# Patches to Seascapes: Advancing Seascape Understanding of Fish Communities in Seagrass Ecosystems and its Applications to Conservation and Restoration

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*A thesis submitted to fulfil the requirements of the degree of Doctor of Philosophy*

I live, work, and play on the lands of the Gadigal people. This work of this thesis was conducted on the lands of Gadigal (where my office and home are based), and the land and sea Country of the Awabakal (**Chapter 2 & 3**) and Worimi people (**Chapter 5**). I would like to acknowledge the Gadigal, Awabakal, and Worimi people and pay my respects to their elders, past, present, and emerging. For more than 70,000 years they have been hunting and fishing on Country and learning about and understanding these systems. I'd also like to thank them for looking after the land and sea Country that we have the privilege to research, understand, and enjoy to this day. Sovereignty of this land and sea country was never ceded; this always was and always will be Aboriginal land.

# Statement of originality

This is to certify that the content of this thesis is my own work. This thesis has not been submitted for any other degree or purpose.

I certify that the intellectual content of this thesis is the product of my own work, and that all assistance received in preparing this thesis and all sources have been acknowledged.

**Christopher Pine**, 14th November 2025

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# Statement of the use of Generative AI

During the preparation of this thesis the author used Microsoft Copilot sparingly for the purposes of copyediting to check and assist with spelling and grammar. Generative AI was never used for the purposes of generating new content wholesale. The author confirms that where text was modified by generative AI, the content was reviewed for possible errors, inaccuracies, and bias. The author takes full responsibility for the submitted thesis and ensures the work is their own and has used generative AI within the parameters of use outlined by the ethical standard set by the University of Sydney.

# Author Attribution Statement

**Chapter 2** of this thesis is currently under review at the *North American Journal of Fisheries Management* as:

> Pine, C, Gribben, P., Bugnot, A. & Figueira W. Optimising sampling to characterise fish population size structure from stereo remote underwater video

All authors contributed to the conception and design of the experiment. I lead the project, collected the data, processed the remote underwater stereo-videos, conducted simulations and statistical analysis. I wrote the manuscript and all co-authors contributed to feedback on the drafts.

**Chapter 3** of this thesis is currently being prepared for submission for publication as:

> Pine, C, Gribben, P., Bugnot, A. & Figueira W. Connectivity to artificial structures shapes fish communities in adjacent seagrass meadows

All authors contributed to the conception and design of the experiment. I lead the project, collected the data, conducted simulations and statistical analysis. I wrote the manuscript and all co-authors contributed to feedback on the drafts.

**Chapter 4** of this thesis is currently being prepared for submission for publication as:

> Pine, C., Swadling, D., Gribben, P., Bugnot, A., Lueck, L. & Figueira, W. Seascape connectivity and configuration often outweigh focal patch characteristics in structuring temperate estuarine seagrass fish assemblages

All authors contributed to the study conception and design. I led the project, conducted data collection, video processing, data processing, design of the statistical approach, and conducted the analysis. Data collection and video processing was also conducted by Leonie Lueck. Daniel Swadling and William Figueira assisted with the data collection. Daniel Swadling assisted with the design of the statistical approach. I wrote the manuscript and all co-authors contributed to feedback on the drafts.

**Chapter 5** of this thesis is presented and styled as a thesis chapter and has the following contributors.

> Pine, C., Bugnot, A., Swadling, D., Gribben, P., Taylor, M.D. & Figueira, W. Strategic restoration planning in marine systems: A generalisable decision-support framework integrating site suitability, seascape understanding, and spatial prioritisation

All authors contributed to the conception of the project. I was responsible for the design of the framework and led the project. I conducted data collection, data processing, and analysis. Daniel Swadling selected the restoration sites used in the baseline scenario. Matt Taylor contributed significant amounts of in-situ environmental data (temperature, salinity, pH) used extensively to develop the data layers required for analysis. Further in-situ environmental data was provided courtesy of the Food Agility CRC Shellfish Transformation Program. I wrote the manuscript and all co-authors contributed to feedback on the drafts.

In **Chapters 2, 3, & 4** I use plural author pronouns (we, our) to reflect the work of my co-authors and as these chapters are in the midst of the publication process. For the other chapters, General Introduction (**Chapter 1**), **Chapter 5**, and the General Discussion (**Chapter 6**), I use singular author pronouns as these are thesis-specific chapters (though **Chapter 5** will be later adapted for publication).

**Christopher Pine**, 14th November 2025

As supervisor for the candidature upon which this thesis is based, I can confirm that the authorship attribution statements above are correct.

**Will Figueira**, 14th November 2025

# List of Publications included as part of this thesis

This thesis has been prepared in a thesis with publications format

| Publication | Chapter | Status | Journal |
|---|---|---|---|
| Pine, C, Gribben, P., Bugnot, A. & Figueira W. (in Review). Optimising sampling to characterise fish population size structure from stereo remote underwater video. | 2 | In Review | North American Journal of Fisheries Management |
| Pine, C, Gribben, P., Bugnot, A. & Figueira W. (in prep). Connectivity to artificial structures shapes fish communities in adjacent seagrass meadows. | 3 | In prep. | Landscape Ecology |
| Pine, C., Swadling, D., Gribben, P., Bugnot, A., Lueck, L. & Figueira, W. (in prep). Seascape connectivity and configuration often outweigh focal patch characteristics in structuring temperate estuarine seagrass fish assemblages. | 4 | In prep. | Landscape Ecology |
| Pine, C., Swadling, D., Bugnot, A., Gribben, P., Taylor, M.D. & Figueira, W. (in prep). Strategic restoration planning in marine systems: A generalisable decision-support framework integrating site suitability, seascape understanding, and spatial prioritisation. | 5 | Presented and styled as thesis chapter | **NA** |

# Other Publication and Presentations During Candidature

## *Peer-reviewed Publications*

McLaren, E., Sommer, B., **Pine, C.,** Miskelly, A., Byrne, M., 2025. Searchin' for Urchins: Utilising Museum Collections and Citizen Science to Assess Species on the Move in the Genus *Tripneustes*. Journal of Biogeography 52, e15092. https://doi.org/10.1111/jbi.15092

Ross, P.M., **Pine, C**., Scanes, E., Byrne, M., O'Connor, W.A., Gibbs, M., Parker, L.M., 2024. Meta-analyses reveal climate change impacts on an ecologically and economically significant oyster in Australia. iScience 27. https://doi.org/10.1016/j.isci.2024.110673

Roncolato, F., Fellowes, T.E., Duce, S., Mora, C., Johansson, O., Strachan, I., Bugnot, A.B., Erickson, K., Figueira, W., Gribben, P.E., **Pine, C**., Morgan, B., Vila-Concejo, A., 2024. Ecomorphodynamics of oyster reefs and their influence on oyster reef morphology. Geomorphology 456, 109213. https://doi.org/10.1016/j.geomorph.2024.109213

**Pine, C.,** Erickson, K., Gribben, P.E., Figueira, W.F., 2022. Observation of juvenile Eastern Blue Groper (*Achoerodus viridis*) on remnant oyster reefs in New South Wales, Australia. Ecology 103, e3824. https://doi.org/10.1002/ecy.3824

## *Conference Abstracts*

**Pine C.,** Swadling D., Gribben, P., Bugnot A,. Lueck L. & Figueira W (2024). A Fishes Guide to Finding a Home: Understanding the Role of the Estuarine Habitat Mosaic and Focal Patch Characterstics on Fish Communities in Seagrass Meadows. Australian Marine Sciences Association Conference 16th-20th September 2024, Hobart, Tasmania, Australia

**Pine C.,** Bugnot A., Swadling D., Gribben, P., Taylor, M. & Figueira W (2025). Strategic Marine Restoration Planning: A decision-support framework for ecological outcomes. Australasian Coastal Restoration Network Symposia 2nd-3rd September 2025, Canberra, Australian National Territory, Australia

**Pine C.,** Erickson K., Gribben P., Bugnot A. & Figueira W. (2022) Oyster Reef Design Rules: Understanding the influence of Reef Characteristics on Fish assemblages to increase the effectiveness of oyster restoration efforts. Australian Marine Sciences Association Conference August 7th-11th 2022, Carins, Queensland, Australia

*"One fish,*

*two fish,*

*red fish,*

*blue fish"*

- *Dr Seuss*

*(*A man who had significant foresight about the day-to-day activities of fish ecologists around the world)

# Acknowledgements

Perhaps one of the most famous openings to a novel of all time is in Charles Dickens' book *A Tale of Two Cities*, which starts with: *"It was the best of times, it was the worst of times, it was the age of wisdom, it was the age of foolishness, it was the epoch of belief, it was the epoch of incredulity, it was the season of light, it was the season of darkness, it was the spring of hope, it was the winter of despair."* Though this quote really is about the juxtaposition between the difficult living conditions of the French peasantry and the luxurious, overindulgent lifestyle of the French aristocracy (a quote that increasingly parallels the modern era), I truly believe that there is no other quote that captures the essence of my experience doing this PhD. It has really been the best of times and the worst of times.

This document is a snapshot of myself at various points over the past few years and shows the progression of my ideas and myself as a scientist. From the minutia of sampling with underwater video all the way through to tackling the – most likely – overly ambitious idea of trying to apply the understanding of seascape ecology into restoration. While it is a great time capsule of my scientific capabilities, what you won't find within the 1.5 spaced lines of 12-point Times New Roman is the stories of the difficult times, the self-doubt, the days spent worrying if I was even "good enough" to be doing this. The sleepless nights, the failure, the gut wrenching anxiety, the days in the field where everything went wrong, the times you hit rock bottom – only to find out there was five more layers of rock bottom to go, and the countless times I almost gave up and walked away.

To put it scientifically. Indeed, the evidence suggests that this may have been among "*the worst of times*".

But what you also won't find within these lines, is the stories of the incredible people that have supported me throughout this entire process, the stories of the times spent joking around and laughing so hard we couldn't breathe, the quiet moments of encouragement, the camaraderie, the lunches shared every day. The friendship, kinship, and love. The moments of triumph, the moments of passion and excitement for science. So, I'd like to take a moment to give these people the thanks and acknowledgement they deserve, as without these people, none of this would be possible.

**Will**, thank you for taking the chance on the naïve kid who never really showed up to class all those years ago (in my defence, it was COVID times), I am incredibly grateful. You have always known when to let me "pull on the leash", so to speak, and let me be free to chase after my scientific squirrels. But you have also known when to reign me in an keep me focused on a singular squirrel at a time. That is no mean feat and takes an extreme amount of skill as a mentor to do. Through all these years working with you, you have led by example to show me that science not only takes a good head, but also a kind heart. Throughout this experience, I know that if my back - or anyone's back for that matter - was up against the ropes, you would always be there (and have always been there) to help when needed most. At times I find it eerie how similar we are (plate O' beef and canned tuna/chicken lunches come to mind, among various other things), but I do hope to one day be half the person and scientist you are. Thank you for your coming along with me on this wild ride and for your mentorship and guidance all these years.

**Paul**, I feel like of all my supervisors you have pushed me the most scientifically. At every turn you have always often asked the most difficult questions. But I thank you for it. I am a better scientist because of it, and for that I am deeply appreciative. Your questions have pushed me to understand my work and the ecology of these systems in a much deeper, more thorough, and considered way than I would have otherwise. You have made me more precise and specific in my scientific writing and my use of language through your feedback. You have also shown me a huge amount of support and kindness over the years and have done so often with great humour. Your dry, blunt, and often sarcastic style of humour has never failed to make me crack a smile (in the cases where I recognise the joke!). I will never forget singing along with you and Will to 'Dad Rock' at AMSA 2022, although I'm not sure how much you remember of it considering the amount we had to drink!

Anyone who knows me knows that I love statistics – often much to my own detriment - and I love experimental design. But I didn't always have this passion. **Ana** was the first person to ever explain and describe statistics to me in a way that I understood; sparking my interest and eventual love for stats. You have this brilliant ability to communicate complex ideas into ways that are easily understood by most people, a skill I hope to possess a fraction of one day. Every time I have walked away from one of our meetings I have left with a feeling of scientific excitement and immense encouragement. I still remember the kindness you showed to me in the first weeks of my Honours, inviting Hannah and I out to group drinks even though – at the time – we felt a bit out of place. That single act of kindness that day helped foster many of the friendships with the people in the office to this day, and for that I am deeply grateful. Thank you so much for your support and mentorship over the past few years.

A key collaborator – and at this point, honorary supervisor – throughout this process has been **Dan**. Your knowledge and mentorship throughout this process has been critical to this entire experience. It was always nice to speak to someone else who has been as deep in the weeds of seascape ecology as I am, and I really appreciated how I always left our conversations with a deeper and more nuanced understanding of whatever we were discussing. The excitement and support you've met many of my ideas with has helped push me along through some of the more difficult stages of my PhD. That being said, you also showed a healthy dose of scepticism to each idea. Something that was invaluable in improving my work, my scientific justification, and guiding the direction of the last two chapters of my thesis. Thank you so much for agreeing to jump on this crazy ship the past little while, I hope you've enjoyed it as much as I have.

These four figures have been instrumental in my growth and trajectory as a scientist; however, the story would be incomplete without mentioning **Katie.** Who knew when I showed up to my first day of fieldwork during my Honours that I would meet, not only the person who taught me almost every practical skill it takes to be a marine ecologist, but also a lifelong friend? You laid the foundations upon which my supervisors have built. I will always cherish the days in the field together, cry-laughing over the same stupid joke for hours on end. You have given me so much support and friendship over the years – often leaving me teary from your kindness - and without it I wouldn't be here finishing my PhD. We have been through absolute hell together, whether that be trudging through waist deep mud, the horrors of Crookhaven, or the long days on the water underneath the hot sun. But there is no person I'd rather have alongside me in hell than you. I hope that maybe one day – once you have forgotten about the horrors of working in academia – that I can convince you to come back and work with me, so the dream team can ride off into the estuary one last time. Thank you for everything.

Perhaps the person who has known me the longest of the people mentioned here is **Hannah**. We have been friends and have been along the same path from our undergrad through to honours, and then throughout our PhDs. It was my hope that we could submit our PhDs on the same day as originally planned, as it would've felt right to end this journey alongside someone who had started this journey with me. We first met doing a group project together in my second year of uni, and I have been a pain in her arse ever since. There is no one I love winding up more than you. But I think you might say the same about winding me up. But despite our relentless back and forth banter, you have been one of the best friends someone could ask for. You have been so kind and supportive throughout all these years. I will always remember our conversations commiserating about our theses, talking for hours about anything and everything on our long drives to and from fieldwork, and the times you have ruthlessly beat me in almost every boardgame we play. You have kept me humble and has never failed to take me down a peg or two when needed. Without your friendship and support I would not be half the person I am today, thank you.

Although **Alex** isn't here to see it (he's off post-doc'ing in Italy), he is another person integral to this story. Need I say more than mention one of the ten commandments we lived by in our house when we lived together. "*Sometimes you gabba, sometimes you goo*". You have been there throughout some of the lowest goos throughout my PhD, but your unwavering hilarity and your energy has always kept me going throughout the darkest of days. I loved our time living together and the brotherhood we shared. You were the best housemate I've ever had – though I regret that I wasn't the same for you! The times we've spent together, staying up so late talking nonsense and laughing that we're exhausted the next day, I will always remember and was integral to me never giving up. Thank you for being un-ashamedly yourself – that has always inspired me – and thank you for your friendship and support all these years. I hope one day we can live in the same city again! Remember, a happy head is a shaved head.

