 11–19.
[24] J. Howard, S. Hoyt, K. Isensee, E. Pidgeon, M. Telszewski, Coastal Blue Carbon: Methods for Assessing Carbon Stocks and Emissions Factors in Mangroves, Tidal Salt Marshes, and Seagrass Meadows, Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union For Conservation of Nature, Arlington, Virginia, USA, 2014.
[25] J.B. Kauffman, C. Heider, T. Cole, K. Dwire, D. Donato, Ecosystem carbon stocks of Micronesian mangrove forests, Wetlands 31 (2011) 343–352.
[26] C.M. Duarte, I.J. Losada, I.E. Hendriks, I. Mazarrasa, N. Marba, The role of coastal plant communities for climate change mitigation and adaptation, Nat. Clim. Change 3 (2013) 961–968.
[27] L. Pendleton, D.C. Donato, B.C. Murray, S. Crooks, W.A. Jenkins, S. Sifleet, et al., Estimating global "Blue Carbon" emissions from conversion and degradation of vegetated coastal ecosystems, PLoS ONE 7 (2012) e43542.
[28] A.E. Sutton-Grier, A.K. Moore, P.C. Wiley, P.E.T. Edwards, Incorporating ecosystem services into the implementation of existing U.S. natural resource management regulations: operationalizing carbon sequestration and storage, Mar. Policy 43 (2014) 246–253.
[29] L.H. Pendleton, A.E. Sutton-Grier, D.R. Gordon, B.C. Murray, B.E. Victor, R. B. Griffis, et al., Considering "Coastal Carbon" in existing U.S. Federal Statutes and Policies, Coast. Manag. 41 (2013) 439–456.
[30] K. Warne, Let Them Eat Shrimp: The Tragic Disappearance of the Rainforests of the Sea, Island Press, Washington DC, 2011.
[31] C. Lovelock, M. Adame, V. Bennion, M. Hayes, J. O'Mara, R. Reef, et al., Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of South East Queensland, Australia, Estuaries Coasts 37 (2013) 763–771.
[32] A.J. Howe, J.F. Rodríguez, P.M. Saco, Surface evolution and carbon sequestration in disturbed and undisturbed wetland soils of the Hunter estuary, southeast Australia, Estuar. Coast. Shelf Sci. 84 (2009) 75–83.
[33] C.J. Sanders, I.R. Santos, D.T. Maher, J.L. Breithaupt, J.M. Smoak, M. Ketterer, et al., Examining 239+240Pu, 210Pb and historical events to determine carbon, nitrogen and phosphorus burial in mangrove sediments of Moreton Bay, Australia, J. Environ. Radioact. 151 (2016) 623–626.
[34] S.J. Livesley, S.M. Andrusiak, Temperate mangrove and salt marsh sediments are a small methane and nitrous oxide source but important carbon store, Estuar. Coast. Shelf Sci. 97 (2012) 19–27.
[35] N. Saintilan, K. Rogers, D. Mazumder, C. Woodroffe, Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands, Estuar. Coast. Shelf Sci. 128 (2013) 84–92.
[36] R.M. Morton, Community structure, density and standing crop of fishes in a subtropical Australian mangrove area, Mar. Biol. 105 (1990) 385–394.
[37] C. Creighton, P.I. Boon, J.D. Brookes, M. Sheaves, Repairing Australia's estuaries for improved fisheries production – what benefits, at what cost? Mar. Freshw. Res. 66 (2015) 493–507.
[38] I.J. Bateman, D. Abson, N. Beaumont, A. Darnell, C. Fezzi, N. Hanleys, et al., Economic values from ecosystems, in: The UK National Ecosystem Assessment Technical Report, United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC), Cambridge, 2011, pp. 1067–1152.
[39] D. Trewin, Year book Australia: 2004, Australian Bureau of Statistics, Australian Government, Canberra, 2004.
[40] B.A. Polidoro, K.E. Carpenter, L. Collins, N.C. Duke, A.M. Ellison, J.C. Ellison, et al., The loss of species: Mangrove extinction risk and geographic areas of global concern, PLoS ONE 5 (2010) e10095.
[41] J.T.P. Tait, I.D. Cresswell, R. Lawson, C. Creighton, Auditing the health of Australia's ecosystems, Ecosyst. Health 6 (2000) 149–163.
[42] N. Saintilan, R.J. Williams, Mangrove transgression into saltmarsh environments in south-east Australia, Glob. Ecol. Biogeogr. 8 (1999) 117–124.
[43] N. Saintilan, R.J. Williams, The decline of saltmarshes in Southeast Australia: results of recent surveys, Wetlands 18 (2000) 49–54.
[44] S. Sinclair, P.I. Boon, Changes in the area of coastal marsh in Victoria since the mid 19th century, Cunninghamia, vol. 12, 2012, pp. 153–176.
[45] L. McLoughlin, Estuarine wetlands distribution along the Parramatta River, Sydney, 1788–1940: implications for planning and conservation, Cunninghamia 6 (2000) 579–610.
[46] L. McLoughlin, Mangroves and grass swamps: changes in the shoreline vegetation of the Middle Lane Cover River, Sydney, 1780's-1880's, Wetlands 7 (1988) 13–24.
[47] K. Rogers, E. Knoll, C. Copeland, S. Walsh, Quantifying changes to historic fish habitat extent on north coast NSW floodplains, Australia, Reg. Environ. Change 16 (2016) 1469–1479.
[48] G.N. Goodrick, A Survey Of Wetlands Of Coastal New South Wales, Technical Memorandum No 5, CSIRO Division Of Wildlife Research, Canberra, 1970.
[49] D.A. Friess, E.L. Webb, Variability in mangrove change estimates and implications for the assessment of ecosystem service provision, Glob. Ecol. Biogeogr. 23 (2014) 715–725.
[50] L. Turner, D. Tracey, J. Tilden, W.C. Dennison, Where river meets sea: exploring Australia's estuaries, CRC for Coastal Zone, Estuary and Waterway Management, Brisbane, 2004.
[51] N. Saintilan, Australian Saltmarsh Ecology, CSIRO Publishing, Collingwood, Melbourne 2009, p. 225 (pp).
[52] N. Saintilan, K. Rogers, The significance and vulnerability of Australian saltmarshes: implications for management in a changing climate, Mar. Freshw. Res. 64 (2013) 66–79.
[53] Geomorphic, OzCoasts habitat mapping shape files for GIS, (accessed 11.01.16), accessed at 2016.
[54] Department of Environment, Natural Resource Management (NRM) Regions,

2015, accessed at ⟨http://www.environment.gov.au/fed/catalog/search/resource/details.page?uuid=%7B60F60282-B651-4B8B-BA4d-ADEF46D42B29%7D⟩, 2016 (accessed 11.01.16).
[55] ARMCANZ (Agriculture and Resource Management Council of Australia and New Zealand), Floodplain Management in Australia: Best Practice Principles and Guidelines, CSIRO Publishing, Collingwood, 2000.
[56] R.W. Galloway, An inventory of Australia's coastal lands, Aust. Geogr. Stud. 19 (1981) 107–116.
[57] R.W. Galloway, Distribution and physiographic patterns of Australian mangroves, in: B.F. Clough (Ed.), Mangrove Ecosystems in Australia: Structure, Function and Management, Australian Institute of Marine Science and Australian National University, Canberra, 1982, pp. 31–54.
[58] M.D. Spalding, F. Blasco, C.D. Field, World Mangrove Atlas, International Society For Mangrove Ecosystems,, Okinawa, Japan, 1997.
[59] FAO, Status and trends in mangrove area extent worldwide. Forest Resources Assessment Paper No 63, Food and Agriculture Organization of the United Nations, 2003.
[60] FAO, The Eorld's Mangroves 1980–2005. FAO Forestry Paper 153, Food and Agriculture Organization of the United Nations, 2007.
[61] M.D. Spalding, M. Kainuma, L. Collins, World Atlas of Mangroves, Earthscan, London, Washington DC, 2010.
[62] Australian Government, Australia's State of the Forests Report 2013: Five-yearly Report, Department of Agriculture and ABARES, Canberra, 2013.
[63] D. Bucher, P. Saenger, An inventory of Australian estuaries and enclosed marine waters: an overview of results, Aust. Geogr. Stud. 29 (1991) 370–381.
[64] OzCoasts, National intertidal/subtidal benthic habitat), accessed on accessed at ⟨http://www.ozcoasts.org.au/nrm_rpt/habitat_extent.jsp⟩, 2009.
[65] R.J. Williams, G. West, D. Morrison, R.G. Creese, Estuarine Resources of New South Wales, New South Wales Department of Primary Industries, Port Stephens, 2006.
[66] Bureau of Rural Services, Australia's State of the Forests Report: Five-yearly report, Australian Government, Department of Agriculture, Fisheries and Forestry, Canberra, 2008.
[67] P. Fairweather, Saltmarshes, In: Marine Parks Scientific Working Group, (Ed.), The Vulnerability of Coastal and Marine Habitats in South Australia, Department of Environment, Water and Natural Resources, Adelaide, 2011, pp. 59–34.
[68] G.W. Carr, Survey of Victorian coastal saltmarsh distribution in relation to the habitat of the Orange-bellied Parrot. Report to Kinhill Planners Pty Ltd and ICI Australia, Ecology Australia, Fairfield, 1979.
[69] DSE, A Field Guide to Victorian Wetland Ecological Vegetation Classes for the Index of Wetland Condition, Department of Sustainability and Environment, Melbourne, 2012.
[70] (WA Department of Fisheries, Fisheries fact sheet: Mangroves, Government of Western Australia, Department of Fisheries, Perth, 2012.
[71] P. Laegdsgaard, Ecology, disturbance and restoration of coastal saltmarsh in Australia: a review, Wetl. Ecol. Manag. 14 (2006) 379–399.
[72] P. Laegdsgaard, J. Kelleway, R.J. Williams, C. Harty, Protection and management of coastal saltmarsh, in: N. Saintilan (Ed.), Australian Saltmarsh Ecology, CSIRO Publishing, Collingwood, Melbourne, 2009, pp. 149–166.
[73] R.J. Williams, F.A. Watford, Change in the distribution of mangrove and saltmarsh in Berowra and Marramarra Creeks. 1941–1992, Report to Hornsby Shire Council, NSW Fisheries Office of Conservation, Fisheries Research Institute, Cronulla, NSW, 1997.
[74] D. Roberts, From Swampland to Farmland: A History of the Koo-Wee-Rup Flood Protection District, Rural Water Commission Of Victoria, Melbourne, 1985.
[75] GHD. Pty Ltd, Western Basin Dredging and Disposal Project: Environmental Impact Statement, GHD Pty Ltd, and Gladstone Ports Corporation, Brisbane, Australia, 2010.
[76] INPEX Browse Ltd, Ichthys Gas Field Development Project: Draft Environmental Impact Statement, Ichthys Joint Venturers (INPEX and Total E&P), Perth WA, 2007.
[77] H. Poffenbarger, B. Needelman, J. Megonigal, Salinity influence on methane emissions from tidal marshes, Wetlands 31 (2011) 831–842.
[78] J. Sammut, M.D. Melville, R.B. Callinan, G.C. Fraser, Estuarine acidification: impacts on aquatic biota of draining acid sulphate soils, Aust. Geogr. Stud. 33 (1995) 89–100.
[79] C.E. Lovelock, M.C. Ball, K.C. Martin, I.C. Feller, Nutrient enrichment increases mortality of mangroves), PLoS ONE 4 (2009) e5600.
[80] A.S. Mandura, A mangrove stand under sewage pollution stress: Red Sea, Mangroves Salt Marshes 1 (1997) 255–262.
[81] B.F. Clough, K.G. Boto, P.M. Attiwill, Mangroves and sewage: a re-evaluation, in: H. Teas (Ed.), Biology and Ecology of Mangroves, Springer, Netherlands, 1983, pp. 151–161.
[82] I. Valiela, J.M. Teal, W.J. Sass, Production and dynamics of salt marsh vegetation and the effects of experimental treatment with sewage sludge: Biomass, production and species composition, J. Appl. Ecol. 12 (1975) 973–981.
[83] K. Edyvane, Pollution: the death knell of our mangroves? SAFISH 16 (1991) 4–7.
[84] K.S. Edyvane, Coastal and marine wetlands in Gulf St. Vincent, South Australia: understanding their loss and degradation, Wetl. Ecol. Manag. 7 (1999) 83–104.
[85] A.P. Belperio, Negative evidence for a mid-Holocene high sea level along the coastal plain of the Great Barrier Reef Province, Mar. Geol. 32 (1979) M1–M9.
[86] H. Kirkman, Mangroves, in: Marine Parks scientific Working Group, (Ed.), The Vulnerability of Coastal and Marine Habitats in South Australia, Department of Environment, Water and Natural Resources, Adelaide, 2011, pp. 30–35.
[87] K. Rogers, K.M. Wilton, N. Saintilan, Vegetation change and surface elevation dynamics in estuarine wetlands of southeast Australia, Estuar. Coast. Shelf Sci. 66 (2006) 559–569.
[88] L. Eslami-Andargoli, P. Dale, N. Sipe, J. Chaseling, Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia, Estuar. Coast. Shelf Sci. 85 (2009) 292–298.
[89] D. Bucher, P. Saenger, A classification of tropical and subtropical Australian estuaries, Aquat. Conserv.: Mar. Freshw. Ecosyst. 4 (1994) 1–19.
[90] N. Saintilan, K. Rogers, Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings, New Phytol. 205 (2015) 1062–1070.
[91] K.W. Krauss, K.L. McKee, C.E. Lovelock, D.R. Cahoon, N. Saintilan, R. Reef, et al., How mangrove forests adjust to rising sea level, New Phytol. 202 (2014) 19–34.
[92] N. Pontee, Defining coastal squeeze: a discussion, Ocean Coast. Manag. 84 (2013) 204–207.
[93] K. Rogers, N. Saintilan, C. Copeland, Managed retreat of saline coastal wetlands: Challenges and opportunities Identified from the Hunter River Estuary, Australia, Estuaries Coasts 37 (2013) 67–78.
[94] J. Burley, R. McAllister, K. Collins, C. Lovelock, Integration, synthesis and climate change adaptation: a narrative based on coastal wetlands at the regional scale, Reg. Environ. Change 12 (2012) 581–593.
[95] P. Peake, J. Fitzsimons, D. Frood, M. Mitchell, N. Withers, M. White, et al., A new approach to determining environmental flow requirements: sustaining the natural values of floodplains of the southern Murray-Darling Basin, Ecol. Manag. Restor. 12 (2011) 128–137.
[96] L. Shoo, J. O'Mara, K. Perhans, J. Rhodes, R. Runting, S. Schmidt, et al., Moving beyond the conceptual: specificity in regional climate change adaptation actions for biodiversity in South East Queensland, Australia, Reg. Environ. Change (2012) 1–13.
[97] K. Rogers, N. Saintilan, Remapping of the SEPP14 wetlands in the Shoalhaven district, Wetlands 20 (2002) 55–65.
[98] E. Asbridge, R. Lucas, C. Ticehurst, P. Bunting, Mangrove response to environmental change in Australia's Gulf of Carpentaria, Ecol. Evol. 6 (2016) 3523–3539.
[99] R.K. Craig, "Stationary is Dead" – Long live transformation: five principles for climate change adaptation law, Harvard Law Review, vol. 34, 2010, pp. 9–73.
[100] NSW Government, Coastal Management State Environmental Planning Policy: Explanation of Intended Effect, NSW Department of Planning and Environment, Sydney, 2015.
[101] K. Rogers, C. Schofield, Responding to changing coasts: The need for fixed and flexible limits and boundaries in the face of sea level rise, in: C. Esposito, J. Kraska (Eds.), Proceedings of the Law of the Sea Institute Meeting, September 2014, Madrid (in press).
[102] C.D. Woodroffe, K. Rogers, K.L. McKee, C.E. Lovelock, I.A. Mendelssohn, N. Saintilan, Mangrove sedimentation and response to relative sea-level rise, Annu. Rev. Mar. Sci. 8 (2016) 243–266.
[103] J.P. Doody, Coastal squeeze and managed realignment in southeast England, does it tell us anything about the future? Ocean Coast. Manag. 79 (2013) 34–41.
[104] J. Bell, M. Baker-Jones, Retreat from retreat – the backward evolution of sea-level rise policy in Australia, and the implications for local government, 19 Local Gov. Law J. 19 (2014) 23–35.
[105] M. O'Kane, Assessment of the science behind the NSW Governments sea level rise planning benchmarks, NSW Chief Scientist And Engineer, Sydney, 2012.
[106] DECCW, Technical note: Derivation of the NSW Government's sea level rise planning benchmarks, Department of Environment, Climate Change and Water, NSW Government,, Sydney, 2009.
[107] NSW Planning, NSW Coastal Planning Guideline: Adapting to Sea Level Rise, NSW Government, Sydney, 2010.
[108] J.G. Titus, Rolling easements, Climate Ready Estuaries Program, United States Environmental Protection Agency, retrieved from: ⟨https://www.epa.gov/sites/production/files/documents/rollingeasementsprimer.pdf⟩, 2011.
[109] N. Abel, R. Gorddard, B. Harman, A. Leitch, J. Langridge, A. Ryan, et al., Sea level rise, coastal development and planned retreat: analytical framework, governance principles and an Australian case study, Environ. Sci. Policy 14 (2011) 279–288.
[110] D.N. Bengston, J.O. Fletcher, K.C. Nelson, Public policies for managing urban growth and protecting open space: policy instruments and lessons learned in the United States, Landsc. Urban Plan. 69 (2004) 271–286.
[111] A.G. Azad, Community Ecology of Mangrove Birds (Ph.D Thesis), Charles Darwin University, accessed at ⟨http://espace.cdu.edu.au/view/cdu:29981/Thesis_CDU_29981_Mohd_Azlan_J.pdf⟩, 2010 (accessed 16.06.16).
[112] DCC, Climate Change Risks to Australia's Coast: A First Pass National Assessment, Department of Climate Change, Canberra, Australia, 2009.
[113] NSW Government, NSW Sea Level Rise Policy Statement, NSW Government, Sydney, 2009.
[114] Northern Territory Government, Northern Territory Climate Change Policy, Northern Territory Government, Darwin, 2009.
[115] Department of Environment and Heritage Protection, Coastal Management Plan, Queensland Government, Brisbane, 2013.
[116] Queensland Department of Environment and Resource Management, Draft Queensland Coastal Plan 2009, Department of Environment and Resource Management, Brisbane, 2009.