**Bella** has been my A11 ride-or-die diva. I am always impressed by your capability to balance your *extremely* quick wit alongside always being so considerate, insightful, and thoughtful. Often, we have gone absolutely insane and stir crazy down the end of our hallway in A11. I have never cried so much laughing than when we refuse to stop bouncing off each other as if we were trying to put on the best comedy night. You have brought so much levity and support to some of the most difficult moments of my PhD/life. I have so many fond memories of our little slice of hell that is our hallway that I will cherish for the rest of my life. Even though I will never **not** find your obsession with putting insets into every figure you make peak comedy (someone *please* take Illustrator away from this woman); you will always have a permanent inset in my heart. Never stop being so authentic and kind.

To "other" **Chris** (though I now bestow upon you "equal" Chris status) & **Emily**, I feel like both of you guys have been my "cool older brother" and "cool older sister" all these years. You both have provided guidance, support, and friendship throughout this entire experience in a way that has left me standing a little bit taller and a little bit prouder each time. I have always loved our hallway and lunch time chats, just shooting the shit and laughing all the time. I love our dynamic where Emily will encourage and play into my chaos, which leads to Chris getting more and more distraught (in a good way). Neither of you know how much the continual *slap on the back* "You got this bud" has meant to me throughout this experience. That small gesture (and other gestures like it that both of you are so good at) have comforted me in the most difficult moments throughout this experience and provided the extra push I've needed to keep going. These small acts of kindness and kinship have been so important to me, and I am incredibly grateful for them. Whoever is lucky enough to hire you for your next steps on your careers in academia will have lucked into the academic equivalent of a Royal Flush. I believe in you both.

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**Agus** - though I like to call her grandma to remind her of their old age – you have brought such light and levity to this office with your wide smile, distinctive laugh, and fun sense of humour. When you leave this building, we will all feel the hole you'll leave behind. Thank you so much for looking out for me and providing encouragement and support when I've needed it most. The small ruffle of my hair you often do as you walk past my desk is a small gesture of support that has kept me going, even when all I want to do is walk away. I know at the moment you don't know where life will take you. But what I do know is that no matter what you choose to do in the future, you will excel.

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To the rest of my crew including **Matt**, **Mon**, **Alex**, **Bernard, Daya**, **Renske**, **Josie**, **Seb**, **Lizzie**, **Luke**, and **Lara**. Thank you for being supportive, friendly, and brilliant people to be around. All of you have contributed to the feeling of this place being a fantastic and fun place to be – and a place that feels like a second family. All the conversations and laughter we've shared will be carried in my heart for a long time, and this wouldn't be possible without you!

**Ronan** & **Freya**, thank you for being so understanding of what this experience has been like over the past little bit! I have loved every opportunity we've had to hang out, and I always leave feeling much happier and energised – even if I get absolutely annihilated in all the games we play together. Ronan you in particular are never afraid to make fun of me, which always reminds me to not take myself/life too seriously. It's always a funny - and often well deserved - reality check. Thank you both for your kindness, support, and friendship.

**Micro**, even though of all the people listed here, you probably know the least about what I "actually" do day-to-day, your support and words of encouragement have always been among the most effective and important to me. Nothing has lifted my spirits up more after a bad day at the PhD factory than a message from you saying things like "Can't believe those fish hurt my boy like that. LET ME ATTEM. I'll beat them up for you." Your support throughout all of this has made this thesis possible. Thank you for all the nights hanging out and chatting, it always helped me take my mind off work. I'm truly grateful to have you as my friend.

I'd also like to thank my family, including my **Mum**, **brother**, and **Grandma Cushion** for supporting me and my education throughout all these years. Thank you for always believing in me!

Lastly, but most certainly not least, **Gems**. Without your support and love I would not be here today. You have been the best partner in crime I could've asked for over these past years. No matter how bad the days at work have gotten, you have been there by my side supporting me every step of the way. Despite the fact I have slaved away writing this thesis for months at this point, this paragraph has been the most difficult thing to write in this entire thesis. It's been so difficult to write as you are absolutely *radiant* in a way that I cannot describe. No scientific finding I'll ever make - or have ever made – is as important as finding my love for you. Your light brings out the best in me. I love you.

Thank you to everyone for putting up with my antics over the past years. This work is as much yours as it is mine, as without everyone's mentorship, support, and kindness, none of this work would be done or here today. If it wasn’t for the rule about authorship requiring “significant intellectual contribution” (damn you rules!), everyone mentioned here would be well deserving of their name as an author and a significant contributor to this work. This work does not exist without you. So, while my name may be on this thesis, your spirits are woven between these lines; your stories left unsaid - but integral nonetheless.

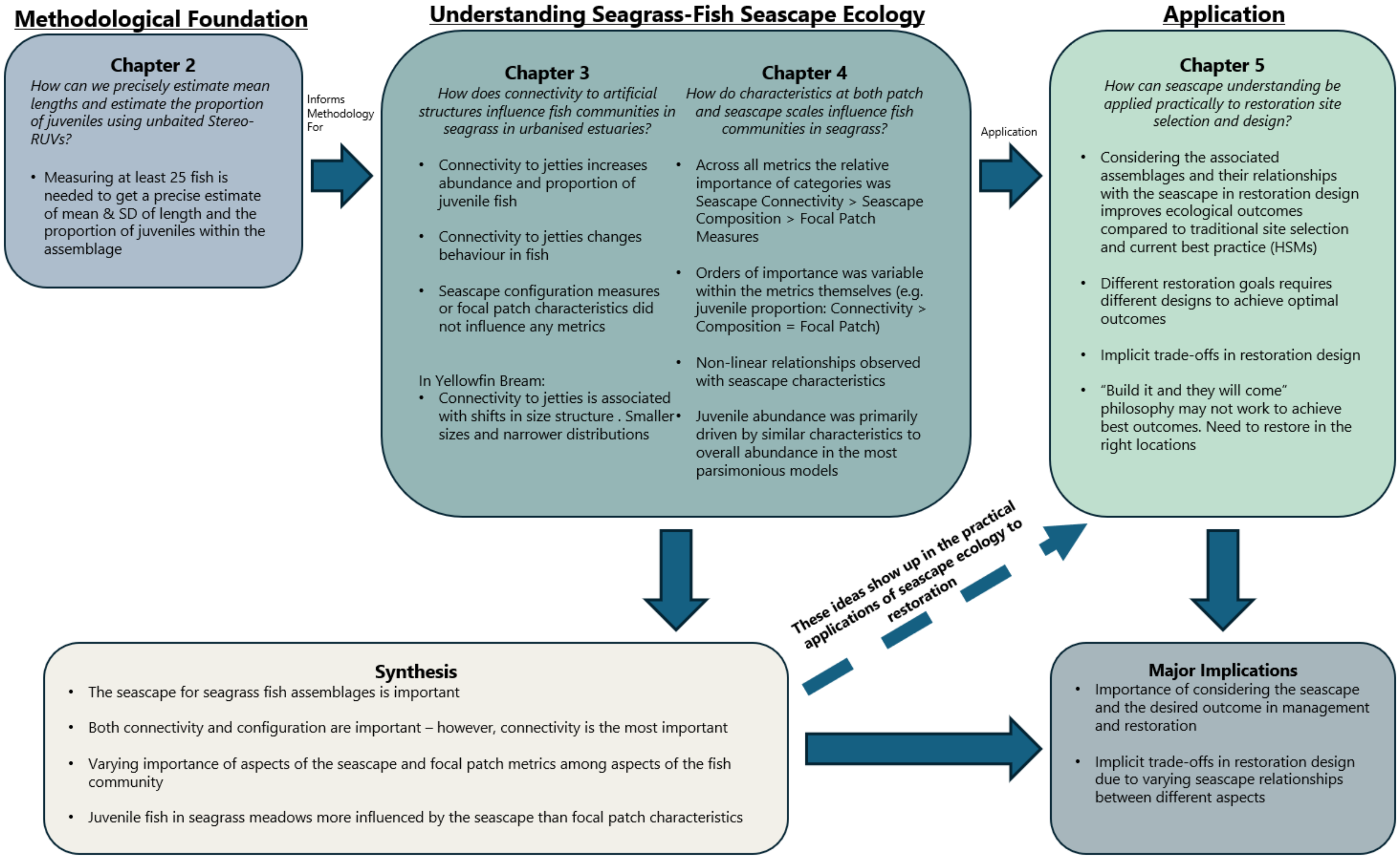
To everyone else not mentioned here by name, you have also been important to my journey and experience throughout this process. Whether it be your friendship, kindness, or words of encouragement; it has not gone unnoticed, and I will always be deeply deeply appreciative and grateful for it. I am just aware that these acknowledgments are already ~3000 words long and I just hear the ghost of Paul’s voice telling me to “get to the point” (rightly so I might add).

So, in conclusion, to put it scientifically. Indeed, the evidence suggests that this may have been “*the best of times*”.

- Chris

# Graphical Abstract

## *How do seascape and focal patch characteristics influence fish communities in temperate estuarine seagrass systems, and how can this understanding be applied and integrated to potentially improve restoration outcomes?*



**Methodological Foundation**

**Chapter 2**

*How can we precisely estimate mean lengths and estimate the proportion of juveniles using unbaited Stereo-RUVs?*

- Measuring at least 25 fish is needed to get a precise estimate of mean & SD of length and the proportion of juveniles within the assemblage

Informs Methodology For

**Understanding Seagrass-Fish Seascape Ecology**

**Chapter 3**

*How does connectivity to artificial structures influence fish communities in seagrass in urbanised estuaries?*

- Connectivity to jetties increases abundance and proportion of juvenile fish
- Connectivity to jetties changes behaviour in fish
- Seascape configuration measures or focal patch characteristics did not influence any metrics

In Yellowfin Bream:

- Connectivity to jetties is associated with shifts in size structure . Smaller sizes and narrower distributions

**Chapter 4**

*How do characteristics at both patch and seascape scales influence fish communities in seagrass?*

- Across all metrics the relative importance of categories was Seascape Connectivity > Seascape Composition > Focal Patch Measures
- Orders of importance was variable within the metrics themselves (e.g. juvenile proportion: Connectivity > Composition = Focal Patch)
- Non-linear relationships observed with seascape characteristics
- Juvenile abundance was primarily driven by similar characteristics to overall abundance in the most parsimonious models

Application

**Application**

**Chapter 5**

*How can seascape understanding be applied practically to restoration site selection and design?*

- Considering the associated assemblages and their relationships with the seascape in restoration design improves ecological outcomes compared to traditional site selection and current best practice (HSMs)
- Different restoration goals requires different designs to achieve optimal outcomes
- Implicit trade-offs in restoration design
- "Build it and they will come" philosophy may not work to achieve best outcomes. Need to restore in the right locations

**These ideas show up in the practical applications of seascape ecology to restoration**

**Synthesis**

- The seascape for seagrass fish assemblages is important
- Both connectivity and configuration are important – however, connectivity is the most important
- Varying importance of aspects of the seascape and focal patch metrics among aspects of the fish community
- Juvenile fish in seagrass meadows more influenced by the seascape than focal patch characteristics

**Major Implications**

- Importance of considering the seascape and the desired outcome in management and restoration
- Implicit trade-offs in restoration design due to varying seascape relationships between different aspects

Thesis overview showing key findings and their integration. Methodological development (**Chapter 2**) enabled investigations demonstrating that seascape characteristics including connectivity and configuration primarily drives fish community structure in seagrass (**Chapter 3-4**), which then helped inform the design of the restoration framework that aimed to apply seascape ecology into restoration practice (**Chapter 5**). Contains synthesis of the various chapters and their associated major implications.

# Thesis Abstract

Seagrass ecosystems in temperate estuaries are declining globally due to anthropogenic pressures such as climate change, coastal sprawl, and direct habitat degradation - including both habitat loss and fragmentation. These declines are particularly concerning given that seagrass meadows support ecologically, economically, and culturally important fish communities, making active habitat restoration increasingly critical for both ecosystem recovery and the restoration of these associated fish assemblages. However, restoration success - particularly in regard to the restored habitat's ability to support its associated biotic assemblage - remains limited partly due to inadequate consideration of the surrounding seascape and associated ecological processes, with less than 13% of projects incorporating seascape context and multi-scale spatial relationships into site selection and restoration design. To design restoration strategies that effectively support fish communities, we first must understand how the seascape influences these assemblages. Yet despite recognition of the role of seascape in shaping fish assemblages from a theoretical perspective, there remains limited understanding of the seascape ecology of fish communities in seagrass meadows in temperate estuarine systems.

This thesis addresses the critical knowledge gap in understanding how seascape and focal patch characteristics influence fish communities in seagrass systems in temperate estuarine systems and develops a framework for applying this understanding to potentially improve restoration outcomes. This research addressed four key questions via a logical progression from methodological foundations, through seascape ecological understanding, to practical application: (i) optimising sampling protocols for seascape-scale fish surveys, (ii) understanding how structural connectivity to artificial structures influences key fish assemblage metrics in seagrass meadows in urbanised estuaries, (iii) examining the relationships between focal patch and seascape characteristics and seagrass-associated fish communities, and (iv) developing a decision-support framework for the application of seascape ecological understanding to strategic restoration planning.

In **Chapter 2**, using computer simulations validated by in-situ stereo remote underwater video (stereo-RUV) analysis, I established that measuring approximately 25 fish from distinct timepoints within a video provide reliable estimates of key fish population parameters such as mean length, standard deviation of length, and the proportion of juvenile fish, when using unbaited stereo-remote underwater video systems. This established a methodological foundation for precise and cost-

effective seascape surveys, ensuring confidence in the precision of video-derived fish population estimates throughout subsequent chapters while improving survey efficiency.

Surveys of fish assemblages using stereo-RUVs in an urbanised estuary (**Chapter 3**) revealed that seagrass meadows with high connectivity to jetties had significantly greater total fish abundance and the proportion of juvenile fish when compared to seagrass far from jetties, while species diversity, species richness, and the multivariate community composition remained unchanged. Analysis of the size structure of a commercially and recreationally important species - *Acanthopagrus australis* (Yellowfin Bream) - showed that populations in seagrass near jetties had significantly smaller mean size with a narrower length distribution compared to populations in seagrass far from jetties. In this study, neither focal patch characteristics nor any measures of seascape configuration influenced these responses.

I then expanded the scope to examine how all habitats within the seascape influence seagrass associated fish assemblages more broadly (**Chapter 4**). Sampling using stereo-RUVs across 50 spatially balanced sites that covered the full range of seascape and focal patch characteristics present at the study site. I employed a full-subsets modelling approach to understand the relative importance of seascape connectivity, seascape configuration, and focal patch characteristics. The results showed that seascape connectivity and seascape configuration were more important than focal patch characteristics for predicting the response of key fish assemblage metrics (abundance, species richness, diversity, and juvenile proportion), with measures of structural connectivity being most important overall. However, the relative importance of these predictor categories varied among specific assemblage metrics, suggesting that different seascape arrangements may lead to variable outcomes. Notably, 40% of the significant relationships observed were non-linear, often with unimodal or U-shaped relationships, suggesting the presence of complex spatial ecological processes and potential threshold effects in fish community responses to seascape characteristics.