[117] Tasmanian Government, Tasmanian State Coastal Policy, Tasmanian Government, Hobart, 1996.
[118] Department of Premier and Cabinet, Tasmanian Coastal Policy Statement: Consultation draft, Tasmanian Government, Hobart, 2013.
[119] Coastal Protection Board, Coast Protection Board Policy Document, South Australia Coastal Protection Board, Keswick, South Australia, 2004.
[120] Victorian Coastal Council, Victorian Coastal Strategy 2014, The State of Victoria, Department of Environment and Primary Industries, Melbourne, 2014.
[121] J.R. Hunter, Derivation of Victorian Sea-Level Planning Allowances, Report for the Victorian Coastal Council, Flexible Contracting Services for the Victorian Coastal Council, Tasmania, at ⟨http://www.vcc.vic.gov.au/assets/media/files/Final_Report_victorian_allowance_app.pdf⟩ (accessed 16.16.16).
[122] Government of Western Australia, State Planning Policy No. 2.6 State Coastal Planning Policy, Western Australian Government, Perth, 2013.
[123] C. Bicknell, Sea Level Change in Western Australia: Application to Coastal Planning, Government of Western Australia, Western Australia, 2010.
[124] C.D. Ives, S.A. Bekessy, The ethics of offsetting nature, Front. Ecol. Environ. 13 (2015) 568–573.
[125] R.E. Turner, Doubt and the values of an ignorance-based world view for restoration: Coastal Louisiana wetlands, Estuaries Coasts 32 (2009) 1054–1068.
[126] R. Elliot, Faking nature, Inquiry 25 (1982) 81–93.
[127] IPCC, Climate Change 2013: The Physical Science Basis, Technical Summary, accessed at ⟨http://www.climatechange2013.org/images/uploads/WGIAR5_WGI-12Doc2b_FinalDraft_TechnicalSummary.pdf⟩, 2013 (accessed 30.10.13).
[128] P. Dwyer, Successful fish habitat protection and rehabilitation projects: Case studies without a funding application in sight, NSW Coastal Conference, NSW Coastal Conference, Tweed Heads, accessed at ⟨http://www.coastalconference.com/2011/papers2011/ Patrick%20Dwyer%20Full%20Paper.pdf⟩, 2013 (accessed 16.06.16).
[129] J. Ruhl, J. Salzman, I. Goodman, Implementing the new ecosystem services mandate of the Section 404 Compensatory Mitigation Program: a catalyst for advancing science and policy, Stetson Law Rev. 38 (2009) 251–272.
[130] H. Levrel, S. Pioch, R. Spieler, Compensatory mitigation in marine ecosystems: which indicators for assessing the "no net loss" goal of ecosystem services and ecological functions? Mar. Policy 36 (2012) 1202–1210.
[131] US Army Corps of Engineers (Department of Defense), Environmental Protection Agency, Compensatory Mitigation for Losses of Aquatic Resources, Federal Register, vol. 73, 2008, pp. 19594–19705.
[132] S. Cork, G. Stoneham, K. Lowe, Ecosystem services and Australian natural resource management (NRM) futures: Paper to the Natural Resource Policies and Programs Committee (NRPPC) and the Natural Resource Management Standing Committee (NRMSC), Australian Government Department of the Environment, Water, Heritage and the Arts: Canberra, Australia, Canberra, 2007.
[133] S. Burgin, BioBanking: an environmental scientist's view of the role of biodiversity banking offsets in conservation, Biodivers. Conserv. 17 (2008) 807–816.
[134] M.D. Spalding, S. Ruffo, C. Lacambra, I. Meliane, L.Z. Hale, C.C. Shepard, et al., The role of ecosystems in coastal protection: adapting to climate change and coastal hazards, Ocean Coast. Manag. 90 (2014) 50–57.
[135] J. Bell, C. Lovelock, Insuring mangrove forests for their role in mitigating coastal erosion and storm -surge: an Australian case study, Wetlands 33 (2013) 279–289.
[136] C.A. Currin, W.S. Chappell, A. Deaton, Developing alternative shoreline armoring strategies: the living shoreline approach in North Carolina, in: H. Shipman, Dethier, M.N., Gelfenbaum, G., Fresh, K.L., Dinicola, R.S., (Eds.) Puget Sound Shorelines and the Impacts of Armoring, U.S. Geological Survey Scientific Investigations Report 2010-5254, 2010, pp. 91–102.
[137] T.E. Bigford, Nature-based remedies to societal woes, Fisheries 40 (2015) 243.
[138] N. McCristal, Love me tender, Wetlands 27 (2015) 35–36.
[139] C.M.A. West Gippsland, Coastal Saltmarsh Protection Project, accessed at ⟨http://www.wgcma.vic.gov.au/our-region/projects/coastal-saltmarsh-protection-project⟩, 2015 (accessed 07.12.15).
[140] National Biodiversity Strategy Review Task Group, Australia's Biodiversity Conservation Strategy 2010–2030, Australian Government, Department of Environment, Canberra, 2010.
[141] NRMMC, Australia's Strategy for the National Reserve System 2009–2030, Natural Resource Management Ministerial Council, Canberra, 2009.
[142] J. Fitzsimons, P. FitzSimons, C. Ashe, Further strategic additions to Victorias public protected area system: 2002–2004, Vic. Nat. 121 (2004) 214–225.
[143] J. Fitzsimons, G. Wescott (Eds.), Big, Bold and Blue: Lessons from Australia's Marine Protected Areas, CSIRO Publishing, Collingwood, Victoria.
[144] B. Rose, Indigenous protected areas – innovation beyond the boundaries, in: P. Figgis, J. Fitzsimons, J. Irving (Eds.), Innovation for 21st Century Conservation, Australian Committee for IUCN, Sydney, 2012, pp. 50–55.
[145] R. Ullman, V. Bilbao-Bastida, G. Grimsditch, Including Blue Carbon in climate market mechanisms, Ocean Coast. Manag. 83 (2013) 15–18.
[146] W.W.Y. Lau, Beyond carbon: conceptualizing payments for ecosystem services in blue forests on carbon and other marine and coastal ecosystem services, Ocean Coast. Manag. 83 (2013) 5–14.
[147] T. Wood, Direct action can be turned into real climate policy, Financial Review, accessed at ⟨http://www.afr.com/opinion/columnists/direct-action-can-be-turned-into-a-real-climate-policy-20150428–1mv5hq⟩, 2015 (accessed 07.12.15).
[148] E. McLeod, G.L. Chmura, S. Bouillon, R. Salm, M. Björk, C.M. Duarte, et al., A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2, Front. Ecol. Environ. 9 (2011) 552–560.
[149] R.G. Newell, W.A. Pizer, D. Raimi, Carbon markets 15 years after Kyoto: Lessons learned, new challenges, J. Econ. Perspect. 27 (2013) 123–146.
[150] J. Siedenburg, S. Brown, S. Hoch, Voices from the field – carbon markets and rural poverty as seen from Madagascar and Mali, Clim. Dev. (2016) 10–15.
[151] Department of Climate Change and Energy Efficiency, National Carbon Offset Standard, Department of Climate Change and Energy Efficiency, Canberra, 2012.
[152] E. Granek, B.I. Ruttenberg, Changes in biotic and abiotic processes following mangrove clearing, Estuar. Coast. Shelf Sci. 80 (2008) 555–562.
[153] C.E. Lovelock, R.W. Ruess, I.C. Feller, CO_2 efflux from cleared mangrove peat, PLoS ONE 6 (2011) e21279.
[154] B.P. Wilson, I. White, M.D. Melville, Floodplain hydrology, acid discharge and change in water quality associated with a drained acid sulfate soil, Mar. Freshw. Res. 50 (1999) 149–157.
[155] W.S. Hicks, G.M. Bowman, R.W. Fitzpatrick, East Trinity Acid Sulfate Soils Part 1: Environmental Hazards. Technical Report 14/99, CSIRO Land and Water, Canberra, 1999.
[156] J.H.M. Wösten, A.B. Ismail, A.L.M. van Wijk, Peat subsidence and its practical implications: a case study in Malaysia, Geoderma 78 (1997) 25–36.
[157] M. Osland, A. Spivak, J. Nestlerode, J. Lessmann, A. Almario, P. Heitmuller, et al., Ecosystem development after mangrove wetland creation: Plant–soil change across a 20-Year chronosequence, Ecosystems 15 (2012) 848–866.
[158] O.J. Eong, Mangroves – a carbon source and sink, Chemosphere 27 (1993) 1097–1107.
[159] R.K. Runting, C.E. Lovelock, H.L. Beyer, J.R. Rhodes, Costs and opportunities for preserving coastal wetlands under sea level rise, Conserv. Lett. (2016), http://dx.doi.org/10.1111/conl.12239.
[160] R.J. Williams, F.A. Watford, Identification of structures restricting tidal flow in New South Wales, Australia, Wetl. Ecol. Manag. 5 (1997) 87–97.
[161] P. Haines, Hydrological modelling of tidal re-inundation of an estuarine wetland in south-eastern Australia, Ecol. Eng. 52 (2013) 79–87.
[162] A. Lewis, L. Lymburner, M.B.J. Purss, B. Brooke, B. Evans, A. Ip, et al., Rapid, high-resolution detection of environmental change over continental scales from satellite data – the earth observation data cube, Int. J. Digit. Earth 9 (2016) 106–111.
[163] J.R. MacKenzie, N.C. Duke, A.L. Wood, The Shoreline Video Assessment Method (S-VAM): Using dynamic hyperlapse image acquisition to evaluate shoreline mangrove forest structure, values, degradation and threats, Mar. Pollut. Bull. 163 (2016) 751–763.
[164] J. Bellamy, Adaptive governance: the challenge for regional natural resource management, in: A.J. Broan, J.A. Bellamy (Eds.), Federalism and Regionalism in Australia: New Approaches, New Institutions, ANU Press, Canberra, ACT, 2007. pp. 95–117.
[165] J.A. Fitzsimons, L. Hale, B. Hancock, M.W. Beck, Developing a marine conservation program in temperate Australia: determining priorities for action, Aust. J. Marit. Ocean Aff. 7 (2015) 85–93.
[166] M. Parry, J. Lowe, C. Hanson, Overshoot, adapt and recover, Nature 458 (2009) 1102–1103.

Sustainability Science (2019) 14:453–467
https://doi.org/10.1007/s11625-018-0575-0

ORIGINAL ARTICLE

Blue carbon in coastal landscapes: a spatial framework for assessment of stocks and additionality

K. Rogers[1] · P. I. Macreadie[2] · J. J. Kelleway[3] · N. Saintilan[3]

Received: 20 July 2017 / Accepted: 27 April 2018 / Published online: 14 May 2018
© Springer Japan KK, part of Springer Nature 2018

Abstract

Efforts to incorporate blue carbon, the carbon associated with marine ecosystems, into carbon accounting and carbon markets are increasing. To fully leverage the capacity of marine ecosystems to sequester carbon requires information to guide prioritisation of coastal landscapes for conservation and regeneration. A comprehensive landscape-scale assessment of mangrove and saltmarsh blue carbon requires information regarding vegetation cover, sedimentological and geomorphological factors. This information should also be integrated with socio-economic factors that alter natural processes of blue carbon accumulation and storage. The purpose of this study was to provide a framework for undertaking a first-pass assessment of blue carbon storage, preservation, generation and permanency in coastal landscapes, and to incorporate socio-economic factors that will influence blue carbon storage in coastal landscapes. This was achieved using readily available datasets that were analysed using a raster-based approach to develop a proxy indication of biophysical and socio-economic factors relevant for mangrove and saltmarsh blue carbon. The approach demonstrated that large catchments were associated with areas highly suitable for blue carbon storage, preservation, generation and permanency. Small catchments associated with mature barrier estuaries had the highest proportional area that provides potential blue carbon ecosystem services and climate mitigation benefits. The qualitative approach used does not replace high-resolution quantitative assessments of blue carbon storage, flux and detailed site-specific assessment of socio-economic factors that may influence blue carbon services; however, it can be used to guide prioritisation of blue carbon landscapes for further assessment prior to conservation and/or regeneration.

Keywords Mangrove · Saltmarsh · Conservation · Ecosystem services · First-pass assessment · GIS

Introduction

The ambitious emission reduction targets set at the Paris Climate Change Conference will require the implementation of a broad range of mitigation measures. Interest in the management of natural ecosystems as a carbon sequestration opportunity has largely focused on the conservation of terrestrial forests. This has been achieved through, for example, programmes under the REDD+ scheme (Reducing Emissions from Deforestation and Forest Degradation) which preserves carbon sinks associated with forests through conservation and is funded under protocols developed by the United Nations Framework Convention on Climate Change (UNFCCC). Recent evidence has demonstrated that sedimentary environments within coastal landscapes that support mangroves, tidal saltmarshes and seagrasses hold carbon reserves an order of magnitude greater than tropical rainforests; a realisation that has led to growing policy and scientific interest in 'Blue Carbon', that is the carbon

Handled by John Edward Hay, Institute for Global Change Adaptation Science, Ibaraki University, Japan.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11625-018-0575-0) contains supplementary material, which is available to authorized users.

✉ K. Rogers
Kerrylee@uow.eud.au

[1] School of Earth and Environmental Sciences, University of Wollongong, Wollongong, NSW 2522, Australia

[2] School of Life and Environmental Sciences, Deakin University, Melbourne, VIC 3125, Australia

[3] Department of Environmental Sciences, Macquarie University, Sydney, NSW 2109, Australia

associated with marine ecosystems (Duarte et al. 2013; McLeod et al. 2011). Initiatives are currently underway to extend REDD+-type schemes to wetlands, with guidance recently published by the Intergovernmental Panel on Climate Change (IPCC) in the 2013 Wetlands Supplement to the 2006 guidelines for national greenhouse gas inventories (Kennedy et al. 2014).

The impetus to incorporate coastal wetlands into carbon accounting is progressing at local, regional and national scales. At the local scale, below-ground carbon storage and flux between the soil and atmosphere can be measured at sites using standard field and laboratory protocols (Howard et al. 2014). These methods have provided a standardised approach to estimation of carbon across environments and the verification of changes in carbon storage following activities to restore ecosystem function. A Verified Carbon Standard (VCS) for Tidal Wetland and Seagrass Restoration (Emmer et al. 2015) has provided a framework for carbon offsets to be applied to wetland projects. At regional to national scales, carbon gained or lost as a result of activities, including land-use and land-cover change or changes to management practices, can be incorporated into national carbon accounting (Hiraishi et al. 2014). At this scale, emission factors associated with specific land-cover types or land management activities need to be understood and modelled in the context of broad-scale monitoring of land-use change (Kauffman et al. 2014). Understanding the links between land-use/land-cover, carbon storage and carbon flux is, therefore, fundamental to accurate reporting and improvement of coastal landscape management for carbon mitigation benefits. To some degree, vegetation cover provides a useful surrogate for those processes operating at the landscape scale relevant to carbon flux and accumulation. The extent of mangrove and saltmarsh, and to a lesser degree seagrass, can be mapped from aerial photography or active and passive satellite sensors (Giri et al. 2011; Lucas et al. 2014). The position of mangrove and saltmarsh in coastal landscapes is a reflection of salinity, hydroperiod and the stability of intertidal sediments, all factors relevant to the long-term storage of carbon in situ. Where mangrove and saltmarsh co-occur, such as the coastlines of Australia, Gulf of Mexico, South Africa, China and Brazil, mangrove generally supports a higher above- and below-ground carbon stock than saltmarsh (Kelleway et al. 2017, 2016a), and where land-cover has transitioned from saltmarsh to mangrove, the increase in below-ground carbon storage is measurable (Kelleway et al. 2016b).

Vegetation cover is an important biological indicator of the capacity to generate blue carbon; however, sedimentological properties are also important predictors of carbon storage and flux (Kelleway et al. 2016a; Serrano et al. 2016). Mangrove and saltmarsh typically grow in sedimentary landscapes that accumulate mineral and carbon-rich organic material over extended time periods (Woodroffe et al. 2016). This is a particularly important consideration in the context of coastal landscapes that have evolved in response to sea-level rise over the Holocene (Allen 2000; Rogers and Woodroffe 2014; Woodroffe et al. 2014). Palaeoecological analyses indicate mangrove and saltmarsh adapt to sea-level rise by accumulating sediments and organic material within coastal bedrock valleys in response to 120 m of Quaternary sea-level rise (Woodroffe et al. 1993). The long history of sea-level stability in Australia has facilitated geomorphological evolution of coastal landscapes. Accordingly, areas that once supported blue carbon ecosystems and facilitated storage within sediments may no longer support these ecosystems, as geomorphological conditions are no longer suitable. In these cases, the carbon within substrates associated with prior blue carbon ecosystems may be preserved; however, further additions of blue carbon within substrates are limited by the absence of a contemporaneous blue carbon ecosystem. Here we refer to this carbon as 'fossil blue carbon'; that is carbon within a coastal landscape sourced from a prior blue carbon ecosystem and stored within sediments that have accumulated over geological timescales within coastal landscapes. This carbon may constitute a significant proportion of blue carbon storage. Drainage of landscapes supporting 'fossil blue carbon' has been implicated in the development of acid sulfate soils and deleterious environmental impacts (Lin and Melville 2010). Geomorphological evolution of blue carbon ecosystems over the Holocene and their sedimentological character are more physically related to landscape geomorphology. Consequently indicating the capacity for storage of fossil blue carbon is not feasible using spectral imagery.