Building on this previous research, I developed a decision-support framework for restoration site selection that integrates habitat suitability modelling for seagrass, with the seascape ecology of fish communities, and spatial prioritisation to help identify optimal restoration sites (**Chapter 5**). I compared different prioritisation scenarios that reflected varying management priorities (from habitat establishment to fish assemblage enhancement), demonstrating how incorporating fish community responses alongside considering the habitat former itself changes predicted ecological outcomes. The results highlighted the importance of considering the associated assemblage alongside the habitat former when selecting sites for restoration, with the scenario prioritising seagrass habitat suitability alongside all the fish assemblage metrics having the best predicted performance across all outcomes. However, I observed significant variation in the location and arrangement of restoration sites selected depending on which assemblage metric(s) were prioritised, with inherent trade-offs when optimising across multiple criteria. These results suggest that there is no “one-size fits all” solution when it comes to restoration and that there are different “optimal” seascapes and restoration sites depending on a project’s desired goals. Importantly, this framework provides a transferable workflow for practitioners to integrate seascape understanding of associated assemblages into restoration planning.

This research collectively supports the importance of shifting from traditional single-scale restoration approaches towards integrated seascape-informed practice. It particularly highlights the need to consider the habitat-forming species alongside their associated fish assemblages in marine restoration, further recognising that different aspects of the assemblage vary in their seascape relationships and therefore require designs that account for this. The findings in this thesis provide both methodological tools and seascape ecological understanding required to design seascape-informed management and restoration strategies that account for such multi-scale ecological relationships. These findings offer actionable frameworks for marine restoration practitioners working to support biodiversity and ecosystem services under accelerating global change.

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# Chapter 1 - General Introduction

## 1.1 | Marine habitat degradation and global context

Fish are among the most important organisms in marine ecosystems worldwide, playing key ecological, economic, and cultural roles (Holmlund and Hammer 1999; Hiddink et al. 2008; Tacon and Metian 2013). As one of the highest order consumers within marine food webs, they are key to maintaining ecosystem stability and provide essential resources for both commercial fisheries and traditional subsistence practices (Holmlund and Hammer 1999; Hiddink et al. 2008; Tacon and Metian 2013). Yet their populations are increasingly threatened by overfishing, environmental degradation, shifting climate patterns, and other anthropogenic impacts (Brander 2013; Belhabib et al. 2018). One of the biggest challenges facing fish communities is the loss and degradation of the key marine habitats that support them (Duarte et al. 2020). Over the past century, approximately 50 % of coral reefs (Hughes et al. 2017), 35% of mangroves (Valiela et al. 2001), 85 % of oyster reefs (Beck et al. 2011), and 19% seagrass meadows (Dunic et al. 2021) have been lost or severely degraded globally (Duarte et al. 2020). The loss of these critical marine habitats disrupts fish population dynamics, food web stability, and the resilience of coastal ecosystems to environmental change (Lotze et al. 2019; Smale et al. 2019; Duarte et al. 2020), with substantial socio-economic impacts on fisheries that contribute $363 billion (USD) annually to the global economy (Sumaila et al. 2019; Food and Agriculture Organisation 2022). One of the key drivers behind the loss of these critical habitats is anthropogenic climate change, which increases the intensity of weather events, average air and sea temperatures, and the rate of ocean acidification (Intergovernmental Panel on Climate Change 2019).

Among these threatened systems, coastal and estuarine environments face significant pressures due to their proximity to human populations and their position as the interface between terrestrial and marine systems (Crossland et al. 2005; Nicholls et al. 2007; Firth et al. 2016). Coastal and estuarine areas support ~40% of the world's population - despite representing less than 5% of the total land area - and have been rapidly urbanised over the past century, creating unprecedented anthropogenic pressures on surrounding and connected marine ecosystems (Crossland et al. 2005; Nicholls et al. 2007; Clewell and Aronson 2012; Firth et al. 2016). Impacts from these pressures include habitat loss and degradation via coastal development (Waycott et al. 2009; Bulleri and Chapman 2010; Dunic et al. 2021), increased sedimentation and turbidity from runoff and construction (Zabarte-Maeztu et al. 2021; Sandberg et al. 2006), altered hydrodynamics (Donatelli et al. 2019), introduction of marine pollution (Weis 2024), noise pollution from shipping and construction (Duarte et al. 2021), and the proliferation of artificial structures that can alter local ecological communities and conditions (Bulleri and Chapman 2010; Dafforn, Glasby, et al. 2015).

As a result of urbanisation around these systems, the number of artificial structures (e.g., pier/jetties, seawalls, moorings, groynes, marinas, boat ramps, swimming enclosures etc) within coastal, estuarine, and marine environments has been rapidly increasing in a process termed "coastal sprawl" (Waltham and Connolly 2011; Firth et al. 2016; Bishop et al. 2017). The impact of these structures extends beyond simple habitat loss and replacement, altering local hydrodynamics and sediment dynamics (Saengsupavanich et al. 2022). These artificial structures often support different biotic communities (particularly in the case of invertebrate and encrusting communities) compared to natural habitats, typically favouring opportunistic and non-native species (Glasby et al. 2007; Dafforn et al. 2009; Airoldi and Bulleri 2011). Furthermore, the cumulative effects of multiple structures create ecological bottlenecks, impede natural coastal processes, and alter connectivity between marine habitats (Adams et al. 2014; Paxton et al. 2019; Lemasson et al. 2024).

The combination of coastal sprawl, climate change, and other anthropogenic pressures associated with the proximity of estuarine and near-coastal systems to dense human populations has increased the loss and fragmentation of key marine habitats and decreased the quality of the habitats (e.g., seagrass meadows, shellfish reefs, rocky reefs, mangrove forests, saltmarsh) within these systems (Waycott et al. 2009; Beck et al. 2011; Duarte et al. 2020; Dunic et al. 2021). This has resulted in negative impacts on the abundance and biodiversity of the associated fish assemblages in these environments and influences the nursery value of these areas (Gillanders et al. 2011; Cloern et al. 2016; Yeager et al. 2019; Arevalo et al. 2023). This is particularly concerning as estuarine systems and the habitats found within them are critical for supporting fish communities, as many species use these areas as a key part of their life histories often settling, recruiting to, and using these areas as nurseries before eventually migrating to marine areas (Beck et al. 2001; Gillanders et al. 2011; Potter et al. 2015; Sheaves et al. 2015; Arevalo et al. 2023). Due to continued coastal sprawl in these estuarine systems, it is important to understand how this impacts the fish assemblages in other nearby connected habitats to inform the design and management of coastal infrastructure in these regions.

# 1.2 | Seagrass meadows - a critically important fish habitat

Seagrasses are marine *Angiosperms* (flowering plants) that act as habit formers, often aggregating into large, forest-like, patches called seagrass meadows (Hemminga and Duarte 2000), spanning both tropical and temperate latitudes across both hemispheres (McKenzie et al. 2020). Seagrass meadows are one of the most important fish habitats globally, supporting diverse and abundant fish communities that provide nursery habitat for 1/5th of the world's largest 25 fisheries (Unsworth et al. 2019). In Australia, it is estimated that one hectare of seagrass produces between 110-1,080kg of fish per year and supports 69-865 fishing trips per year, with each hectare of seagrass providing a combined fisheries production and recreational value of an estimated 5.5 million AUD (Jänes et al. 2021).

As fish habitat, seagrass meadows provide an abundance and diversity of food resources, alongside providing a refuge from predation and hydrodynamic stress (Heck Jr and Orth 1980; Orth et al. 1984). The three-dimensional structure of the seagrass canopy creates microhabitats, while simultaneously disrupting the foraging efficiency of visual predators (Edgar and Shaw 1995; Jackson et al. 2001). These habitats further support fisheries by facilitating larval settlement and recruitment (Ford et al. 2010). This is important given that a large number of fish species that spawn offshore and settle in estuarine waters as larvae, transitioning from a planktonic to nektonic stage (Potter et al. 2015). The combination of environmental stability, food availability, and shelter provided by seagrass meadows makes these habitats ideal for juvenile fish, often supporting greater levels of juvenile growth, survival, and density in comparison to other estuarine habitats (Whitfield 2017; McDevitt-Irwin et al. 2016; Heck et al. 2003), with this effect being more prominent in temperate seagrass meadows (McDevitt-Irwin et al. 2016). As a result, seagrass meadows have often been referred to as nursery habitats throughout the literature (Whitfield 2017; McDevitt-Irwin et al. 2016; Heck et al. 2003). However, few species spend their entire life history within seagrass habitats, often spending their juvenile stages in these habitats before migrating to other habitats and coastal areas as a part of a natural ontogenetic shift (Werner and Gilliam 1984; Gillanders and Kingsford 1996; Gillanders et al. 2003; Pittman and McAlpine 2003; Nagelkerken 2009). There is some evidence to suggest that this is even observed within different seagrass meadows comprised of different seagrass species (Middleton et al. 1984). In Middleton et al. (1984) they observed smaller fish in *Zostera capricorni* meadows, while observing larger fish in *Posidonia australis* meadows in Gamay Bay (Sydney NSW), with this shift occurring throughout the year – potentially indicating a natural ontogenetic shift from *Zostera* to *Posidonia* meadows.

Beyond their direct impact on fish communities associated with the seagrass meadows themselves, they often provide benefits to the wider seascape. Seagrass meadows exist as components of broader habitat mosaics, often connected to mangroves, rocky reefs, and unvegetated areas through fish movement, larval dispersal, and nutrient flows (Swadling et al. 2019; Henderson et al. 2017; Olds et al. 2012; 2017). As seagrass meadows act as a nursery habitat that increase the supply of recruits into the adult fish population, they play an important role in maintaining and supplying the fish population to connected habitats such as rocky reefs (Swadling et al. 2019), mudflats (Whitlow and Grabowski 2012), and coral reefs (Du et al. 2020). Understanding these landscape-level connections has become increasingly important for effective conservation and restoration planning (Pittman 2017b; Pittman et al. 2021; Wedding et al. 2025), yet the understanding of the seascape ecology of fish communities in temperate seagrass meadows – particularly within estuarine systems – remains limited.

# 1.3 | Theoretical framework: from patches to seascapes

Understanding fish communities in seagrass ecosystems requires examining ecological processes across multiple spatial scales. Traditionally, marine ecology has focused on discrete patches and their associated characteristics in relation to biotic communities (Sale and Douglas 1984; Bell and Westoby 1986; Smith 2009; Smith et al. 2010; Jackson et al. 2017), however, growing recognition of spatial ecology has highlighted that the broader landscape context fundamentally shapes ecological patterns and processes, often in context-dependent ways (Turner 2005; Pittman 2017b; Fletcher and Fortin 2018). As such, integrated understanding of the ecological processes occurring at both the patch & seascape scale – and how one may influence the other - is needed to understand the relationships exhibited between fish assemblages and these characteristics. This section outlines the theoretical progression from patch-level to seascape-scale understanding of fish communities that underpins this thesis.

## *1.3.1 Patch-level ecology*

Patch ecology examines how the characteristics of discrete habitat units influence local ecological processes and associated communities (Wiens 1976; Wu and Loucks 1995; Thornton et al. 2011). These approaches tend to ignore broader landscape context and looks at patches as distinct spatial units with defined boundaries, with each patch having unique environmental conditions that create specific ecological niches (Wiens 1976; Forman 1995). Historically, the patch-scale view of marine ecology has proven particularly valuable (Jackson et al. 2017), as many marine organisms exhibit strong habitat associations and often are limited in their mobility during critical life stages such as larval and juvenile stages (Cowen and Sponaugle 2009). Fish communities in particular have often shown distinct relationships with specific patch types and characteristics, making patch-scale analyses critical for understanding community structure and dynamics (Connell and Jones 1991; Sale 1991; Hixon and Beets 1993). This patch centric view has dominated ecology for decades, providing a fundamental foundation into species-habitat relationships and local population dynamics (Levin 1992; Jackson et al. 2017). Two of the key drivers of the ecology observed within habitat patches are edge effects and habitat complexity (often referred to also as structural complexity).

### 1.3.1.1 Edge effects and patch size

Edge effects, which describe the ecological changes from the edge to the core of the patch, represent one of the core concepts of patch-level ecology (Murcia 1995; Ries et al. 2004). Edges effects are common across terrestrial and aquatic ecosystems and often have differential influences that are species and habitat specific (Fagan et al. 1999; Ries and Sisk 2004; Ries et al. 2004). These effects result from differential environmental conditions at patch boundaries, where adjacent habitats/habitat matrices create gradients in physical parameters such as light, temperature, waterflow, and exposure (Murcia 1995; Ries and Sisk 2004; Ries et al. 2004; Laurance et al. 2007). This then has flow on influences to the behaviour and distribution of associated organisms in and around the patch (Murcia 1995; Ries and Sisk 2004; Ries et al. 2004; Laurance et al. 2007). Edge habitats often represent areas of increased resource availability, altered predation pressures, and enhanced connectivity between habitat types leading to distinct community assemblages compared to patch interiors (Murcia 1995; Ries et al. 2004; Ries and Sisk 2004; Laurance et al. 2007). The magnitude and direction of edge effects can also vary substantially depending on the contrast between adjacent habitat types and matrices, with greater habitat contrast typically producing more pronounced edge effects in either direction (positive or negative; Ries et al. 2004; Ries & Sisk 2004).

Edge effects are particularly influential in determining how patch size affects communities, as smaller patches have proportionally more edge habitat relative to core area. When patches become smaller, edge effects proliferate more throughout the patch, altering ecological processes such as predation, resources availability, and competitive interactions (Ries and Sisk 2004; Laurance et al. 2007; Laurance 2008). These effects vary with patch size, orientation, and depth and can be predicted based on habitat characteristics at boundaries (Ries and Sisk 2004; Smith et al. 2008; Smith 2009; Macreadie et al. 2009; 2010). Seagrass systems in particular exhibit pronounced edge effects, with increased densities and richness of fish found along edges (Smith et al. 2008; Smith 2009; Macreadie et al. 2009; 2010), primarily attributed to altered predator-prey interactions and increased predation rates compared to patch interiors (Smith et al. 2011).

### 1.3.1.2 Habitat structure and complexity

Habitat structural complexity refers to the three-dimensional structure of habitats and represents one of the most important drivers of community structure across ecosystems (MacArthur and MacArthur 1961; August 1983; Tokeshi and Arakaki 2012; Graham and Nash 2013). Structural complexity influences ecological processes in multiple different ways by creating diverse microhabitats that support different species, providing refugia from predation and environmental stressors, and modifications to physical processes such as waterflow and light penetration (MacArthur and MacArthur 1961; August 1983; Tokeshi and Arakaki 2012; Graham and Nash 2013). The relationships between structural complexity and associated biotic assemblages has been documented across both terrestrial and marine ecosystems, from coral reefs, seagrass meadows, and kelp forests to terrestrial forests (Tews et al. 2004; Tokeshi and Arakaki 2012). Generally, increased structural complexity provides a greater number of ecological niches and is associated with greater species diversity and abundance (MacArthur and MacArthur 1961; McCoy and Bell 1991; Tokeshi and Arakaki 2012). However, this relationship is not always linear, with large amounts of complexity impeding movement and foraging for some species, creating trade-offs that vary among taxa and ecological contexts (Almany 2004).