Evidence indicates that carbon storage in wetland and floodplain environments varies in predictable ways in association with geomorphological factors. For example, whether a coastal wetland is a greenhouse gas (GHG) source or sink is highly dependent on the soil chemical and physical characteristics. Anaerobic wetland soils in freshwater settings are prone to the production of methane and nitrous oxides. Their production may offset the benefits of CO_2 sequestration (Megonigal et al. 2005). In sandy environments where soils are well drained, oxidation leads to the rapid loss of carbon (Kelleway et al. 2016a; Saintilan et al. 2013). However, in saline, fine-grained environments where oxidation is lower and conversion to carbon dioxide is inhibited, methane and nitrous oxide production is also greatly reduced, and carbon sequestration and storage conditions are ideal. These changes are thought to be microbially mediated (Emerson et al. 1999). In particular, sulfur-reducing bacteria compete with methanogenic bacteria, effectively shutting down methane production in sites inundated by sulfate-rich waters of half seawater salinity or greater (Poffenbarger et al. 2011). In addition, coastal processes, such as erosion, may pose

a physical threat to the long-term retention of soil carbon in situ. Coastal wetland soils can erode as a result of changes to the direction of river-flow, wind direction and the prevalence of coastal currents (Alongi 2011), as well as storm wave erosion and the gradual impact of sea-level rise (Kirwan and Megonigal 2013). Once remobilised, organic carbon may be either transported to new locations for burial, or remineralised in transit (DeLaune and White 2012; Kirwan and Mudd 2012; Macreadie et al. 2013, 2015). Few studies have considered the proportion of carbon reburied following erosion. Sampere et al. (2008) point to the relatively low macrophyte carbon content of seabeds of the Louisiana continental margin following Hurricane Ivan; these seagrass beds were thought to be the destination of material eroded from the Mississippi delta during storms. Low carbon preservation on inner shelf sediments in several locations suggests low preservation for transported material (DeLaune and White 2012; White et al. 2009).

Human activities in coastal landscapes also exert both direct and indirect pressure on blue carbon and have the capacity to limit blue carbon generation and preservation (McLeod et al. 2011). The effect of human activities on blue carbon is only accounted for in land-use/land-cover mapping in the broadest sense. This is achieved by quantifying direct impacts, such as development and land-use conversion, which reduces the capacity for blue carbon generation, and may also provide the means for mobilisation of in situ blue carbon within sediments (Macreadie et al. 2013). Indirect effects on blue carbon caused by human activities in coastal landscapes may also be significant (Coverdale et al. 2014). To this end, three management activities were recently proposed that may optimise coastal blue carbon sequestration: reducing anthropogenic nutrient inputs; reinstating top-down control of bioturbator populations; and restoring hydrology to blue carbon ecosystems (Macreadie et al. 2017).

Current vegetation-based assessments of blue carbon, including land-use/land-cover mapping, are particularly effective at indicating the capacity for blue carbon generation, yet do not adequately describe blue carbon storage or preservation in coastal landscapes. Sediments rich in fossil blue carbon may no longer support blue carbon ecosystems due to landscape evolution to another ecosystem type (e.g. freshwater wetland or low-lying terrestrial forest), or conversion to another land-use (e.g. urbanization and agriculture) at times pre-dating the earliest record of aerial photography, and are typically excluded from analyses of blue carbon in coastal landscapes. The effect of coastal processes at smaller spatial scales that influence storage and preservation, such as methanogenesis and erosion are assumed to be either homogenous or irrelevant within analyses. In addition, the indirect effects of human activities are rarely considered in assessments targeted towards improving blue carbon management. A comprehensive landscape-scale assessment of blue carbon that is useful for both carbon accounting and prioritising management activities, therefore, requires consideration of vegetation cover, geomorphological and sedimentological factors and processes, and indirect effects of human activities that are likely to influence long-term carbon retention or loss. We provide a framework for the synthesis of commonly collected datasets that can be used in a first-pass assessment to indicate vegetation, geomorphological and sedimentological factors crucial for blue carbon storage, preservation, generation and permanency in coastal landscapes. Estuarine geomorphological units have been mapped in the estuaries of NSW, Australia, at a scale similar to the mapping of mangrove and saltmarsh. In addition, as current land management can significantly influence carbon stocks and the capacity for blue carbon sequestration, we have also integrated socio-economic factors in to the first-pass assessment, using land-use mapping as an indication of current land management practices and the indirect effect of human activities on blue carbon permanency. This study represents the first efforts to integrate biophysical factors and socio-economic factors that may influence blue carbon within an integrated framework.

Defining coastal blue carbon landscapes

Blue carbon, and in particular, the carbon associated with mangrove and saltmarsh, accumulates and decomposes in coastal landscapes at varying rates. Carbon has accumulated within coastal bedrock valleys in conjunction with sedimentary infill of estuaries that occurred after the last marine transgression. In southeastern Australia this process of estuarine infill commenced approximately 7 ka when sea levels stabilised at levels near mean sea level, though may have been up to 2 m higher (Lewis et al. 2013; Sloss et al. 2007). The existence of fossil blue carbon is dependent upon two primary factors: space for storage (i.e. sedimentary volume) and preservation of stored carbon (i.e. anaerobic conditions). Geological and morphological information, particularly the provenance and composition of Quaternary sediments in coastal landscapes and land elevations with respect to past sea levels, has been used as indicators of vulnerability to climate change (Rogers and Woodroffe 2016) and distribution of pre-European wetland habitats (Rogers et al. 2016a), and may act as a proxy indicator of fossil carbon storages.

A recent study of carbon accumulation indicated that blue carbon was primarily generated by autochthonous accumulation in mangrove and saltmarsh (Saintilan et al. 2013). The preservation of this carbon is also dependent upon inundation to create anaerobic conditions and supply of sulfates that suppress methanogenesis (Poffenbarger et al. 2011). The capacity for blue carbon generation in coastal landscapes can be indicated by mapping the current distribution of mangrove and saltmarsh across coastal landscapes with varying

degrees of accuracy, precision and resource efficiency using field or remote-sensing techniques. Accuracy and precision may be reduced in favour of resource efficiency when assessments are undertaken at regional or national scales. As mangrove and saltmarsh are typically positioned between mean sea level and highest astronomical tide (Clarke and Hannon 1967), landscape elevation data complemented with information about sediment composition may be applied as proxy indicators of the current capacity for blue carbon generation.

The ongoing preservation of carbon and future carbon sequestration is dependent upon the capacity for carbon to continue accumulating in coastal landscapes. Climate change, and in particular erosion and inundation associated with sea-level rise and altered storm regimes, may limit the capacity for ongoing sequestration of carbon within coastal landscapes and facilitate the removal of carbon. Projecting the effect of climate change on blue carbon ecosystems is complex and requires a high degree of information about rates of sea-level rise, sediment supply, land subsidence, plant productivity and future landscape management (Rogers et al. 2012; Woodroffe 1990). Rogers and Woodroffe (2016) characterised the vulnerability of estuaries to climate change using geological and morphological information that was applied to the vulnerability framework advocated in the third assessment report of the IPCC. This framework characterises vulnerability on the basis of exposure to climate change drivers, sensitivity of assets to these drivers and the adaptive actions implemented to offset any potential impacts (Parry et al. 2007). Exposure to climate change drivers may suitably indicate the ongoing permanency of carbon in the twenty-first century.

In this study, we have focused on the three timescales relevant for management of blue carbon within coastal landscapes: geological, contemporary and future. As such, we have developed a pixel-based approach that can be applied in GIS, whereby raster cells are ranked and summed according to specific criteria. This approach uses readily available spatial datasets to indicate blue carbon storage, preservation, generation and permanency within coastal landscapes. We have applied this technique at a large spatial scale, though the technique may be refined to use high-resolution datasets and more complex models as indicators. Spatial data layers were generated to characterise biophysical parameters that influence blue carbon within coastal landscapes. These include the following:

- *Storage* defined as the volume of blue carbon within coastal sediments. The premise of this raster layer is that larger volumes, which have accumulated extensive quantities of carbon over the Holocene will store more carbon-rich sediment. Consequently, mature estuaries, with broad coastal plains that have accumulated significant volumes of mineral and organic material, will store more blue carbon that was generated over geological timescales than immature estuaries that have larger water bodies and have undergone less estuarine infill with sediments. In addition, coastal barrier sediments are highly dynamic and exposed to hydrodynamic conditions more typical of the open ocean; reworking of carbon within coastal barriers can be a significant limiting factor for carbon storage. Conversely, alluvial/fluvial sediments have had the longest period to accumulate, under reduced energy conditions and are reported to store greater volumes of carbon than estuarine or marine sediments (Saintilan et al. 2013).
- *Preservation* defined as the capacity for coastal blue carbon to be stored within sediments and soils. There is evidence to indicate that carbon storage is greater in silts and clays, typical of sediments of estuarine and alluvial origins. Coastal barrier sediments that are typically dominated by sands store less carbon due to greater oxidation of sediments (Kelleway et al. 2016a). Due to significant decline in hydrodynamic energy as tributaries enter estuaries, fluvial deltas are composed predominantly of finer grain sizes, yet are influenced by tidal inundation, resulting in saline conditions ideal for ongoing preservation of stored carbon.
- *Generation* defined as the capacity for existing ecosystems to generate biomass and store carbon within living biomass, dead organic material or soil organic carbon. Several reviews suggest that carbon sequestration is greater by mangrove than saltmarsh (Chmura et al. 2003; Pendleton et al. 2012). In southeastern Australia, where both ecosystems co-occur, mangrove is associated with estuaries and lower positions in the tidal frame, while saltmarsh occurs at higher elevations in the tidal frame. Carbon sequestration by saltmarsh is spatially variable, and can be particularly high near the landward margins where vegetation may be dominated by rushes of *Juncus krausii*, or trees and shrubs such as *Casuarina glauca* or *Melaleuca* species (Northam 2016; Saintilan et al. 2013). Furthermore, carbon stored within sediments of fluvial origin typically have higher carbon storage than sediments of estuarine or marine origin (Kelleway et al. 2016a; Saintilan et al. 2013).
- *Permanency* defined as the capacity for carbon to remain in situ. In the context of projections of sea-level rise and increased storminess, the permanency of carbon has been questioned (DeLaune and White 2012; Kirwan and Mudd 2012). In this sense, lower elevations associated with shorelines exhibit greater exposure to erosive wave action, while coastal barrier sediments where wave energy is high, and tidal attenuation is low receive near full exposure to marine drivers that will limit translocation and reworking of coastal blue carbon (Alongi 2008).

These biophysical factors were subsequently intersected with land-use mapping to characterise the compatibility of blue carbon in coastal landscapes with socio-economic factors that may influence blue carbon storage, preservation, generation and permanency. To validate this first-pass assessment, we also investigated whether relationships could be established between outcomes from the first-pass assessment and geomorphological factors such as catchment size, and estuary type and estuary maturity, as defined by Roy et al. (2001).