In marine systems, structural complexity is commonly provided by habitat formers such as corals, seagrasses, macroalgae, and shellfish reefs. In seagrass meadows specifically, the complex structure of seagrass meadows provides refugia from predation by disrupting the sighting ability of visual predators (Edgar and Shaw 1995; Jackson et al. 2001). As such, the level of protection provided by a particular meadow is dependent on the density and structure of the seagrass itself, with increased shoot density being associated with decreases in predation pressure (Jackson et al. 2006; Larkum et al. 2006). Beyond predator-prey dynamics, denser seagrass canopies attenuate more wave energy (Fonseca and Cahalan 1992; Reidenbach and Thomas 2018; Vettori et al. 2024), creating energetically favourable conditions that reduce physiological stress on fish and allow greater energy allocation to growth (Duffy and Hay 2001; Stoll and Fischer 2011). This wave attenuation capacity may be particularly important for patches located near the estuary mouths or in areas with greater exposure to wave energy. Due to this trade-off between protection and predation, different seagrass complexities lead to a shift in the fish communities associated with them (Jackson et al. 2001; Jelbart et al. 2007). For example, less dense seagrass meadows may be more ideal for predatory fish that require more open foraging areas, while denser meadows may better suit prey fish who want to avoid predation (Werner and Hall 1988). Greater seagrass cover is also associated with increased levels of species richness, potentially due to the increased diversity of niches available within a more complex meadow (Heck Jr and Wetstone 1977; Gratwicke and Speight 2005; Jelbart et al. 2007; Smith et al. 2008). This relationship between structural complexity and diversity further emphasises the importance of understanding seagrass condition and structure when evaluating the ecological function of seagrass meadows within the broader seascape.

## *1.3.2 From patches to landscapes*

While patch-level characteristics have been shown to fundamentally influence fish communities (Wiens 1976; Heck Jr and Orth 1980; Wu and Loucks 1995; Thornton et al. 2011; Jackson et al. 2017), these local effects operate within broader spatial contexts that can modify, amplify, or override local patterns (Jackson et al. 2017; Fletcher and Fortin 2018). The limitations of a purely patch-based view of ecology became apparent as ecologists increasingly observed that patches with similar local characteristics often supported different communities and ecological relationships depending on spatial context (Pulliam 1988; Turner 1989; Bradley et al. 2019; 2020), that species distributions and abundances could not be explained by local patch characteristics alone (Levin 1992; 2000; Sheaves 2009), and observed that ecological processes such as dispersal, migration, and spillover effects operated across patch boundaries (Pulliam 1988; Wiens 1997; Lester et al. 2009; Cowen and Sponaugle 2009). This recognition has driven the emergence of spatial ecology as a framework for understanding ecological systems across multiple scales, acknowledging that ecological patterns and processes are inherently spatial phenomena that cannot be fully understood without considering the broader landscape context (Jackson et al. 2017; Fletcher and Fortin 2018).

### 1.3.2.1 Spatial ecology & seascape ecology

Spatial ecology takes a broad view of ecological systems and is a subset of ecology that focuses on the role of space on ecological processes and in turn how space influences ecological patterns (Fletcher and Fortin 2018). This interdisciplinary field encompasses biogeography (Lomolino et al. 2017), landscape ecology (Turner 2005), movement ecology (Nathan et al. 2008), meta-ecology (i.e, metapopulation dynamics (Pulliam 1988; Massol et al. 2011), and landscape genetics (Manel et al. 2003; Fletcher and Fortin 2018).

Landscape ecology - defined as the study of spatial and temporal patterns and their ecological consequences - is one of the key pillars of spatial ecology and originated in terrestrial systems (Fletcher and Fortin 2018). Concepts and the frameworks within landscape ecology are underpinned by foundational ecological theories including island biogeography theory (MacArthur and Wilson 2001) and metapopulation dynamics (Levins 1969; Wiens 1997). This field takes a wider view of ecological processes within an ecosystem, acknowledging that fundamental ecological processes that influence and structure associated biotic communities are determined not only by the characteristics of the habitat patch itself, but also its associated surroundings, context, and connectivity (Forman and Godron 1986; Turner 2005).

The marine application of the principles of landscape ecology, combined with quantitative marine ecology and geosciences, has given rise to seascape ecology as an interdisciplinary field (Pittman 2017b; 2017a). Historically, landscape ecology's application to marine systems was limited by difficulties in obtaining data of high enough resolution and over broad enough scales (Boström et al. 2011; Wedding et al. 2011; Pittman 2017a). However, recent advances in remote sensing techniques, high-resolution datasets across large scales, and marine sampling methods have made the study and research of seascape ecology increasingly accessible (Pittman et al. 2021). Consequently, seascape ecology represents a relatively new but rapidly growing field, with exponential increases in the number of publications per year over the past two decades (Figure 1.1).

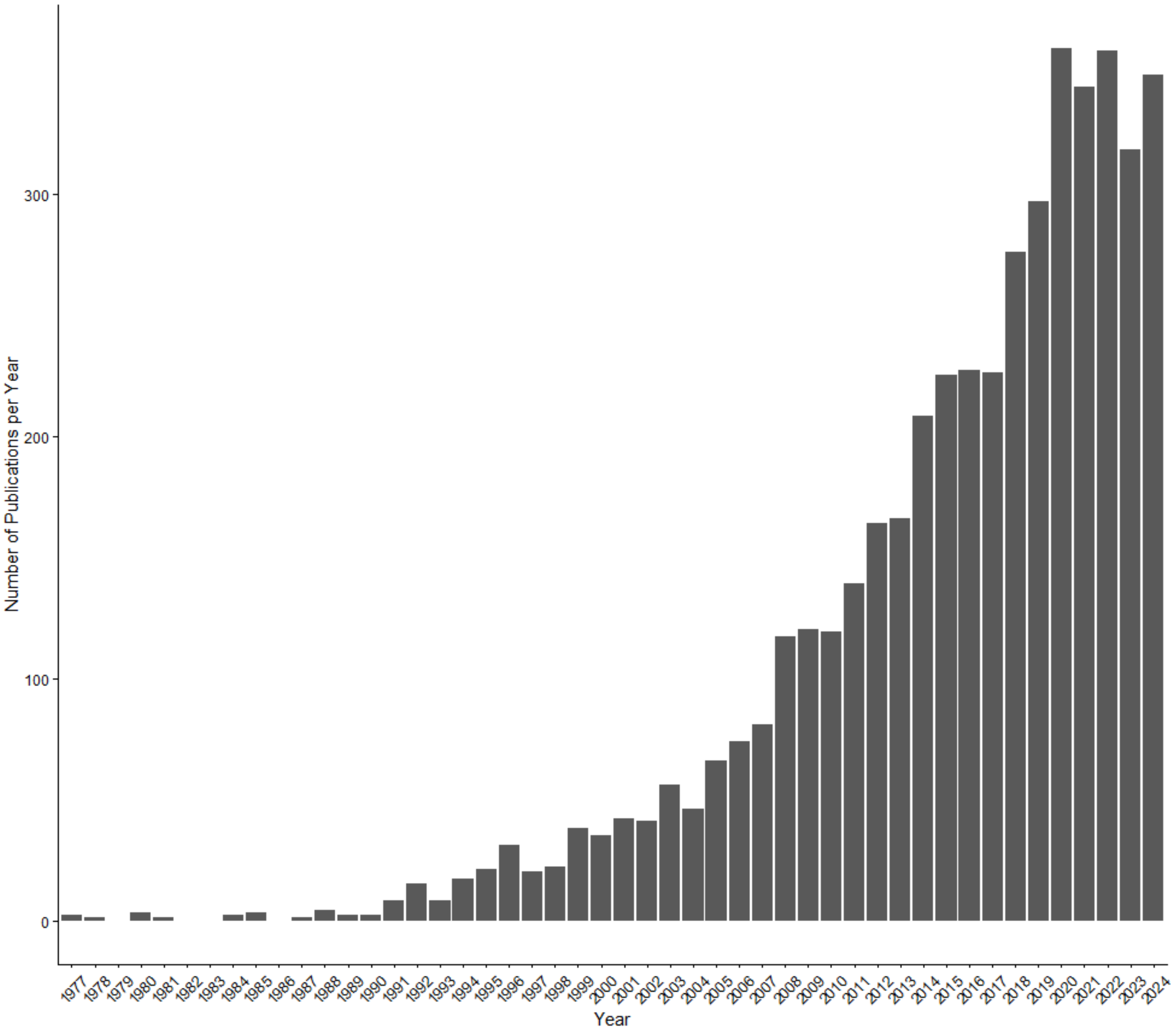


**Figure 1.1** – Number of publications published per year on the topic of seascape ecology in peer-reviewed journals from 1977-2024. Data sourced from Web of Science using the search terms: "Seascape Ecology", "Marine Landscape Ecology", and "Marine Spatial Ecology" searching the topic, abstract, and title of published manuscripts. Accessed on 28/10/2025.

## 1.3.2.2 Defining the seascape and the 4Cs framework

Pittman (2017a) defines the term seascape as a "*spatially heterogeneous and dynamic marine space that can be delineated at a wide range of scales in time and space, where human influence is integral to a system but not necessarily central*", and comprises of what has been described by Pittman et al. (2021) as the "4Cs": **C**ontext, **C**onfiguration (inclusive of seascape composition), **C**onnectivity, and **C**onsideration of scale. Each component influencing underlying ecological processes that drive marine systems and shape biotic assemblages, providing a framework in which we can understand the spatial dynamics of these complex marine ecosystems (Pittman et al. 2021).

### *1.3.2.2.1 Seascape context*

Seascape context refers to the environmental conditions and the surrounding events that influence a focal site across both temporal and spatial scales (Pittman et al. 2021; Wedding et al. 2025), including historical extreme weather events, terrestrial land-use patterns (e.g., agriculture and urbanisation), tidal regimes, and hydrodynamic conditions (Pittman 2017a; Bradley et al. 2020). Growing evidence demonstrates high geographic variability in ecological patterns and context-dependent influences varying the magnitude, shape, and direction of relationships (Bradley et al. 2020). For example, studies examining the relationships between fish/invertebrate communities and patch characteristics (e.g., size, shape, isolation, 3-dimensinal complexity) in estuarine remnant oyster reef systems show significant variability between different estuaries (Leong et al. 2024; 2025), highlighting the importance of seascape context on the ecological relationships between habitat characteristics and its associated assemblages, particularly in estuarine systems.

Estuaries exemplify complex contextual environmental gradients, featuring distinct ecotones from the mouth to the upper regions that significantly influence habitat function and fish assemblages (Mateus et al. 2008; Whitfield, Panfili, et al. 2012; Basset et al. 2013; Baillie et al. 2015). These gradients encompass changes in salinity, temperature, pH, depth, wave energy, and turbidity, often producing distinct environmental conditions across the estuarine continuum (Mateus et al. 2008; Whitfield, Panfili, et al. 2012). For example, patches near estuary mouths typically experience greater stability in water quality, but are more exposed to wave action, while upper estuary patches face greater fluctuations in water quality and conditions but are exposed to less hydrodynamic stress (Mateus et al. 2008; Whitfield, Panfili, et al. 2012). As a result, habitats along this gradient experience different stressors and disturbance regimes, potentially mediating how seascape factors influence fish communities. Yet, despite its ecological importance, these context-dependent relationships remain poorly understood, with most studies examining patch characteristics and the estuarine gradient separately rather than modelling interactive effects (Jelbart et al. 2007; Sheaves 2009; Gilby, Olds, Connolly, Maxwell, et al. 2018), potentially explaining varying findings in the literature regarding the influence of seascape characteristics on fish assemblages in estuarine systems.

##### *1.3.2.2.2 Seascape configuration & composition*

Seascape configuration refers to the arrangement of structural elements (habitat patches) throughout the seascape, including their size, shape, proximity, and degree of fragmentation, directly influencing ecological connectivity and associated processes (Pittman et al. 2021; Wedding et al. 2025). In contrast, seascape composition refers to the types and distribution of habitats constituting the seascape (Pittman et al. 2021; Wedding et al. 2025). Together, these factors influence ecological processes such as landscape complementation/supplementation, source-sink dynamics, and neighbourhood effects operating at particular patches depending on configuration and composition.

Landscape complementation occurs when connected patches provide different but complimentary resources, allowing landscapes to support larger populations than individual patches could maintain independently (Tilman 1982; McIvor and Odum 1988; Dunning et al. 1992). This process depends primarily on the landscape composition rather than spatial arrangement of the patches as different habitat types provide complementary - yet distinct – resources (Tilman 1982; McIvor and Odum 1988; Dunning et al. 1992). Conversely, landscape supplementation occurs when populations access supplementary resources from connected patches, depending on both spatial distribution and connectivity (Werner et al. 1983; Dunning et al. 1992). As fragmentation increases, individuals may expend more time and energy moving across the landscape matrix while facing greater predation risk to access complimentary and/or supplementary resources (Laurance 2008; Fahrig 2017), resulting in increased mortality rates, decreased growth rates, and consequently lower abundance.

Source-sink dynamics occur when productive patches (“sources”) provide emigrants to less productive patches (“sinks) that cannot sustain populations independently (Pulliam 1988; Pulliam and Danielson 1991; Pulliam et al. 1992). Source-sink structure is characterised by patches with strong variation in local demographics and/or varying levels of connectivity, where a patch can function as a sink if it is deficient in either of these two aspects (Figueira and Crowder 2006; Figueira 2009). However, demographic potential of a patch has been shown to be more important in determining patch contribution to overall population dynamics (Figueira 2009). These dynamics - particularly in marine systems - depend on a species' dispersal ability, with more mobile species being better able to locate source patches (Pulliam and Danielson 1991; Figueira and Crowder 2006). In landscapes dominated by sink habitats, a "needle in the haystack" effect may make it difficult for individuals to locate source patches (Pulliam et al. 1992), potentially leading to population declines as individuals become trapped in unsuitable habitats (known as ecological traps that cannot support reproduction or survival (Robertson and Hutto 2006; Hale and Swearer 2016). While landscape composition (source-sink ratio) primarily drives these dynamics, the spatial distribution of patches (landscape configuration) becomes increasingly important when the dispersal ability of an individual species is limited or reduced by factors such as anthropogenic disturbance or habitat loss (Pulliam and Danielson 1991; Figueira and Crowder 2006).

Neighbourhood effects represent a mechanism whereby individuals are primarily influenced by immediate surroundings rather than distant landscape features (Addicott et al. 1987). This reflects how many animals and fish typically utilise seascapes, residing within core areas where they access local resources (Powell and Mitchell 2012; Welsh et al. 2013; Childs et al. 2015), influencing how species respond to habitat heterogeneity, resource distribution, and environmental gradients at fine spatial scales (Addicott et al. 1987).

Despite the recognition of the importance of seascape configuration and its associated ecological processes on fish assemblages in marine systems, there remains limited understanding of the influence of this in seagrass systems. Filling this knowledge gap is critical to further our understanding of the seascape ecology of these systems and effectively apply this understanding to management and restoration. Throughout this thesis, I use the term "seascape configuration" to be inclusive of both seascape configuration and composition, in line with established lexicon in the literature (Pittman 2017b; Pittman et al. 2021).

#### *1.3.2.2.3 Connectivity*

Seascape connectivity represents one of the central principles underpinning seascape ecology due to its association with all other aspects of the field (seascape configuration & composition, context, and scale; Olds et al. 2017; Pittman et al. 2021; Wedding et al. 2025). Connectivity occurs at a variety of different scales from an individual organism, population, metapopulation, or a full distribution of a species and is inherently habitat and species-specific (Moilanen and Nieminen 2002; Olds et al.

2017; Santos et al. 2019; Moilanen et al. 2022). However, understanding connectivity requires distinguishing between its structural and functional aspects.

Structural connectivity refers to the physical arrangement of habitat patches across a seascape, measured purely based on the spatial configuration of habitat elements using metrics like patch density and least-cost paths (Kindlmann and Burel 2008; Wedding et al. 2011; Boström et al. 2011; Olds et al. 2017; Treml and Kool 2017). This form of connectivity is heavily associated with seascape configuration and composition (Boström et al. 2011; Wedding et al. 2011; Treml and Kool 2017; Olds et al. 2017), with greater structural connectivity characterised by shorter distances between patches and more continuous habitat arrangements (Kindlmann and Burel 2008). However structural connectivity alone does not guarantee connectivity in reality, as it assumes all species respond to spatial arrangement regardless of their specific traits and behaviour (Kindlmann and Burel 2008; Wedding et al. 2011).

Functional connectivity describes how seascape structure actually facilitates or impedes organism movement (Cowen and Sponaugle 2009; Weersing and Toonen 2009; White et al. 2019; Treml and Kool 2017), involving metapopulation level processes like gene flow and demographic exchange (Cowen and Sponaugle 2009; White et al. 2019; Treml and Kool 2017). This is driven by individual species' dispersal capabilities and movement patterns (Cowen and Sponaugle 2009; White et al. 2019; Treml and Kool 2017), meaning that highly mobile species may perceive distant habitat patches as functionally connected, while less mobile species may remain functionally isolated from nearby patches. Environmental factors such as water depth, current patterns, temperature gradients, and habitat quality can further modify functional connectivity by creating barriers to movement (White et al. 2019). Consequently, while structural and functional connectivity are related, they can differ substantially in reality, with structurally connected habitats being functionally isolated for certain species, and vice versa (Kindlmann and Burel 2008).

Due to these varying distinctions, connectivity is inherently species- and habitat-specific (Moilanen and Nieminen 2002; White et al. 2019). This species-specific habitat connectivity mean that some habitats may facilitate functional connectivity to a greater degree by providing safer movement corridors, while species-specific dispersal capabilities determine effective connectivity ranges (Anadón et al. 2013; Cecino et al. 2021). Functional connectivity is typically measured through animal tracking studies, genetic analysis, or population modelling (Weersing and Toonen 2009; Hussey et al. 2015; Treml et al. 2015), while structural connectivity is usually measured through indices of isolation and/or measures of distances between habitat patches (Moilanen and Nieminen 2002).

Despite its importance, seascape connectivity's influence on associated assemblages remains poorly understood, with minimal understanding as to how ecological functions are modulated by connectivity patterns (Olds et al. 2016; 2017; Weeks 2017; Pittman et al. 2021). This knowledge gap has been identified as a high priority research theme in seascape ecology (Olds et al. 2017; Pittman et al. 2021), emphasising the need to understand both structural and functional connectivity for deeper ecological understanding of these systems and effective restoration and conservation planning.

#### *1.3.2.2.4 Consideration of scale*

Scale - both temporal and spatial - is another core concept in all ecological disciplines, as different ecological processes are known to occur at different scales (otherwise known as scale-dependence; Schneider 2001; Lecours 2017; Schneider 2017; Pittman et al. 2021). Functional connectivity exemplifies this scale-dependence, operating locally (individual patch-to-patch movement) and across large spatial scales (mass migrations, larval/genetic supply across biogeographic regions; Pulliam 1988; Manel et al. 2003). Temporal variability also influences connectivity, as seasonal conditions may alter hydrodynamic patterns resulting in changes to seascape connectivity, while long-term changes (e.g., increased urbanisation and anthropogenic climate change) may create system-level shifts in connectivity and associated landscape processes (Wolkovich et al. 2014; Schneider 2017; Pittman et al. 2021). Due to the scale-dependence of many ecological relationships, different patterns can emerge when analysing data at different spatial scales (Meentemeyer 1989; Cumming et al. 2006). However, despite scale's importance, it is rarely examined adequately in marine ecology, leaving our understanding of how various scales influence seascape ecological relationships sparse (Schneider 2001; Wedding et al. 2011; Lecours 2017; Schneider 2017; Pittman et al. 2021).

Without proper scale consideration, there is a potential to mislead decision-making and reach incorrect conclusions about ecological relationships (Meentemeyer 1989; Cumming et al. 2006; Pittman et al. 2021; Wedding et al. 2025). Consequently, considering both temporal and spatial scales in seascape ecology is essential, particularly when applying this understanding into multi-scale management and restoration solutions (Lagabrielle et al. 2018). One way to address this potential pitfall is to define the scale of your seascape prior to undertaking the analysis (Pittman 2017a; Schneider 2017). Throughout this thesis, I used an organism-based approach (Wiens 1989) to setting the scale of the seascape following best practice principles outlined by Pittman et al. (2017) & Schneider (2017) when movement behaviour is known for the organisms studied. My seascape sampling unit (SSU) encompassed a 300m circular radius around the survey point (where the underwater remote video camera was deployed). I chose this 300m circular radius as it represents the 95th percentile of home ranges sizes estimated for the most common species (Yellowfin Bream; Swadling et al. 2024) observed in study. This radius also encompasses typical home range estimates for other common species in systems studied, including Luderick *(Girella* tricuspidata), Australasian Snapper (*Chrysophrys auratus*), Eastern Blue Grouper (*Achoerodus viridis*), and various other *Labrids* which demonstrate notable site fidelity in similar habitats (Curley et al. 2013; Ferguson et al. 2013; Harasti et al. 2015; Lee et al. 2015; Ferguson et al. 2016; Fetterplace et al. 2016; Taylor et al. 2017; 2018; Becker et al. 2023). The seascape sampling unit was the unit at which all seascape metrics characterising seascape composition and configuration were derived throughout this thesis.

### 1.3.2.3 The seascape nursery concept

The critical nursery function that seagrass meadows provide has received considerable attention throughout the literature, often with focussing on studies on validating their status as nursery habitats using the Nursery Role Hypothesis as a framework (Beck et al. 2001; Heck et al. 2003; Nagelkerken 2009; Sheaves et al. 2015). The Nursery Role Hypothesis defines nursery habitats as those contributing disproportionately more juvenile individuals per unit area to adult populations than other habitats (Beck et al. 2001). Thus, for the hypothesis to be supported, habitats must support greater contributions to the adult population via any of the following: greater juvenile density, growth, survival, and movement to adult habitats (Beck et al. 2001). Many studies confirm that seagrass meadows generally fulfil this criterion, supporting greater abundance, growth, and survival of juvenile fish than unstructured habitats, with similar rates to that of other structured habitats (Jackson et al. 2001; Heck et al. 2003; McDevitt-Irwin et al. 2016; Lefcheck et al. 2019). However, this body of literature has predominantly focused on patch-level characteristics in isolation, neglecting the influence of broader seascape on nursery function. This single-scale approach may provide an incomplete understanding of nursery value, as it fails to account for how connectivity, seascape configuration, and spatial context modify local patch performance. This could potentially result in management and restoration strategies focusing on nursery function targeting the wrong areas and patches for conservation of nursery value and an incomplete understanding of nursery ecology.

Recent literature has evolved toward the emerging seascape nursery concept (Nagelkerken et al. 2015; Litvin et al. 2018), which combines the concept outlined by the Nursery Role Hypothesis (Beck et al. 2001) with seascape ecology. The seascape nursery concept posits that nursery value emerges from the interaction between local habitat quality and broader landscape context, aligning with our growing understanding of the importance of seascape ecology in influencing these processes (Nagelkerken et al. 2015; Litvin et al. 2018). For example, connectivity facilitates movement between nursery and adult habitats (Cowen and Sponaugle 2009; White et al. 2019), while seascape configuration provides complementary resources and refuge opportunities that may enhance juvenile survival and growth beyond what an individual patch can provide (Tilman 1982; Pulliam et al. 1992; Dunning et al. 1992). Configuration effects, such as fragmentation and patch isolation, may also influence predation risk and resource accessibility (Fahrig 2003; Laurance 2008; Fahrig 2017), thereby modifying the effective nursery value of individual patches. By integrating patch connectivity and seascape context, this concept evolves beyond traditional single-patch evaluation toward a more comprehensive understanding of nursery value within seascapes. This represents a critical theoretical advancement that bridges patch-scale ecology with seascape ecology, providing a more thorough understanding of how nursery function emerges across seascapes. However, despite the conceptual advancement, substantial knowledge gaps remains on how this concept plays out in reality (Nagelkerken et al. 2015; Litvin et al. 2018). While seagrass meadows are generally accepted as nursery habitat (Heck et al. 2003; McDevitt-Irwin et al. 2016; Whitfield 2017), we lack understanding of how seascape connectivity and configuration alongside focal patch characteristics influence the capacity of a seagrass meadow to support juvenile fish and the relative importance of each of these components (Nagelkerken et al. 2015; Whitfield 2017; Olds et al. 2017). This knowledge gap limits our ability to effectively manage and conserve seagrass nursery habitats within the broader seascape context. More critically, it constrains our capacity to design restoration plans that optimise nursery function at seascape scales, potentially leading to suboptimal restoration outcomes.

#### 1.3.2.4 Toward multi-scale understanding

This theoretical framework “from patches to seascapes” (described above) illustrates the underlying theory and evidence of how fish communities in marine systems are shaped by processes operating across multiple spatial scales - from fine-scale habitat structure to broad seascape context. The progression from patch-level to broad seascape thinking highlights that local ecological patterns cannot be fully understood without considering their broader spatial surrounds. Edge effects, habitat complexity, and patch size create the foundation for community structure, but these local effects are modified by seascape configuration, connectivity, and environmental context in ways that may be non-linear and system specific. This thesis builds upon this theoretical foundation to examine how patch-level and seascape-scale factors interact to influence fish communities in temperate Australian seagrass systems in estuaries, providing the ecological understanding needed to advance evidence-based restoration and management practice.

#### 1.3.2.5 The application of seascape ecology to restoration and management - integration and implications for restoration

The complex interplay between seascape configuration, patch characteristics, and estuarine position likely creates ecological trade-offs that influence restoration and conservation outcomes. These trade-offs may manifest as different seascape configurations optimising for different ecological metrics - for example larger patches may be suited for high fish abundance but may not be ideal for maximising diversity. While ecological theory suggests such trade-offs should exist, they remain poorly understood in seagrass systems (Sheaves 2009; Bradley et al. 2019; 2020). Understanding these potential trade-offs is particularly important for evidence-based restoration, as practitioners often face decisions about prioritising different ecological objectives with limited resources (Maron and Cockfield 2008; De Groot et al. 2013; Reed et al. 2013; Cordingley et al. 2016).

Integrating these ideas into restoration to try to improve the efficiency and cost-effectiveness of restoration is of the upmost importance given the significant economic constraints surrounding marine habitat restoration (Bayraktarov et al. 2016; Abelson et al. 2020). The cost to carry out marine restoration is high, with one study reporting the median cost of restoration of one hectare of marine habitat being around $80,000 USD, with suggestions that in reality the real cost is likely to be two to four times greater (~$160,000 USD - ~$320,000 USD; Bayraktarov et al. 2016). These values are up to eight times greater than the maximum costs estimated for the restoration of most terrestrial habitats (Armsworth 2014; Bayraktarov et al. 2016). It has been proposed that this is most likely due to marine systems being highly variable and dynamic, with significant variability in environmental conditions (e.g., wave energy, temperature, salinity, light availability, nutrient availability, exposure) on both daily and yearly temporal scales due to impacts of storms, run off, changes in current flow (Cloern et al. 2016; Pansch et al. 2022), alongside the comparatively greater logistical challenges associated with working in a marine environment (Bayraktarov et al. 2016; Abelson et al. 2020; Thomson and Gerwing 2023). Furthermore, unlike terrestrial systems, greater economic investment in marine restoration projects is not correlated with restoration success, likely associated with ecological understanding and restoration techniques not being sufficiently mature enough to yield high levels of return on investment in marine systems (Ruiz-Jaen and Mitchell Aide 2005; Bayraktarov et al. 2016). This is compounded by marine restoration's focus on the habitat former itself rather than the recovery of the associated biotic assemblages (such as fish communities) that restoration often ultimately aims to support (Hagger et al. 2017; Cross et al. 2020). These economic limitations alongside limited scope of restoration highlights the importance of maximising restoration efficiency by incorporating seascape ecology into restoration design. By understanding the relationships between fish communities and the seascape in seagrass systems, restoration efforts could strategically select sites and restoration designs that optimise for fish community outcomes while working within economic constraints.

## 1.4 | Methodological considerations in fish community assessment

Seascape-level marine research requires precise and scalable survey methods that can reliably characterise fish communities across broad spatial scales. While traditional extractive methods like seine netting and trawling remain efficient for fisheries assessments, their destructive nature and habitat limitations make them unsuitable for research in ecologically sensitive areas or structured habitat (National Research Council et al. 2006; McGeady et al. 2023). These methods also introduce various sampling biases, including mesh size selectivity that favours certain size classes, differential catch rates among species and life stages, and escape by larger more mobile species (National Research Council et al. 2006). Additionally, these methods are often time-intensive in the field, limiting researchers' ability to achieve broad spatial coverage necessary for seascape studies within practical sampling windows.

The limitations of extractive sampling have driven increased adoption of non-extractive alternatives in marine research (Whitmarsh et al. 2017; Langlois et al. 2020; McGeady et al. 2023). Baited remote underwater video systems (BRUVs) offer broad applicability, but single camera systems cannot capture any size data that is critical for understanding population demographics (Whitmarsh et al. 2017; Langlois et al. 2020). Stereo-BRUV systems address this limitation through stereoscopic measurement (Harvey et al. 2001; Langlois et al. 2020), yet the bait plumes associated with baited systems often create artificial fish aggregations that bias both abundance estimates and size measurements (Hardinge et al. 2013), particularly when using the standard MaxN (defined as the maximum number of individuals of a particular species observed within the video at one time point; Schobernd, Bacheler & Conn 2013) methodology (Williams et al. 2022). These biases become more pronounced with increasing fish abundance, decreasing camera viewing area, and when fish school by age and/or length, potentially compromising the reliability of community assessments across variable seascape contexts (Williams et al. 2022). Unbaited stereo-RUVs avoid the behavioural modifications and biases in length associated with bait attraction and can provide more representative samples of natural fish communities (Langlois et al. 2020). However, their application in marine ecology is limited by lengthy video processing times and the lack of validated sampling protocols for reliable population parameter estimation. Specifically, researchers lack guidance on the minimum number of individual fish measurements required to generate precise estimates of key population metrics such as mean length and the proportion of juveniles within the fish assemblage. This uncertainty creates a trade-off between sampling effort (and thereby cost) and statistical reliability that limits the scalability of unbaited stereo-RUV methods for broad seascape-level research, as often studies conducting surveys at seascape-level scales require significantly greater sample sizes on account of their broader spatial scale, significantly increasing the cost and time associated with conducting these studies.