Method

Study region

In southeastern Australia, estuaries form predominantly behind sand barriers on a wave-dominated coastline, and rivers prograde fluvial deltas into open mud basins (Roy et al. 2001). Intertidal mud basin and fluvial deltaic environments offer the potential of high carbon preservation (Saintilan et al. 2013), and mangrove and saltmarshes in these settings support the highest stocks of carbon in the upper metre of soils, twice that of sandy marine deltas (Kelleway et al. 2016a). Over time, the infilling of estuaries results in further accretion of intertidal habitat to supratidal floodplain, within which intertidal peats may be preserved for thousands of years (Hashimoto et al. 2006; Saintilan and Wilton 2001). The South Coast of New South Wales, Australia is a wave-dominated coastline that extends from the Illawarra region to the NSW-Victorian border (Fig. 1). The coastline is characterised by rocky headlands, pocketed beaches, a few larger embayments and many estuaries positioned behind coastal barriers. Roper et al. (2011) identify more than 100 well-defined estuarine waterbodies. Coastal landscapes are demarcated by the Southern Tablelands and Southern Highlands which confine many smaller coastal catchments. Only the larger catchments of the Shoalhaven, Clyde, Moruya, Tuross, Bega and Towamba Rivers drain areas on the highlands and tablelands.

Due to the high wave energy and dominant southeasterly wave direction, coastal blue carbon ecosystems (i.e. mangrove, saltmarsh and seagrass) are restricted to larger coastal embayments or within estuaries, behind coastal barriers. Conceptual models of the geomorphological evolution of these estuaries have been developed by Roy (1980) and redefined by Roy et al. (2001). These models describe the zonation of estuaries on the basis of dominating processes (i.e. river, wave or tide energy), and the evolution of estuaries on the basis of sedimentary infill of bedrock valleys and the development of flood-tide and fluvial deltas. Accordingly, seagrass habitats are conceptualised to be more extensive in immature estuaries due to larger sub-tidal estuarine areas, while mangrove and saltmarsh are more extensive in mature estuaries where sedimentary infill of bedrock valleys has facilitated the development of intertidal floodplains (Roy et al. 2001).

First-pass assessment

A raster-based approach using the spatial analyst extension in ARCGIS was used to undertake the first-pass assessment of blue carbon landscapes. Input geological and morphological spatial data sets were used as proxy indicators of blue carbon storage, preservation, generation and permanency. As this study was undertaken at a regional scale and focused on coastal landscapes rather than individual ecosystems, we used Quaternary and bedrock geology mapping (Troedson et al. 2004) and Shuttle Radar Topography Mission-derived 1 s Digital Elevation Model (SRTM-DEM). High-resolution measurements of soil and sediment provenance, carbon content at various soil depths and high resolution elevation data, such as DEMs derived from light detection and ranging (LiDAR) or elevations derived from real time kinetic—global positioning systems may provide improved accuracy. Similarly, complex hydrodynamic modeling may provide additional information about exposure to climate change drivers. However, these approaches are data intensive and cost inefficient and consequently cannot be readily applied at the landscape or regional scale.

The SRTM_DEM has the largest spatial resolution of all data sets used in the assessment, with a raster cell size of approximately 30 m × 30 m. Consequently, the SRTM_DEM was used as the template for cell position and cell size when converting vector-based bedrock and Quaternary geology data sets to raster layers. The SRTM_DEM does not reliably indicate elevations below 0 m (Australian Height Datum), which approximates mean sea level; consequently, the first-pass assessment focused only upon landscape surfaces higher than 0 m AHD. Following conversion of all spatial data to raster format, choropleth raster maps were prepared to indicate blue carbon storage, preservation, generation and permanence. These maps were generated according to the geological and morphological criteria detailed in Table 1. For simplicity, we chose to characterise the capacity of blue carbon landscapes to store, preserve, generate and permanently retain blue carbon according to a relatively simple scale of high, moderate or low capacity. In doing so, this approach reduced processing resource requirements in favour of increasing the factors incorporated into the analysis. The extract function was used to identify relevant cells, which were subsequently reclassified according to their capacity for storage, preservation, generation or permanency.

To characterise the biophysical factors related to blue carbon within coastal landscapes a blue carbon indicator

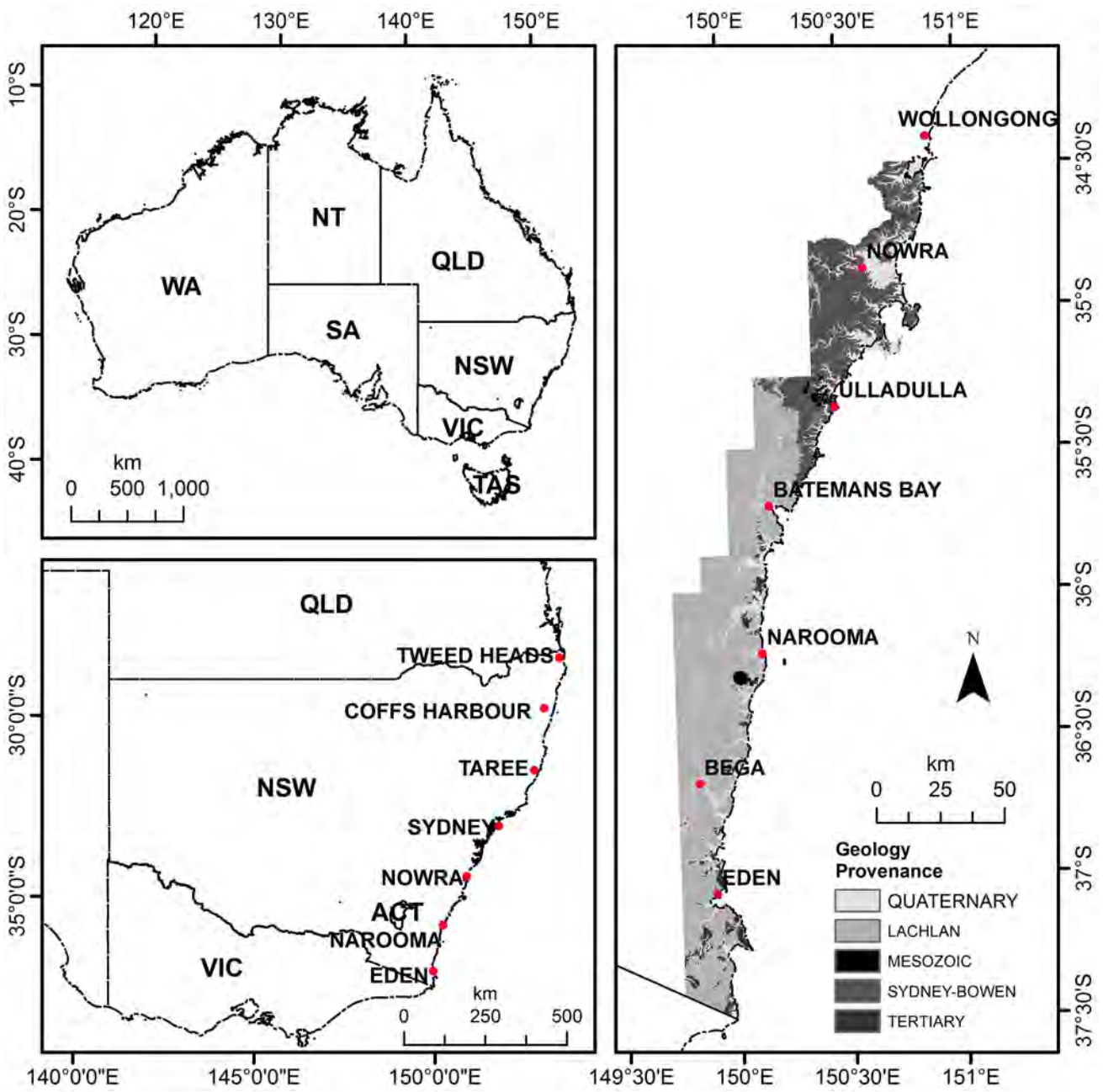


Fig. 1 Location of study site on the southeastern coast of New South Wales, and the bedrock, tertiary and quaternary geology of the region. The map boundary indicates the spatial extent of available datasets

choropleth (BCI) map was prepared using the raster calculator to add the prior choropleth maps of blue carbon storage, preservation, generation and permanency together. Cell values ranged between three and 12. To assist with interpretation of the BCI map and remove bias from classification, the generated choropleth map was reclassified to produce a final blue carbon indicator map using the equal interval classification, with classes labelled:

- High when cell values were greater than 9;
- Moderately high when cell values were 7–8;
- Moderate when cell values were 6;
- Moderately low when cell values were 4–5;
- Low when cell values were 3; and
- Nil when cell values were 0 (i.e. no blue carbon likely to be in the landscape).

Table 1 Approach applied to determining biophysical indicators of blue carbon potential including storage, preservation, generation and permanency within estuaries. In combination, these factors were used to generate BCI maps

BCI component	Geomorphic indicator	Description of indicator	Cell label (value)	Cell description
Storage	Elevation, geology (sedimentary and bedrock)	Mature estuaries have larger volume of sediment accumulated over the Holocene compared to immature estuaries Quaternary sediments in mature estuaries have more areas with low slopes (low topographic relief) Finer grained sediments associated with alluvial and estuarine plains store more carbon than sandy sediments associated with coastal barriers	High (3)	Alluvial plain/estuarine plain + elevation 2–5 m
			Moderate (2)	Alluvial plain/estuarine plain + elevation 0–2 m; or alluvial plain/estuarine plain + elevation > 5 m
			Low (1)	Coastal barrier
			Nil (0)	Bedrock geology
Preservation	Geology (sedimentary and bedrock)	Estuarine sediments exhibits ideal anaerobic and saline conditions for carbon preservation Alluvial sediments increasingly brackish Marine sediments increasingly oxidised or reworked	High (3)	Estuarine plain sediments
			Moderate (2)	Alluvial plain sediments
			Low (1)	Coastal barrier sediments
			Nil (0)	Bedrock geology
Generation	Elevation, geology (sedimentary and bedrock)	Lower intertidal areas support mangrove; upper intertidal areas support saltmarsh Saltmarsh in fluvial environments have higher generation capacity than estuarine and marine environments	High (3)	Quaternary deposits + elevation 0–1 m
			Moderate (2)	Alluvial plain + elevation 2–5 m
			Low (1)	Coastal barrier/estuarine plain + elevation 1–2 m
			Nil (0)	Bedrock geology
Permanency	Elevation, geology (sedimentary and bedrock)	Lower elevations and shorelines exhibit greater exposure to wave action Marine drivers exhibit history of operating near coastal and estuarine quaternary deposits	High (3)	Coastal barrier/estuarine plain + elevation > 5 m; or Alluvial plain
			Moderate (2)	Estuarine plain + elevation < 5 m
			Low (1)	Coastal barrier + elevation < 5 m
			Nil (0)	Bedrock geology

Integration with socio-economic factors

The BCI map was integrated with NSW land-use maps (DECC 2007) to identify where socio-economic factors may provide additional benefit or risk for blue carbon generation, preservation or storage. This was achieved by converting vector-based land-use maps to raster surfaces on the basis of the major land-use category. As detailed in Table 2, these categories were subjectively reclassified to have values of high, medium and low that represented their compatibility with the generation, preservation and storage of blue carbon. The resulting categorised map indicated blue carbon compatibility (BCC). The raster calculator tool was used to multiply the BCI and BCC maps to provide an overall indication of locations within the coastal landscape of south-eastern NSW where blue carbon was indicated to be high (i.e. BCI map) and existing land-use would enable continued generation, preservation and storage (i.e. BCC map). Again, to aid interpretation and remove bias from classification, this map was reclassified using the equal interval classification to create a blue carbon potential (BCP) map.