This methodological gap has significant implications for seascape ecology research, where understanding this multi-scale ecological relationships requires consistent, reliable data collection across numerous sites and spatial scales (Boström et al. 2011). Without optimised sampling protocols, researchers risk either under-sampling videos (leading to imprecise parameter estimates) or over-sampling (inefficient use of limited resources), both of which compromise the quality and scope of seascape studies. Addressing this methodological foundation is therefore essential before undertaking comprehensive studies of fish community responses to seascape characteristics using unbaited stereo-RUVs. Furthermore, in marine ecology, where logistical constraints frequently limit sample sizes due to factors such as weather, equipment costs, and vessel availability, methodological optimisation becomes particularly crucial for ensuring that limited sampling effort translates into reliable and meaningful ecological insights that can inform both scientific understanding and management decisions.

## 1.5 | Thesis overview and aims

The overall goal of the thesis was to get a greater understanding of the seascape ecology of fish communities in seagrass systems within temperate estuaries in Australia, with the aim of then applying this understanding to restoration/conservation contexts. This research is particularly pertinent as restoration is increasingly being used to mitigate the negative impacts of anthropogenic pressures on these declining ecosystems and to bring back what was once lost (Gillies et al. 2015; Saunders et al. 2020). While applying seascape ecology principles to restoration has the potential to significantly improve restoration outcomes (Wedding et al. 2025), we must first understand the complex spatial relationships that govern fish communities in these systems.

This thesis addresses this critical knowledge gap by examining how fish assemblages respond to habitat characteristics across multiple spatial scales and ultimately tries to outline a way this could be applied to restoration. Specifically, this thesis addresses four key research questions underneath the broader overarching question "how do seascape and focal patch characteristics influence fish communities in temperate estuarine seagrass systems, and how can this understanding be applied and integrated to potentially improve restoration outcomes?": (i) What sampling effort is required for reliable assessment of key fish population parameters (mean and standard deviation of length, the proportion of juveniles) using stereo-RUV systems to enable precise cost and time efficient seascape level surveys? (ii) How does connectivity to artificial structures alongside seascape and focal patch characteristics influence fish communities in seagrass within a highly urbanised estuary? (iii) How do both focal patch and seascape characteristics more broadly influence fish community responses? (iv) How can this multi-scale ecological understanding be operationalised for strategic restoration planning that considers outcomes for associated organisms (fish in this case), as well as the target habitat itself? My thesis follows a logical progression from methodological foundation through ecological understanding to practical application: (1) establishing robust methodological protocols necessary for reliable seascape-scale research (**Chapter 2**); (2) using these methods to understand multi-scale ecological relationships/seascape ecology of fish communities in seagrass meadows in temperate estuarine systems (**Chapter 3 & 4**); and (3) applying this understanding into evidence-based restoration frameworks (**Chapter 5**).

This thesis comprises four data chapters (**Chapter 2 -5**), of which **Chapters 2, 3,** and **4** are prepared as stand-alone manuscripts formatted for publication. **Chapter 2** is currently under review at *North American Journal of Fisheries Management*. **Chapters 3 & 4** are in the process of being prepared as a manuscript for *Landscape Ecology*. **Chapter 5** is prepared and styled as a thesis chapter and thus contains references to other chapters throughout the methodology to reduce repetition of methodologies throughout the thesis.

In **Chapter 2**, I aim to optimise sampling methods to assess key fish population metrics from unbaited stereo-remote underwater video and assess the number of observations required to get a reliable estimate of the mean and deviation of fish lengths and to estimate the number of juveniles within the population. Both of which were integral to understand to conduct the fish assemblage surveys in later chapters.

In **Chapter 3**, I examined how proximity to artificial structures (specifically jetties) and various focal-patch and seascape habitat characteristics influenced key fish assemblage metrics (total abundance, species richness, diversity, proportion of juvenile fish within the assemblage), size-structure, and behaviour in adjacent seagrass meadows. This understanding is critical as urbanisation of marine and estuarine systems continues to accelerate, and the need to inform sustainable development and management of these systems becomes more important.

In **Chapter 4**, I broaden the scope from solely connectivity to artificial structures to examine how seascape configuration and structural connectivity alongside focal-patch characteristics shape fish assemblage structure. Unlike the previous chapter's focus on specific features, this chapter aims to develop a broader understanding of seascape ecological relationships across a natural seascape. Understanding these relationships is critical to inform seascape-aware conservation and restoration strategies.

In **Chapter 5**, I integrate seascape understanding into a systematic decision-support framework for restoration site selection/planning that considers outcomes for both associated assemblages and the habitat former, combining habitat suitability modelling, spatial prioritisation, and multi-criteria optimisation. This framework aims to address key restoration bottlenecks including opportunistic site selection, inadequate consideration of seascape context, and lack of quantitative approaches for optimising restoration design.

Finally, in the General Discussion (**Chapter 6**), I synthesise the key findings across all chapters, discuss broader implications, and provide recommendations for future research directions. This research provides both fundamental ecological insights and practical tools for evidence-based restoration, with applications extending beyond seagrass systems to other marine restoration contexts where spatial considerations will be critical for success

# Chapter 2 - Optimising sampling to characterize fish population size structure from stereo remote underwater video

# Abstract

Length data from fish populations is crucial for understanding ecosystem integrity and informing fisheries management decisions, with stereo Remote Underwater Video systems (stereo-RUVs) emerging as a powerful non-extractive sampling tool to do so. However, the optimal sampling effort required to obtain precise population parameter estimates from stereo-RUV footage for fish remains poorly understood. We investigated the minimum number of fish that need to be sampled to precisely characterise population metrics mean and standard deviation of length, and proportion of juveniles across different population structures. Using simulation studies across four distinct population size distributions, combined with validation through in-situ stereo-RUV deployments, we identified consistent patterns in sampling requirements. Our results demonstrate that measuring approximately 25 replicate fish - ideally from 25 distinct timepoints/different schools - provides precise estimates of the studied population metrics across diverse underlying length-frequency distributions. This sampling threshold remained robust even when the underlying population structure was unknown. This study provides the first empirically validated sampling protocol for stereo-RUV surveys of key population parameters such as mean and standard deviation of lengths, and the proportion of juveniles within the population, offering a workflow that optimizes the balance between sampling effort and precision. These findings will enhance the reliability of non-extractive fish population monitoring, which is particularly valuable for tracking ecosystem responses to anthropogenic impacts and climate change.

## 2.1 | Introduction

Fish play vital ecological, economic, and cultural roles in marine ecosystems worldwide, and as key components of marine food webs, they constitute some of the highest order consumers, are key to maintaining ecosystem integrity and resilience, and support both commercial fisheries and traditional subsistence practices (Holmlund and Hammer 1999; Hiddink et al. 2008; Tacon and Metian 2013). However, fish populations face mounting pressures from direct harvest, habitat degradation, climate change, and other anthropogenic impacts (Brander 2013; Belhabib et al. 2018), making the understanding of their population biology increasingly critical for effective conservation and management (Queirós et al. 2018).

The study of population biology requires systematic surveys to measure key metrics such as abundance, species richness, diversity, behaviour, body size, and size/age distributions (Maunder and Punt 2013; Ono et al. 2015). These metrics enable researchers and managers to track population trends, assess ecosystem stability via keystone species, understand the underlying ecology, and make informed decisions about conservation and resource management, such as setting sustainable catch limits, identifying critical nursery habitats for protection, establishing effective marine protected areas, and developing species-specific recovery plans for depleted populations (Ono et al. 2015). Various techniques have been employed to conduct such surveys, each with distinct advantages and limitations. Extractive methods such as hook-and-line fishing, trawling, or seine netting are traditionally used in fisheries stock assessments (National Research Council et al. 2006). However, these methods are limited by biases related to mesh size selection (particularly smaller size classes such as juveniles) and often can be destructive and/or damaging, restricting their use in certain habitats (National Research Council et al. 2006). Consequently, non-extractive techniques, such as diver-based underwater visual census (UVC) and remote underwater videos (RUVs), have gained preference in the research community (Whitmarsh et al. 2017; Langlois et al. 2020).

Remote underwater videos (RUVs) have become increasingly prevalent tools for surveying fish populations, particularly in areas where traditional extractive methods are unsuitable or prohibited (Langlois et al. 2020; Erickson et al. 2023; McGeady et al. 2023). The use of multiple RUVs can increase the ability to conduct sampling more rapidly, with greater sample sizes, and at larger spatial scales by being deployed simultaneously or consecutively in the field (Whitmarsh et al. 2017; Langlois et al. 2020), thus increasing efficiency and reducing the cost associated with conducting fish surveys. Furthermore, stereo remote underwater videos (stereo-RUVs), which use two cameras at a fixed angle and distance apart, enable precise, in situ, non-extractive measurements of fish body size (Harvey et al. 2001; Langlois et al. 2020). This capability allows researchers to collect detailed demographic data including size frequencies and metrics of population structure such as the proportions of juvenile fish within a population (Langlois et al. 2020). As a result, stereo-RUVs have emerged as a valuable tool to provide a method that is both cost-effective and statistically powerful for detecting spatio-temporal changes in fish populations, particularly for monitoring relative abundance, length distributions, and biomass patterns of fish assemblages across marine ecosystems.

There are two primary methods for estimating fish abundance from RUVs: MaxN and MeanCount. MaxN, defined as the maximum number of fish observed in a single video frame, is commonly used with baited RUVs (BRUVs) to estimate relative fish abundance (Whitmarsh et al. 2017; Langlois et al. 2020; McGeady et al. 2023). This metric has the benefit of being relatively quick to calculate, reducing the processing time of BRUVs, and provides a conservative estimate of the number of fish at a given site, ensuring that an individual fish contributes to the metric only once during a video (Schobernd et al. 2013). However, a key challenge in analysing BRUV footage is the temporal dynamics of fish attraction to bait, where fish numbers typically increase over time, with this accumulation rate varying with environmental conditions (Hardinge et al. 2013). MaxN addresses this challenge by providing a single snapshot of maximum fish numbers, making it the predominant metric for BRUV analysis (McGeady et al. 2023). When measuring fish lengths from BRUV footage, researchers typically measure all fish present in the MaxN frame as a logical extension of this approach (Johansson et al. 2008; Langlois et al. 2020). However, recent studies suggest these MaxN-derived length estimates may show potential bias under certain conditions, such as high fish abundance, low field of view, and high schooling density (Williams et al. 2022). Moreover, the number of fish that need to be measured to obtain reliable length estimates remains poorly understood.

For unbaited RUVs, where temporal accumulation is not expected, MeanCount offers an alternative approach by sampling a set number of frames throughout the video and then calculating the average number of fish observed per frame (Schobernd et al. 2013). Multiple studies demonstrate MeanCount's linear relationship with true abundance across various scenarios, as such it provides a more accurate assessment of site-relative abundance in unbaited systems (Schobernd et al. 2013; Stobart et al. 2015; Erickson et al. 2023). The repeated sampling nature of MeanCount also enables collection of length data from more fish throughout the video, with studies indicating that it may provide a more unbiased mean length estimates compared to MaxN (Williams et al. 2022). However, MeanCount requires significantly more processing time than MaxN, as analysts must count, identify, and measure fish across all sampling frames. Additionally, the optimal sampling intensity for both abundance estimates and length measurements using MeanCount remains undetermined.

Though both methodologies have been used to estimate population characteristics from underwater videos, neither the MaxN nor MeanCount approaches fully address how many fish measurements are needed to precisely estimate population parameters such as mean length or the proportion of juveniles/adults within a population. For example, when sampling particular frames or just the MaxN frame, researchers may only measure 1-5 fish, potentially introducing bias due to small sample size (Tversky and Kahneman 1971; Underwood and Chapman 2003). Currently, the number of fish that need to be measured to get a precise estimate of mean length, the standard deviation of the lengths, or the proportion of any specific subset of the length distribution (juveniles for instance) within a population using stereo-RUVs has not been determined. Addressing this knowledge gap is essential for optimising fish video analysis workflows and ensuring reliable population assessments.

While machine learning techniques have shown promise for analysing entire videos without subsampling (Ditria et al. 2020; Lopez-Marcano et al. 2021), current workflows require large, size and species-specific training datasets, making subsampling methods still necessary. Additionally, fully autonomous length measurement from RUVs remains under-developed and computationally expensive, requiring either manual length annotation or semi-automated methods with human input (Marrable et al. 2023). Consequently, studies using machine learning for fish identification often still choose to limit length measurements to the MaxN frame or combine MaxN with randomly sampled frames to determine these parameters (Sheaves et al. 2020; Connolly et al. 2024). Understanding optimal sampling requirements therefore remains crucial even as automated methods continue to develop.

This study aims to identify the optimal sample size for deriving precise estimates of size structures and the proportion of juveniles within a given fish population sampled using stereo-RUVs. We evaluated sampling optimisation under four simulated population structures with known size distributions and population sizes, validating our findings using a case study dataset derived from in-situ stereo-RUV deployments.

# 2.2 | Methods

This analysis comprised two components: one based on four simulated populations with differing age-frequency distributions (and thus different length-frequency distributions), and another based on a case study dataset collected in the field. The simulation component was designed to understand how the underlying age/length-frequency distribution of a population might affect the number of fish that must be sampled in order to precisely estimate size structure - such as mean and standard deviation of lengths, and the proportion of juveniles. This was critical as the underlying distribution of a population can affect the likelihood of encountering less common fish sizes, especially at the extremes of the distribution, due to lower abundance within the population (assuming a non-biased and random sampling methodology). This approach was necessary because the true underlying distribution in the case study dataset was unknown. The case study dataset was used to validate the results of the simulation study and provided an in-situ example of whether the optimal sample size derived from the simulation study could be achieved in practice.

## *2.2.1 Generating datasets*

### 2.2.1.1 Simulation study

We generated four sample populations following the same approach used by Williams et al. (2022) for simulating populations for fisheries analysis. In our population, each age ranged from 1 to 20 years, with consistent/stable recruitment year to year. Each of the four populations had a different annual natural morality rate (*M*: 0.2, 0.4, 0.6, 0.8; Table 2.1), which were selected to generate a variety of age-frequency distributions (Figure 2.1), covering a wide range of natural mortality scenarios that may be encountered in the field. The population size was set at 50,000 to ensure that the simulated populations accurately reflected theoretical distributions. Ages were converted to lengths using a von Bertalanffy growth model (Von Bertalanffy 1957) with the following parameters: $L\infty = 1000$, $K = 0.25$, $t0 = -0.5$ (Table 2.1). Variability within the size at age for each fish was modelled using a normal distribution with a coefficient of variation (0.2) that was consistent for each age (as per Williams, Shertzer & Bacheler 2022). In the simulation studies, juvenile fish were defined as those below 33% of the population's maximum length, as this is a rough estimate of size at maturity for many fish species (Piggott et al. 2020). All simulations were conducted in R for reproducibility (R v4.4.2; R Core Team 2025).

**Table 2.1** - Parameters used to generate the simulated populations

| **Biological Factor** | **Parameter** | **Values** |
|---|---|---|
| Age range ($y$) | $a$ | 1-20 |
| Natural Mortality Rates ($y^{-1}$) | $M$ | 0.2-0.8 |
| Asymptotic length (length units) | $L\infty$ | 1000 |
| Growth Rate ($y^{-1}$) | $K$ | 0.25 |
| Spawning Adjustment ($y$ ) | $t_0$ | -0.5 |
| Variability in length-at-age | $cv$ | 0.2 |

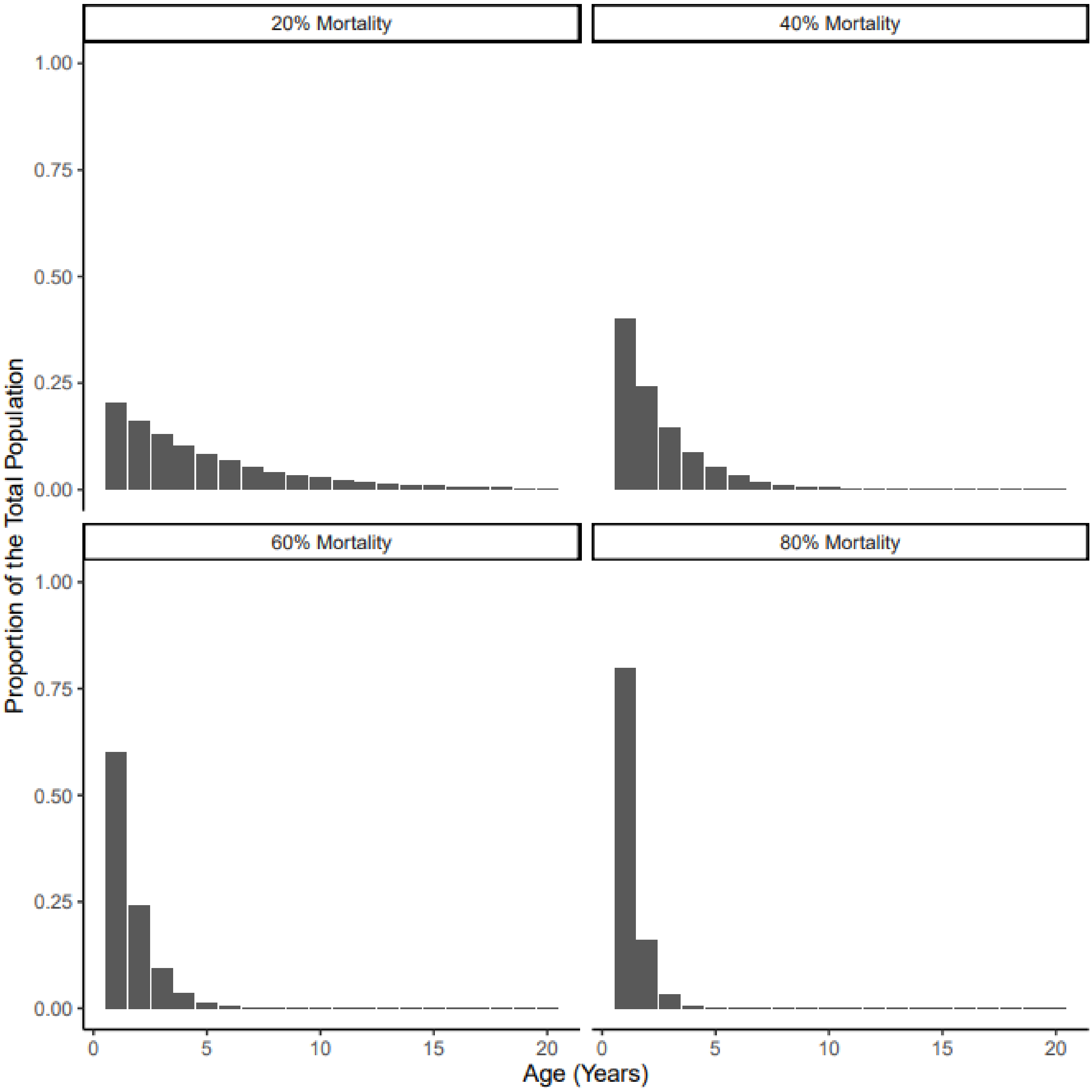


**Figure 2.1** - Age-frequency distributions of the simulated population at various levels of mortality (*M*) - 20% (0.2 *M*), 40% (0.4 *M*), 60% (0.6 *M*), and 80% (0.8 *M*).

### 2.2.1.2 Case study

Ten unbaited stereo-remote underwater video systems (stereo-RUVs) were deployed for 1.5 hours during high tide within seagrass, *Zostera capricorni*, meadows throughout a temperate estuary (Lake Macquarie) in New South Wales, Australia in Austral autumn (April) 2023. This deployment time was chosen to cover most of the tidal slack period around high tide, minimising potential confounding effects from incoming or outgoing tides. GoPro cameras (Hero 11 and 12 set to 1080p, 60fps, wide field of view) on the stereo-RUVs were positioned 800 mm apart with a 4.5° inward angle, creating an optimal measuring distance of 2-8 meters from the frame centre (Langlois et al. 2020). Stereo-RUVs were calibrated using a standard 1x1x1m SeaGIS calibration cube in the CAL software prior to deployment (v1.2; SeaGIS 2024a). The resulting videos were sampled every 30 seconds for 60 minutes (including the starting point at 0 minutes), yielding 121 frames per video for analysis. This interval was chosen as it represents a high level of temporal resolution while avoiding potential autocorrelation between samples.

Each frame was annotated using EventMeasure software (v6.42; SeaGIS, 2024b), where fish were counted, identified to species level, and had their fork lengths (mm) measured. Yellowfin Bream (*Acanthopagrus australis,* Sparidae) were chosen as model species for analysis due to their ubiquity throughout all videos and common presence in seagrass habitats within eastern Australian estuaries (Curley et al. 2013). The juvenile size cut-off for Yellowfin Bream was defined as 190mm which is equal to the FL50 (length at which 50% of the individuals in the population have reached sexual maturity; Chen & Paloheimo 1994) for this species in the samples.

We focused on one species rather than the full fish assemblage as mean length for a population should always be considered at a species level rather than a whole assemblage level due to inter-specific variation in length and length at maturation (Policansky 1983; Caley et al. 1996). Similarly, for juvenile counts, while some studies may choose to focus on the overall number of juveniles across all species, many studies choose to focus on a few common or important species due to the inherent biological differences and habitat preferences between species and across their ontogeny (Bronwyn et al. 2003; Nagelkerken et al. 2015; Piggott et al. 2020).

### *2.2.2 Sampling the datasets*

Length datasets derived from the four simulated populations (mortality rates = 0.2, 0.4, 0.6, 0.8) as well as each of the videos (10 in total) were sampled via a bootstrap method (with replacement) to generate 10,000 simulated datasets for each sample size (ranging from 1 to 100 fish measured) available within a dataset. This was done using a custom function in R (R v4.4.2; R Core Team 2025; see code in 10.5281/zenodo.14641960; Pine et al., 2025). For each of the simulated datasets, we calculated three population metrics: mean length, standard deviation of the length, and proportion of juveniles. The precision of these estimates was assessed using the raw coefficient of variation (standard deviation divided by the mean - CV) calculated for each metric at each sample size.

Note that we have not attempted to assess accuracy within our analysis as this is not possible in the primary application, the field study, where the true population structure is unknown. However, previous work looking at sample size analysis shows that when sampling methodologies are unbiased, an increase in precision generally leads to an increase in accuracy (Andrew and Mapstone 1987; Underwood 1997; Underwood and Chapman 2003), and indeed accuracy also usually improves more quickly with increases in sample size compared to precision (e.g., Erickson, Bugnot & Figueira 2023).

### *2.2.3 Identifying the optimal number of fish to sample*

When the CV stabilises, additional increases in sample size do not significantly enhance precision, despite increased sampling effort (Andrew and Mapstone 1987; Underwood 1997). To optimize sampling effort, we defined the point at which the CV stabilises as the optimal sample size for achieving the highest degree of precision in our study. To approximate the instantaneous rate of change of CV with sample size, we calculated the finite central derivative for each data point, representing the percentage improvement in CV from one point to the next. For a sample size of one the forward derivative was calculated. For the maximum sample size, the backward derivative was used due to the lack of data points on either side required for the central derivative calculation. We defined the cut-off point beyond which sampling additional fish is not useful at 0.5% instantaneous rate of change in CV. This threshold was used to determine when further increases in sample size yielded diminishing returns in precision and represents a practical balance between achieving robust precision in our population structure estimates while acknowledging the substantial resource investment required for each additional sample. This point is ultimately arbitrary and should be set *a* *priori* by an investigator as this level will vary based on how sensitive/conservative an investigator is to levels of precision their analysis/project requires (Andrew and Mapstone 1987; Underwood 1997; Anderson and Santana-Garcon 2015). For the case studies, in situations where the 0.5% cut-off was never reached due to insufficient sample size, the video was excluded from further analysis and the calculation of the mean, median, and max optimal sample size.

## *2.2.4 Statistical analysis*

To understand if the population size structure (different mortality values) significantly influenced the number of measurements required to reach the *a priori* cutoff in the simulation study, a one-way ANOVA was conducted (with different mortality values as a factor with four levels) using the *car* package (Fox et al. 2012) in R (R v4.4.2; R Core Team 2025). A tukey post-hoc analysis was conducted also using the package *car* (Fox et al. 2012) to see which populations varied significantly from one another where required.

# 2.3 | Results

## *2.3.1 Simulation study*

Across all three metrics (mean length, standard deviation of lengths, and proportion of juveniles), the coefficient of variation (CV) showed consistent patterns over all four simulated populations. All metrics demonstrated rapid initial improvement in precision, with CV decreasing to $\leq 50\%$ of initial values within the first 10 samples (Figure 2.2 A, B, & C). The point of diminishing returns occurred at sample sizes between 20 and 30 for all metrics (Table 2.2). For mean length this occurred at 23.8 ± 0.7 fish, it occurred for standard deviation at 27.4 ± 1.3 fish, and proportion of juveniles at 24.2 ± 0.8 fish (Table 2.2). No significant differences were found in these cut-off points among populations with different mortality rates (ANOVA, $p > 0.05$ for all metrics). Final CV values stabilised at approximately 0.05 for mean length, 0.1-0.25 for standard deviation, and 0.1-0.4 for proportion of juveniles, with higher mortality rates generally associated with lower final CV values (Figure 2.2).

**Table 2.2** - Summary table of the mean, standard error, 95% confidence interval, median, and max point of diminishing returns (derived the last occurrence of the 0.5% central derivative) for each metric analysed for various population structures within the simulation study (Mortality Rate: 0.2, 0.4, 0.6, 0.8).

| **Mortality Rate** | **Metric** | **Mean** | **SE** | **95% CI** | **Median** | **Max** |
|---|---|---|---|---|---|---|
| 0.2 | Mean Length | 21.7 | 0.88 | 19.9 - 23.4 | 22 | 23 |
| | SD Length | 22.3 | 0.33 | 21.7 - 23.0 | 22 | 23 |
| | Juvenile Proportion | 24.7 | 1.20 | 22.3 - 27.0 | 24 | 27 |
| 0.4 | Mean Length | 25.3 | 1.33 | 22.7 - 27.9 | 24 | 28 |
| | SD Length | 27.7 | 2.73 | 22.3 - 33.0 | 26 | 33 |
| | Juvenile Proportion | 27.0 | 2.08 | 22.9 - 31.1 | 28 | 30 |
| 0.6 | Mean Length | 23.7 | 1.86 | 20.0 - 27.3 | 25 | 26 |
| | SD Length | 30.3 | 2.85 | 24.8 - 35.9 | 28 | 36 |
| | Juvenile Proportion | 22.0 | 1.00 | 20.0 - 24.0 | 21 | 24 |
| 0.8 | Mean Length | 24.3 | 0.33 | 23.7 - 25.0 | 24 | 25 |
| | SD Length | 29.3 | 0.67 | 28.0 - 30.6 | 30 | 30 |
| | Juvenile Proportion | 23.0 | 0.58 | 21.9 - 24.1 | 23 | 24 |
| All Groups Combined | Mean Length | 23.8 | 0.66 | 22.4 - 25.1 | 24 | 28 |
| | SD Length | 27.4 | 1.26 | 24.9 - 29.9 | 27.5 | 36 |
| | Juvenile Proportion | 24.2 | 0.81 | 22.6 - 25.7 | 23.5 | 30 |

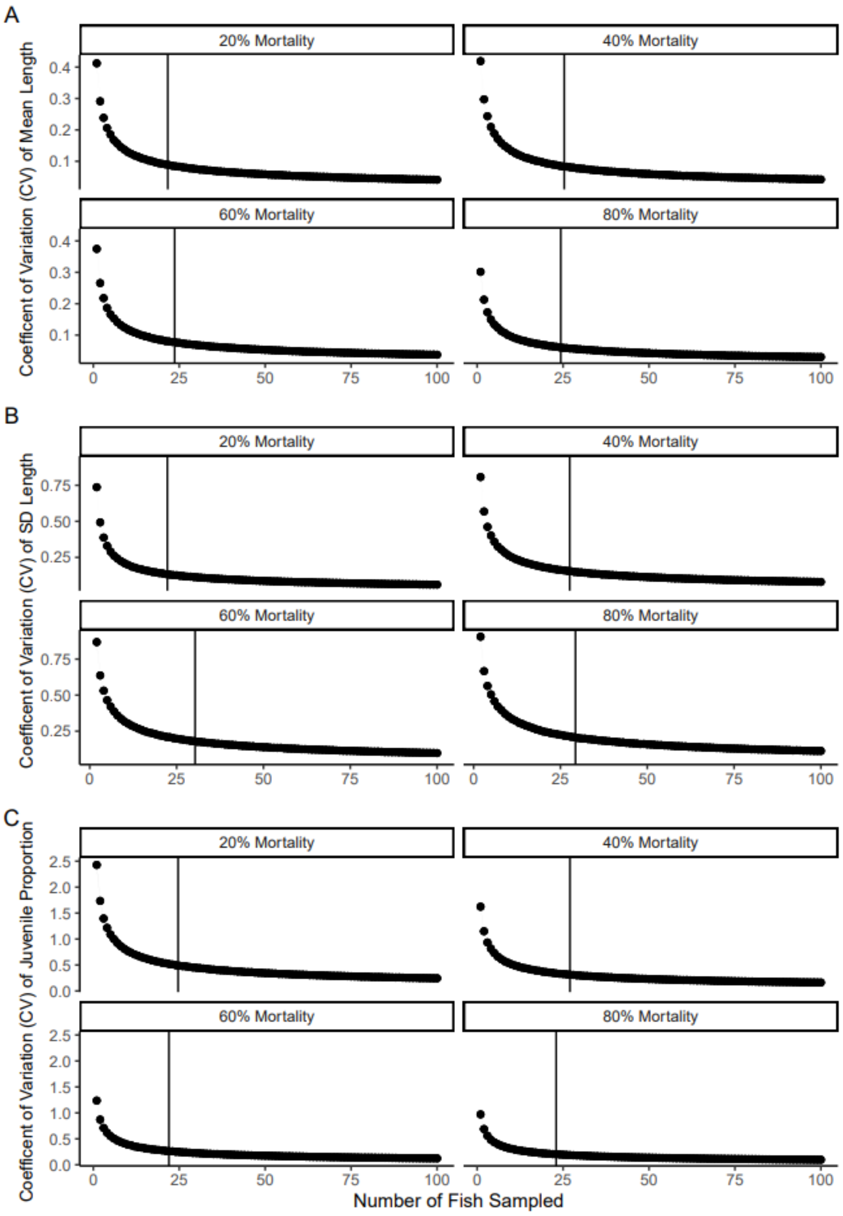


**Figure 2.2** - Precision (coefficient of variation, CV) curves based on the number of fish sampled for three key population traits within four populations with varying mortality rates (M=0.2, 0.4, 0.6, 0.8). A) Mean length B) Standard deviation of fish lengths C) Proportion of juveniles within the population. Vertical lines (when present) represent the point of diminishing returns for that particular group calculated using the central derivative approach described in the methods.