Statistical analysis

To aid interpretation of maps, the area (ha) of BCI, BCC and BCP values was calculated for each catchment and converted to a proportion of the total catchment area. This conversion provided the means to undertake further statistical analyses that would provide insight into the landscape factors that contributed to higher BCI, BCC, and BCP scores. Statistical analyses were initially undertaken to identify whether linear relationships existed between the generated map variables and catchment size using regression analyses. The premise of this analysis was that a threshold catchment size might be required to maximise blue carbon potential. For example, analyses investigated whether a correlation could be established between the proportion of a catchment identified as having blue carbon potential based on the BCP map and

Table 2 Approach applied to determining socio-economic indicators of blue carbon potential and to generate BCC maps

Major land-use category	Cell label (value)	Description of land-use category
Conservation area	High (3)	Crown reserve, cultural heritage site, foreshore land, marine park, national park, nature reserve, conservation area, riparian reserve, regeneration area, state forest, state recreation area, tree lot
Cropping	Low (1)	Continuous or rotation cropping, or with fixed irrigation system, sometimes within ephemeral wetland or lake, may include large crop areas of fodder, rice, sugar cane
Grazing	Moderate (2)	Occurs in range of landscapes including flood runners, firebreaks, agroforestry, ephemeral wetland, native vegetation, riparian land, irrigated pastures, rangelands, cleared land, and grassland
Horticulture	Low (1)	Plantations of banana, bamboo, eucalypt, cut flowers, grass, nursery, olives, orchards, tea tree, tea, coffee, turf, vegetables, vineyard
Intensive animal production	Low (1)	Poultry, abattoirs, cattery, animal production of beef, dairy, poultry, piggery, horse studs, sale yards
Mining/quarrying	Low (1)	Derelict and abandoned mines and quarries, grassland within mining lease, mine and quarry sites, restored mining land
Power generation	Moderate (2)	Energy corridors, abandoned power stations, substations, gas supply, and green power
River drainage system	Moderate (2)	Channels, estuarine waters, dams, lakes and lagoons, evaporation basins, marinas, river training, navigation structure, river channel filled with aquatic vegetation, water supply channel, weir
Special category	Moderate (2)	Beach, cliff, crown reserve with public access, defense utilities, foreshore protection, aboriginal land, levees, sand spits
Transport	Low (1)	Airports, railway, communication facilities, roads and road reserves, trig stations, beacons
Tree/shrub cover	High (3)	Hardwood, pine, poplar, rainforest, softwood plantations, native forest, logged and regenerated native forest, native woody shrub, riparian vegetation, tree lot, tree corridor
Urban	Low (1)	Residential, rural residential, landfill, abandoned urban or industrial land, aboriginal settlements, caravan parks, cemeteries, waste dump, recreation, tourism, education
Wetland	High (3)	Floodplain swamp, mangrove, mudflat, oyster leases, saltmarsh freshwater swamp

the catchment area. Full factorial ANOVAs were also used to determine whether geomorphological characteristics of estuaries predicted the observed patterns in the first-pass assessment. Geomorphological characteristics included estuary type and the degree of infill or maturity. The classification applied was based on Roy et al. (2001) with estuary type being either: type I Bays, II tide-dominated estuaries, III wave-dominated estuaries or IV intermittent estuaries. Estuary maturity was classified as either: (A) youthful, (B) intermediate, (C) semi-mature, or (D) mature. As there were only two type I estuary catchments included in the first-pass assessment (i.e. Ulladulla Harbour and Batemans Bay; Jervis Bay was divided into sub-catchments of Cararma Inlet, Currambene Creek and Moonee Moonee Creek) and one type II estuary (i.e. Clyde River), these estuaries were excluded from the ANOVAs to improve the degrees of freedom.

Results

The estuaries' maximum and minimum area (ha) of high BCI, BCC and BCP are provided in Table 3a. Shoalhaven River (Fig. 2) exhibited the highest BCI and BCP; however, the Clyde River exhibited the highest BCC. With respect to

Table 3 (a) Estuaries with maximum and minimum area of high BCI, BCC and BCP (area in brackets); and (b) Estuaries with maximum and minimum proportion of their catchment with high BCI, BCC and BCP (% area of estuaries in brackets)

	High BCI	High BCC	High BCP
(a) Catchment (Area in ha)			
Min	Meringo Creek (0.35)	Wrights Creek (18)	Werri Lagoon (0.087)
Max	Shoalhaven River (7800)	Clyde river (113 000)	Shoalhaven River (1900)
(b) Catchment (proportion)			
Min	Mollymook Creek (0%), Ulladulla Harbour (0%)	Ulladulla Harbour (0%)	Mollymook Creek (0%), Ulladulla Harbour (0%), Wrights Creek (0%)
Max	Cararma Inlet (18%)	Merrica River (100%), Table Creek (100%), Nadgee Creek (100%)	Cararma Inlet (16%)

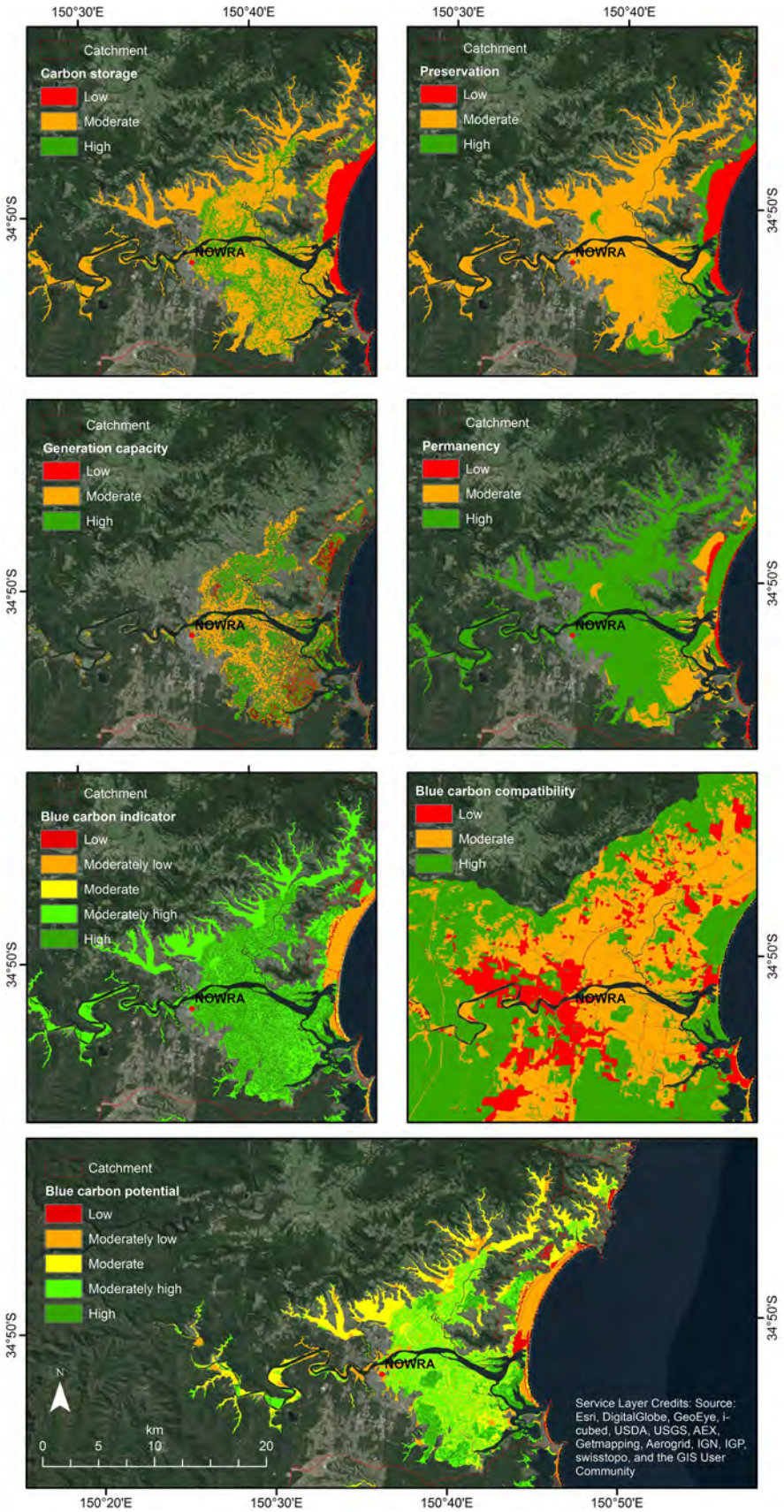


Fig. 2 Generated blue carbon indicator (BCI), compatibility (BCC) and potential (BCP) maps for the Shoalhaven River catchment

the proportion of the total catchment area, Cararma Inlet (Fig. 3) had the maximum proportion of high BCI and BCP within its catchment, while a number of small creeks whose catchments lie entirely within land-use categories receiving a high BCC score, such as national park or nature reserve, exhibited the highest BCC (Table 3b). For detailed maps of BCI, BCC and BCP for the study region see Supplementary Figures. For detailed quantification of the area of blue carbon storage, preservation, generation, permanency, BCI, BCC and BCP by catchment see Supplementary Tables 1 and 2, respectively.

Significant relationships were established between high and total BCI, BCC and BCP and catchment area (Model 1: Table 4); however, the coefficient of determination for the relationship between high and total BCC and catchment area was relatively low. The large catchments of the Shoalhaven, Clyde, and Bega Rivers, with catchment areas greater than 50,000 ha, exceeded individual confidence intervals for regression models (Fig. 4), indicating that relationships between BCI, BCC, BCP and catchment area weaken as the catchment size increases. This relationship is associated with a greater proportion of the catchment being outside of the coastal low-lands. Full factorial ANOVAs indicated that relationships between biophysical and socio-economic factors important for a first-pass assessment of blue carbon potential were improved when accounting for the influence of estuary type and estuary maturity (Model 2: Table 4b) (See supplementary Table 3 for full factorial effects tests).

Discussion

Readily available datasets were used to present a spatial prioritisation of likely blue carbon stocks and their relation to land tenure and usage. This analysis assists with prioritisation at the regional and estuary scales. At the regional scale it enables distinguishing between estuaries on the basis of the scale of potential activities, such as restoration or conservation, that may enhance blue carbon sequestration. At the estuary scale, it facilitates distinguishing between geomorphic settings that have great BCP when focusing on-ground activities to enhance blue carbon storage. On the basis of this approach, we have identified some generalisations regarding prioritisation; large catchments have the greatest extents categorised as having high BCI and BCP, while small catchments, and particularly those located within reserves have the highest proportion of the catchment categorised as having high BCI and BCP. In addition, strong relationships were established between catchment size, estuary type and estuary maturity; large mature barrier estuaries, in particular, had the greatest area of all mapped variables.

Several opportunities to include blue carbon in wetland management and restoration exist under current national legislation and policy in many countries, even though no specific mention of this ecosystem service may be obvious (Rogers et al. 2016b; Sutton-Grier et al. 2014). For example, in the United States, the *Federal Water Pollution Control Act* (1948), also known as the Clean Waters Act, requires that compensatory wetlands be established *in lieu* of wetland destruction or modification. Sutton-Grier et al. (2014) argue that the restoration of carbon ecosystem services can and should be considered in determining the nature of compensatory wetland habitats being created under the provisions of the Clean Waters Act. Specifically, the carbon within a lost saltmarsh and the carbon sequestration potential of the wetland should be quantified by the US Army Corp of Engineers when establishing specifications for an equivalent wetland. Implementation of these policy initiatives is contingent upon an understanding of the distribution of blue carbon in coastal landscapes, and the potential of sites to continue sequestering carbon. The landscape-scale analysis of variability in blue carbon storage, preservation, generation and permanency presented in this study, which accounts for both biophysical and socio-economic factors, allows for the identification of hotspots for conservation. In addition, favourable candidate sites for investment in remediation or restoration for carbon sequestration benefits can also be identified. Validation of the suitability of hotspot sites for remediation or restoration can subsequently be undertaken through field-based analysis of potential sites. As spatial variability in carbon storage, preservation and permanence are considered; our approach goes a long way towards identifying the suitability of settings for compensatory works.

Coastal blue carbon can also contribute to national and regional priorities in wetland conservation and restoration. Additions to the reserve system, such as coastal national parks, the National Estuarine Research Reserve System in the United States, or internationally significance wetlands designated under the Ramsar Convention, are currently prioritised against a range of values including ecological values, representativeness, condition and opportunity. Carbon storage and sequestration is an additional value that could be considered when increasing conservation efforts. Funds made available by Federal and State/Regional governments for wetland restoration could consider not only long-term viability under climate change but carbon sequestration potential as a condition of grants, or a factor in assessment and selection of proposals. Sutton-Grier et al. (2014) show how this could be applied to the assessment of Coastal Zone Enhancement Grants in the USA. In the context of south-eastern NSW, our analysis would suggest, for example, that the Bega River, the Shoalhaven River (Fig. 2) and Tuross Lakes are sites would provide a range of attractive options for improving blue carbon benefits, and these benefits could be incorporated into conservation programs. These estuaries are located within wide coastal valleys that are largely

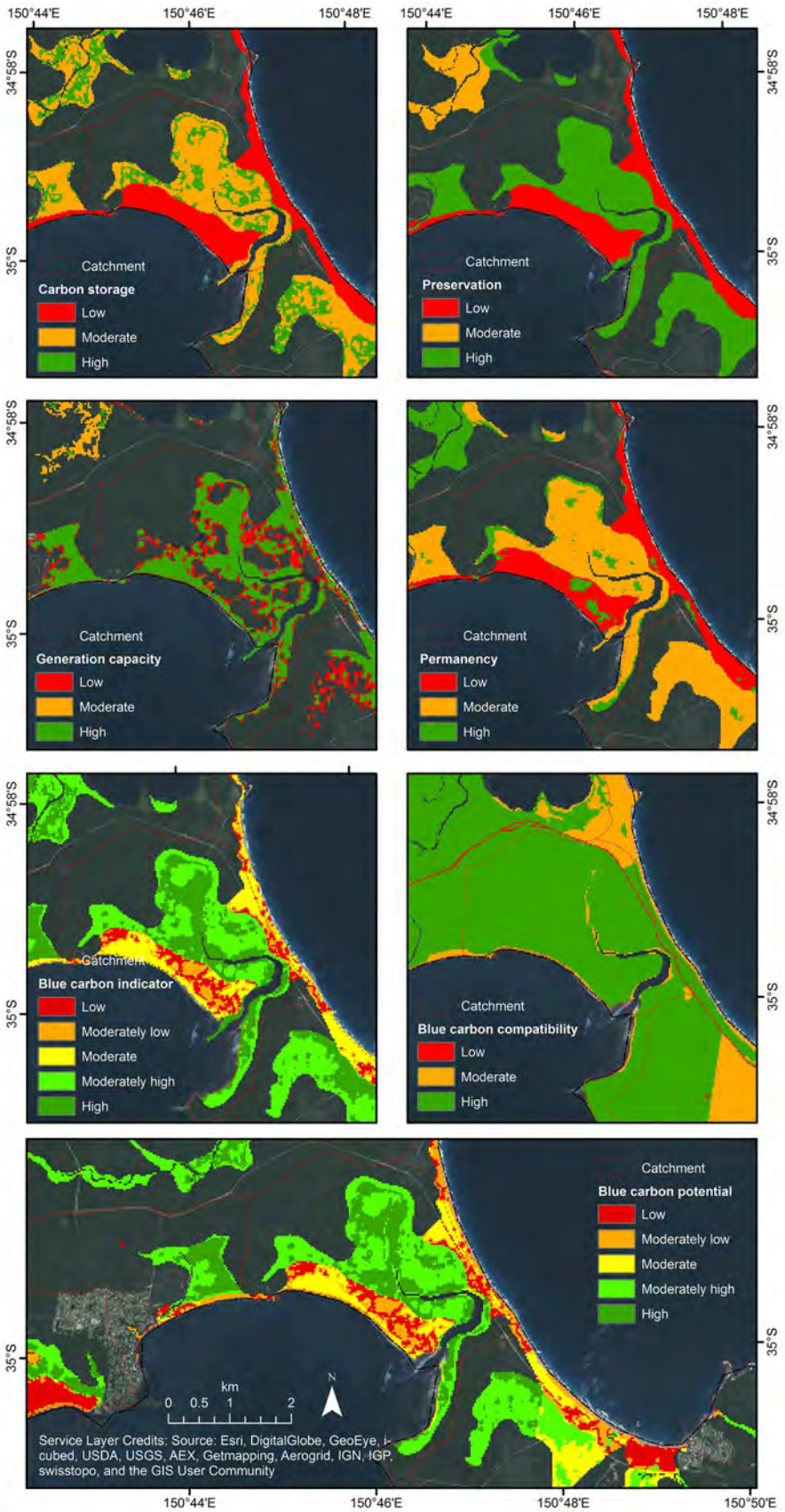


Fig. 3 Generated BCI, BCC and BCP maps for the Cararma Inlet catchment

Table 4 (a) Statistical results from linear regression analysis of the area of high and total BCI, BCC and BCP and catchment area; and (b) statistical results from factorial ANOVA of high and total BCI, BCC and BCP and catchment area, estuary type and estuary maturity

(a) Model 1: linear regression						
Fixed parameter	Catchment area (ha)					
Response variable	BCI high (ha)	BCI total (ha)	BCC high (ha)	BCC total (ha)	BCP high (ha)	BCP total (ha)
R^2	0.94	0.91	0.37	0.54	0.92	0.92
F ratio	976.97	681.48	381.17	76.41	745.16	723.10
p value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
(b) Model 2: full factorial ANOVA						
Fixed parameters	Catchment area (ha) Estuary type (III or IV) Estuary maturity (A, B, C, D)					
Response variable	BCI high (ha)	BCI total (ha)	BCC high (ha)	BCC total (ha)	BCP high (ha)	BCP total (ha)
R^2	0.97	0.97	0.93	0.93	0.95	0.97
F ratio	121.99	96.38	45.85	41.08	68.96	96.40
p value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Effect tests from full factorial analysis in Supplementary Table 3

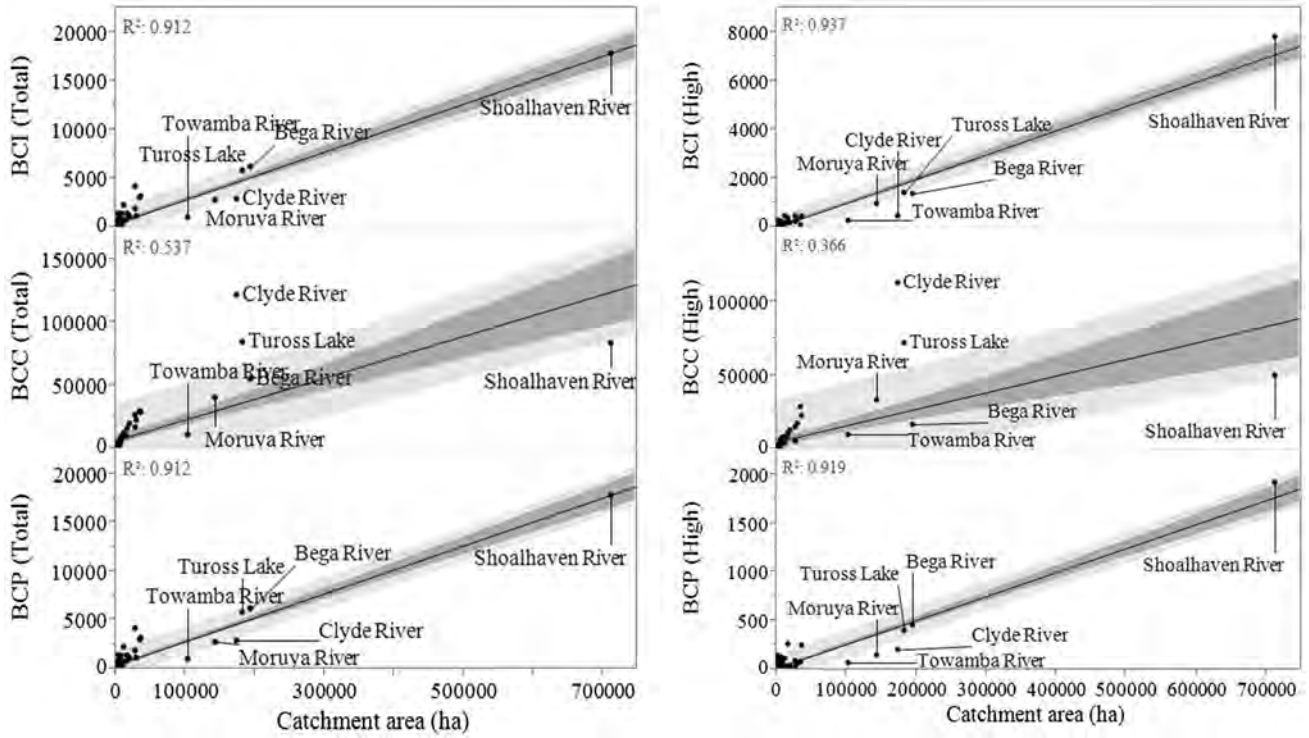


Fig. 4 Regression analyses and confidence intervals (95% confidence of fit and confidence of prediction) of the fixed parameter catchment area (ha) and first-pass assessment outputs of area with high BCI, BCC and BCP scores, and total area with BCI, BCC and BCP scores

infilled by Quaternary sediments, and support extensive areas of mangrove and saltmarsh on deltas proximal to the coast. In addition, land-use (i.e. cattle grazing and forested areas) around these estuaries is compatible with carbon preservation. Unlike the many smaller sand-dominated estuaries forming behind coastal barriers on the coastline of south-eastern NSW, these larger riverine coastal floodplains are likely to provide the geomorphological characteristics and spatial extent required for commercially viable blue carbon projects. Conversely, these are also sites particularly

vulnerable to carbon losses where land-use practices have changed. On many NSW floodplains, the construction of artificial drainage networks and the isolation of floodplains from natural sediment sources have led to the oxidation of soils, acid sulfate discharges, remineralisation and loss of carbon, and subsidence (Rogers et al. 2016b). These have been particularly severe where soils contain high carbon and sulfur levels typical of palaeo-mangrove and saltmarsh deposits (Lin and Melville 2010). The approach presented here identifies hot spots of likely high fossil carbon storage and was achieved with greater resolution than previous topography based assessments.

The carbon variation across coastal landscapes indicated in this study was predicated by spatial data projected on raster cells of 30 m × 30 m, a relatively coarse dimension given the spatial scales over which blue carbon can vary (Owers et al. 2016a, b). Whilst the approach presented in this first-pass assessment is a qualitative assessment that can be used to guide prioritisation of blue carbon landscapes for further assessment; it only provides an indication of blue carbon potential and does not replace high-resolution quantitative assessments of blue carbon storage and flux. Nor does it replace detailed site-specific assessment of socio-economic factors that may influence blue carbon potential at the project scale, both now and in the future. We advocate the use of high-resolution analyses of plant productivity and soil carbon properties, and integration of this information across coastal landscapes to improve predictive models of blue carbon potential. This would provide the essential information needed by coastal planners and managers to account for the carbon sequestration ecosystem service provided by coastal landscapes.

The approach adopted in our first-pass assessment of blue carbon potential on the south coast of NSW covers 68 estuaries and incorporates hundreds of geomorphologically distinct wetlands. This spatial coverage was made possible by the prior mapping of land-use/land-cover, mangrove and saltmarsh vegetation mapping, and the availability of supporting data about Quaternary geology, elevation, estuary types and the degree of maturity. Unlike previous efforts to spatially delineate blue carbon ecosystems based on the extent of mangrove and saltmarsh cover, we have taken a broader approach by mapping blue carbon within coastal landscapes, thereby recognising 'fossil blue carbon' associated with prior blue carbon ecosystems that may have been replaced by non-blue carbon ecosystems due to landscape evolution or converted to other land-uses. Exclusion of these areas from assessments increases the risk that these stocks will be lost due to future development activities. Similar to assessments of coastal vulnerability that use indicator approaches (Nguyen et al. 2016), analyses of blue carbon rarely consider the influence of socio-economic factors on blue carbon, and this approach provided the means of layering pertinent land-use information with the spatial patterning evident in biophysical information. In doing so, we have demonstrated the capacity to identify blue carbon hotspots, including those areas that do not currently support blue carbon ecosystems, but provide an archive of prior blue carbon or offer considerable capacity to support blue carbon ecosystem restoration. While it is fortunate to have such a wealth of data to undertake this first-pass assessment, spatial data of this type are becoming more widely available through agencies such as the US Geological Survey and NASA. For example, the US Geological Survey's Quaternary Geological Atlas of the United States (https://gec.cr.usgs.gov/data/quatatlas/index.shtml) and the US Fish and Wildlife Service's National Wetlands Inventory (https://www.fws.gov/wetlands/) provide data consistent with many of the elements of this analysis at similar spatial scales.

Acknowledgements This research was supported by the South East local Lands Service, UOW Global Challenges Program and the Australian Research Council (for KR: FT130100532).

References

Allen JRL (2000) Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. Quat Sci Rev 19:1155–1231

Alongi DM (2008) Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. Estuar Coast Shelf Sci 76:1–13

Alongi DM (2011) Carbon payments for mangrove conservation: ecosystem constraints and uncertainties of sequestration potential. Environ Sci Policy 14:462–470

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. Glob Biogeochem Cycles 17:1111

Clarke LD, Hannon NJ (1967) The mangrove swamp and salt marsh communities of the Sydney district: I. Vegetation, soils and climate. J Ecol 55:753–771

Coverdale TC, Brisson CP, Young EW, Yin SF, Donnelly JP, Bertness MD (2014) Indirect human impacts reverse centuries of carbon sequestration and salt marsh accretion. PLoS One 9:e93296

DECC (2007) Land use: New South Wales. A data set of land use between June 2000 and June 2007 for New South Wales. Department of Environmental and Climate Change, NSW, Sydney

DeLaune R, White J (2012) Will coastal wetlands continue to sequester carbon in response to an increase in global sea level?: a case study of the rapidly subsiding Mississippi river deltaic plain. Clim Change 110:297–314. https://doi.org/10.1007/s10584-011-0089-6

Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marba N (2013) The role of coastal plant communities for climate change mitigation and adaptation. Nat Clim Change 3:961–968. https://doi.org/10.1038/nclimate1970. http://www.nature.com/nclimate/journal/v3/n11/abs/nclimate1970.html#supplementary-information

Emerson D, Weiss JV, Megonigal JP (1999) Iron-oxidizing bacteria are associated with ferric hydroxide precipitates (Fe-plaque) on the roots of wetland plants. Appl Environ Microbiol 65:2758–2761

Emmer I, von Unger M, Needelman B, Crooks S, Emmett-Mattox S (2015) Coastal blue carbon in practice: a manual for using the VCS methodology for tidal wetland and seagrass restoration

VM0033. In: Simpson S (ed). Restore America's Estuaries and Silvestrum, Arlington
Giri C et al (2011) Status and distribution of mangrove forests of the world using earth observation satellite data. Glob Ecol Biogeogr 20:154–159. https://doi.org/10.1111/j.1466-8238.2010.00584.x
Hashimoto TR, Saintilan N, Haberle SG (2006) Mid-holocene development of mangrove communities featuring rhizophoraceae and geomorphic change in the Richmond river estuary, New South Wales, Australia. Geographical Research 44:63–76
Hiraishi T et al (2014) 2013 supplement to the 2006 IPCC Guidelines for national greenhouse gas inventories: wetlands. Intergovernmental Panel on Climate Change, Geneva
Howard J, Hoyt S, Isensee K, Pidgeon E, Telszewski M (eds) (2014) Coastal blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrass meadows. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature, Arlington
Kauffman JB, Heider C, Norfolk J, Payton F (2014) Carbon stocks of intact mangroves and carbon emissions arising from their conversion in the Dominican Republic. Ecol Appl 24:518–527. https://doi.org/10.1890/13-0640.1
Kelleway JJ, Saintilan N, Macreadie PI, Ralph PJ (2016a) Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes. Ecosystems 19:865–880
Kelleway JJ, Saintilan N, Macreadie PI, Skilbeck CG, Zawadzki A, Ralph PJ (2016b) Seventy years of continuous encroachment substantially increases 'blue carbon'capacity as mangroves replace intertidal salt marshes. Glob change Biol 22:1097–1109
Kelleway JJ et al (2017) Review of the ecosystem service implications of mangrove encroachment into salt marshes. Glob Change Biol 23:3967–3983
Kennedy H, Alongi DM, Karim A (2014) Coastal wetlands. In: Hiraishi T, Krug T, Tanabe K, Srivastava N, Jamsranjav B, Kujuda M, Troxler T (eds) 2013 supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: wetlands. IPCC, Geneva, p 55
Kirwan ML, Megonigal JP (2013) Tidal wetland stability in the face of human impacts and sea-level rise. Nature 504:53–60. https://doi.org/10.1038/nature12856
Kirwan ML, Mudd SM (2012) Response of salt-marsh carbon accumulation to climate change. Nature 489:550–553
Lewis SE, Sloss CR, Murray-Wallace CV, Woodroffe CD, Smithers SG (2013) Post-glacial sea-level changes around the Australian margin: a review. Quat Sci Rev 74:115–138. https://doi.org/10.1016/j.quascirev.2012.09.006
Lin C, Melville M (2010) Mangrove soil: a potential contamination source to estuarine ecosystems of Australia. Wetlands (Australia) 11:68–75
Lucas R et al (2014) Contribution of L-band SAR to systematic global mangrove monitoring. Marine Freshw Res 65:589–603. https://doi.org/10.1071/MF13177
Macreadie PI, Hughes AR, Kimbro DL (2013) Loss of 'blue carbon'from coastal salt marshes following habitat disturbance. PloS One 8:e69244
Macreadie PI et al (2015) Losses and recovery of organic carbon from a seagrass ecosystem following disturbance. Proc R Soc B 282:20151537
Macreadie PI et al (2017) Can we manage coastal ecosystems to sequester more blue carbon? Front Ecol Environ 15:206–213
McLeod E et al (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Front Ecol Environ 9:552–560. https://doi.org/10.1890/110004
Megonigal J, Mines M, Visscher P (2005) Linkages to trace gases and aerobic processes. Biogeochemistry 8:350–362
Nguyen TT, Bonetti J, Rogers K, Woodroffe CD (2016) Indicator-based assessment of climate-change impacts on coasts: a review of concepts, methodological approaches and vulnerability indices. Ocean Coast Manag 123:18–43
Northam KJ (2016) Influence of entrance regim on vegetation profiles and carbon storage in south-eastern New South Wales ICOLLs. Bachelor of Environemntal Science (Honours), University of Wollongong
Owers CJ, Rogers K, Mazumder D, Woodroffe CD (2016a) Spatial variation in carbon storage: a case study for Currambene Creek, NSW, Australia. J Coast Res 75(SI):1297–1301
Owers CJ, Rogers K, Woodroffe CD (2016b) Identifying spatial variability and complexity in wetland vegetation using an object-based approach. Int J Remote Sens 37:4296–4316
Parry MK, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (2007) Appendix 1: Glossary. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge
Pendleton L et al (2012) Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. PLoS One 7:e43542. https://doi.org/10.1371/journal.pone.0043542
Poffenbarger H, Needelman B, Megonigal J (2011) Salinity influence on methane emissions from tidal marshes. Wetlands 31:831–842. https://doi.org/10.1007/s13157-011-0197-0
Rogers K, Woodroffe CD (2014) Tidal flats and salt marshes. In: Masselink G, Gehrels R (eds) Coastal environments and global change. Wiley, Oxford
Rogers K, Woodroffe CD (2016) Geomorphology as an indicator of the biophysical vulnerability of estuaries to coastal and flood hazards in a changing climate. J Coast Conserv 20:127–144
Rogers K, Saintilan N, Copeland C (2012) Modelling wetland surface elevation and its application to forecasting the effects of sea-level rise on estuarine wetlands. Ecol Model 244:148–157
Rogers K, Knoll E, Copeland C, Walsh S (2016a) Quantifying changes to historic fish habitat extent on north coast NSW floodplains, Australia. Reg Environ Change 16(5):1469–1479. https://doi.org/10.1007/s10113-015-0872-4
Rogers K et al (2016b) The state of legislation and policy protecting Australia's mangrove and salt marsh and their ecosystem services. Marine Policy 72:139–155
Roper T et al (2011) Assessing the condition of estuaries and coastal lake ecosystems in NSW, Monitoring, evaluation and reporting program Technical Report Series, Office of Environment and Heritage. NSW Office of Environment and Heritage, Sydney
Roy PS (1980) Quaternary depositional environments and stratigraphy of the Fullerton Cove region, central New South Wales. Rec Geol Surv NSW 19:189–219
Roy PS et al (2001) Structure and function of south-east Australian estuaries. estuarine. Coast Shelf Sci 53:351–384
Saintilan N, Wilton K (2001) Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. Wetlands Ecol Manag 9:409–420
Saintilan N, Rogers K, Mazumder D, Woodroffe C (2013) Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. Estuar Coast Shelf Sci 128:84–92. https://doi.org/10.1016/j.ecss.2013.05.010
Sampere TP, Bianchi TS, Wakeham SG, Allison MA (2008) Sources of organic matter in surface sediments of the Louisiana Continental margin: effects of major depositional/transport pathways and Hurricane Ivan. Cont Shelf Res 28:2472–2487
Serrano O et al (2016) Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? Biogeosciences 13:4915–4926. https://doi.org/10.5194/bg-13-4915-2016

Sloss CR, Murray-Wallace CV, Jones BG (2007) Holocene sea-level change on the southeast coast of Australia: a review. Holocene 17:999–1014

Sutton-Grier AE, Moore AK, Wiley PC, Edwards PET (2014) Incorporating ecosystem services into the implementation of existing U.S. natural resource management regulations: Operationalizing carbon sequestration and storage. Marine Policy 43:246–253. https://doi.org/10.1016/j.marpol.2013.06.003

Troedson A, Hashimoto TR, Jaworska J, Malloch K, Cain L (2004) New south wales coastal quaternary geology. prepared for the comprehensive coastal assessment (DoP) by the NSW Department of Primary Industries. Mineral Resources, Maitland

White J, DeLaune R, Li C, Bentley S (2009) Sediment methyl and total mercury concentrations along the Georgia and Louisiana inner shelf, USA. Anal Lett 42:1219–1231

Woodroffe CD (1990) The impact of sea-level rise on mangrove shorelines. Prog Phys Geogr 14:483–520

Woodroffe CD, Mulrennan ME, Chappell J (1993) Estuarine infill and coastal progradation, southern van Diemen Gulf, Northern Australia. Sed Geol 83:257–275

Woodroffe CD, Lovelock CE, Rogers K (2014) Mangrove shorelines. In: Masselink G, Gehrels R (eds) Coastal Environments Glbal Change. Wiley, West Sussex, UK

Woodroffe CD, Rogers K, McKee KL, Lovelock CE, Mendelssohn IA, Saintilan N (2016) Mangrove sedimentation and response to relative sea-level rise. Annu Rev Marine Sci 8:243–266