### *2.3.2 Case study*

Analysis of the in-situ stereo-RUV deployments revealed similar patterns to the simulation study, though only six (SD of length and juvenile proportion) and seven (mean length) of the ten videos contained sufficient fish numbers to identify points of diminishing returns (Figure 2.3; Figure 2.4; Figure 2.5). All metrics showed the same rapid improvement in precision within the first 10 samples as observed in the simulation study. The point of diminishing returns occurred at consistent sample sizes across metrics. It occurred for mean length at 24.4 ± 1.48 fish (range: 20-31, n=7 videos), standard deviation at 25.16 ± 1.42 fish (range: 21-23, n=6), and proportion of juveniles at 24.6 ± 1.82 fish (range: 21-33, n=6; Table 2.3). Final CV values stabilized between 0.05-0.15 across all metrics.

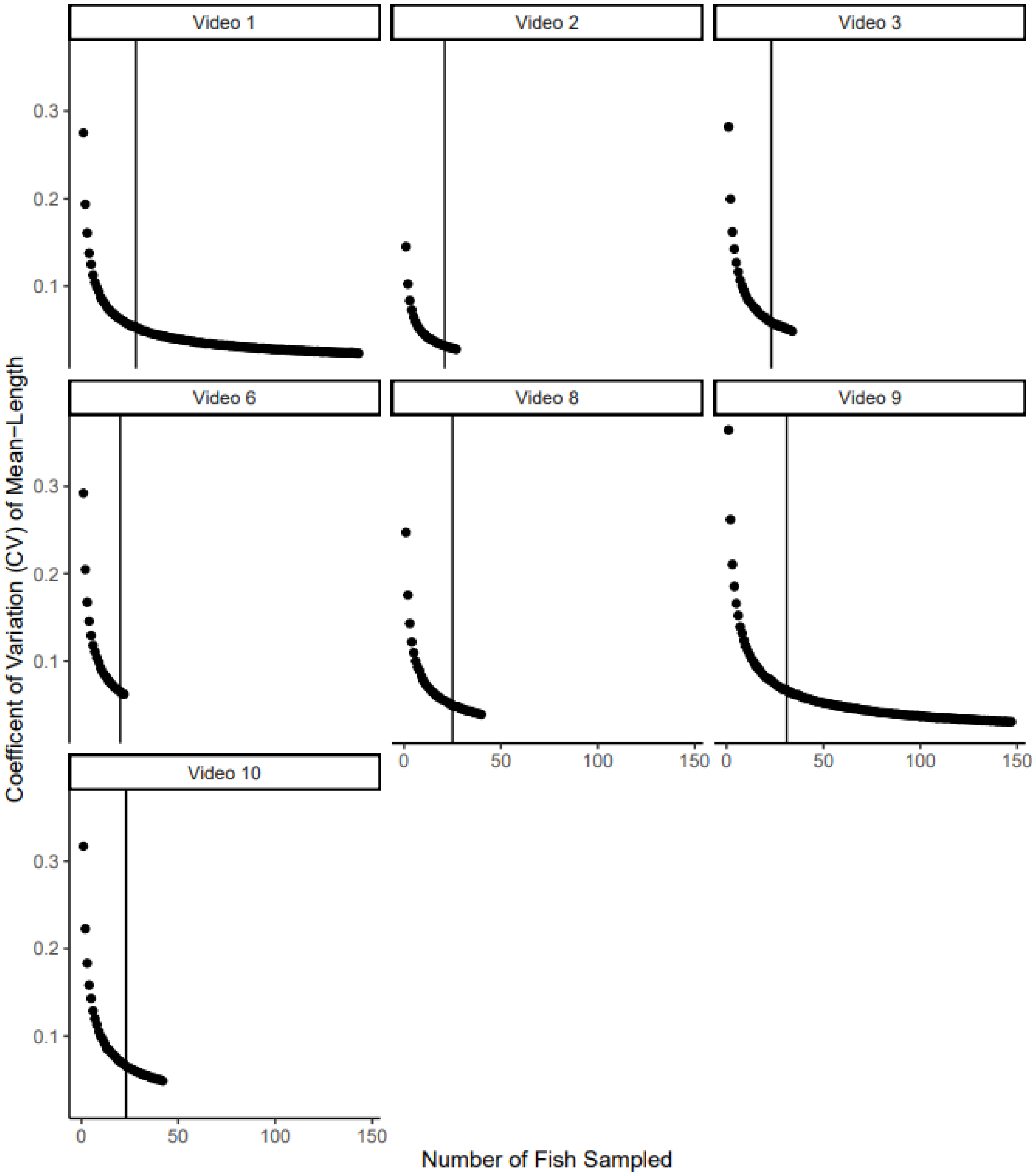


**Figure 2.3** - Precision (coefficient of variation, CV) curves for the mean length of Yellowfin Bream based on the fish sampled. Each plot is represented by a video ID. Vertical lines (when present) represent the point of diminishing returns for that particular video calculated using the central derivative approach described in the methods.

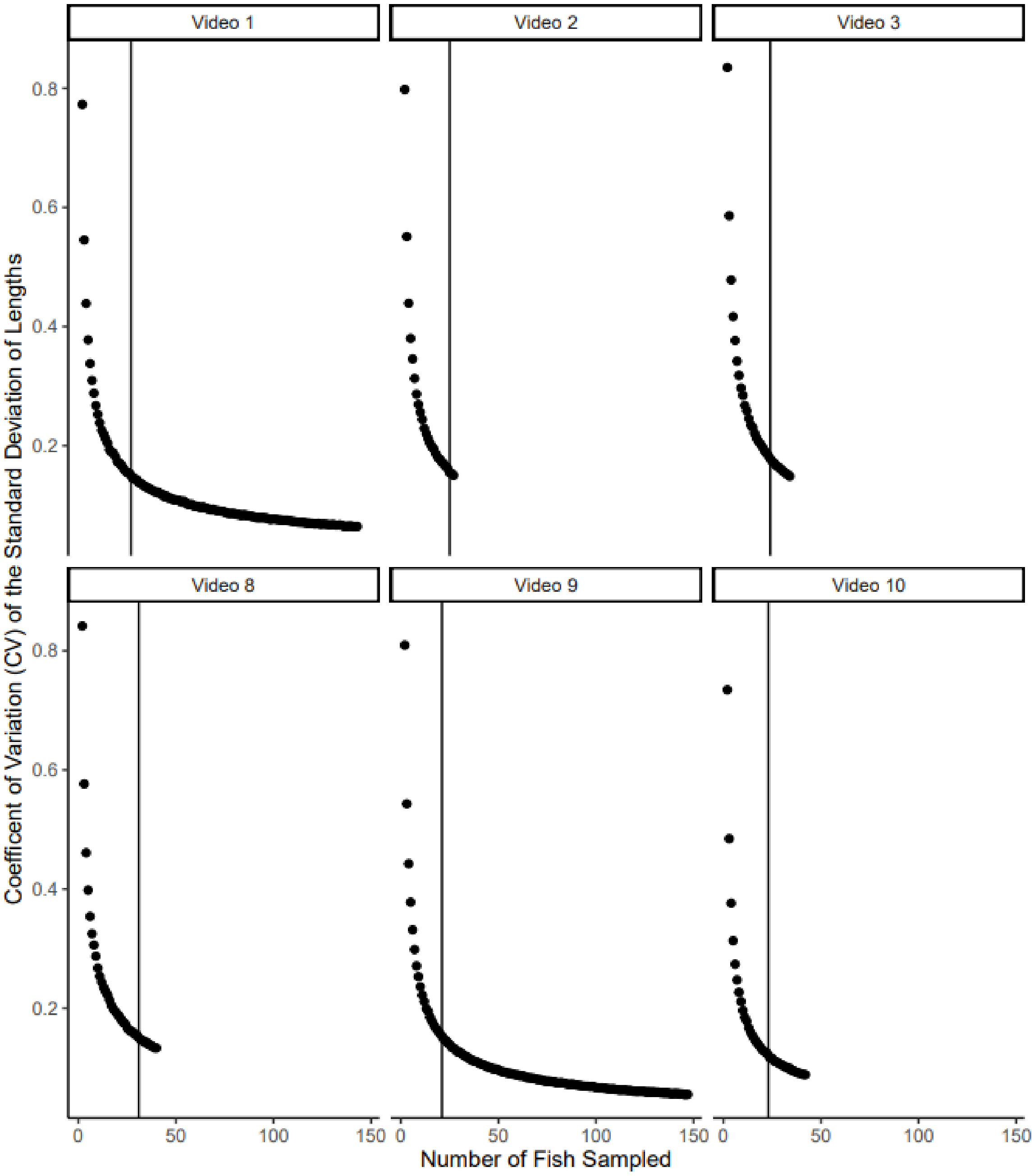


**Figure 2.4** - Precision (coefficient of variation, CV) curves for the standard deviation (+/-SD) of Yellowfin Bream lengths based on the number of fish sampled. Each plot is represented by a video ID. Vertical lines (when present) represent the point of diminishing returns for that particular video calculated using the central derivative approach described in the methods.

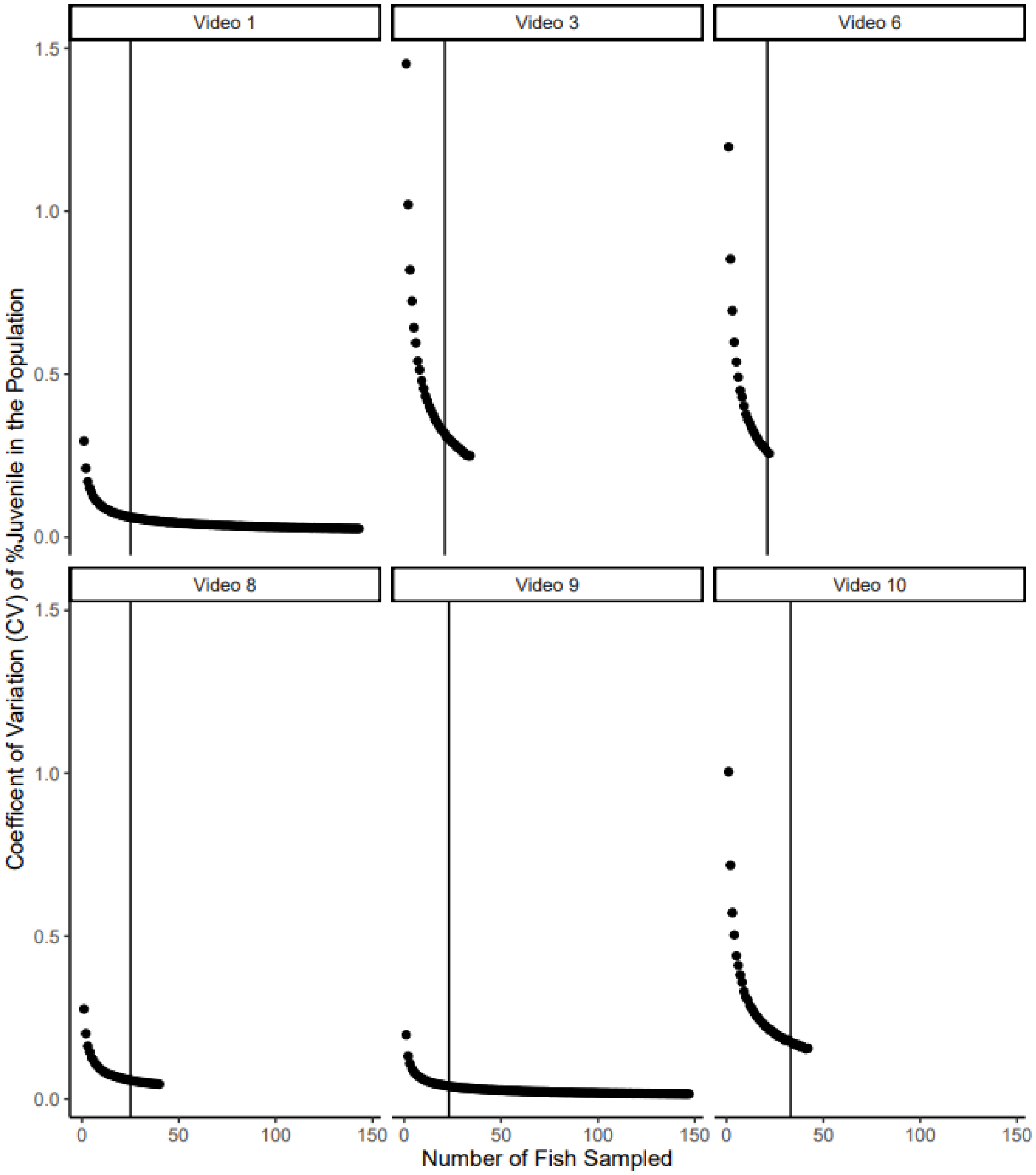


**Figure 2.5** - Precision (coefficient of variation, CV) curves for the proportion of juvenile Yellowfin Bream within the population based on the number of fish sampled. Each plot is represented by a video ID. Vertical lines (when present) represent the point of diminishing returns for that particular video calculated using the central derivative approach described in the methods.

**Table 2.3** - Summary table of the mean, standard error, median and max point of diminishing returns (derived the last occurrence of the 0.5% central derivative) for each metric analysed in the case study.

| Metric | Mean | SE | 95% CI | Median | Max |
|---|---|---|---|---|---|
| Mean Fish Length | 24.43 | 1.48 | 21.53-27.32 | 23 | 31 |
| SD of Fish Length | 25.16 | 1.42 | 22.37-27.95 | 24.5 | 31 |
| Proportion of Juveniles within the Population | 24.66 | 1.82 | 21.1-28.23 | 24 | 33 |

## 2.4 | Discussion

Given the time and effort required to extract video data, understanding the optimal number of replicate fish measurements needed to obtain precise population metrics is crucial for efficient and reliable stereo-RUV surveys. Through a combination of simulation studies and field-based case studies, we investigated the relationship between sample size and precision for three key population metrics: mean length, standard deviation of lengths, and proportion of juveniles. Our analysis revealed a consistent optimal sample size of approximately 25 fish measurements across these metrics, emerging both from our simulation studies across multiple length frequency distributions (~22-27 fish; Table 2.2) and our case study analysis (~24-25 fish; Table 3). The alignment with central limit theorem, which suggests sample means approximate normal distribution at samples sizes around 30 when sampling is representative of the underlying population (Rosenblatt 1956), provides theoretical support for this empirically derived threshold. Additionally, our results parallel findings from extractive fisheries sampling, where precise estimates of mean length and standard deviations were achieved with 25 fish measurements (Kritzer et al. 2001). While not unexpected, the alignment of the optimal sample size derived in this study with these suggests that stereo-RUV surveys reliably sample a random and representative sample of the population.

This recommendation of 25 fish measurements represents a substantial increase from current practices in stereo-RUV studies, where measurements typically range from 3-15 fish within the MaxN frame (Whitmarsh et al. 2017; Langlois et al. 2020). This disparity suggests that previous studies may have achieved lower precision than optimal and highlights an opportunity to enhance the reliability of future research through more comprehensive sampling protocols. Of particular note is the consistency of this optimal sample size across all measured metrics, including the proportion of juveniles in the population - a metric for which no prior sampling guidelines existed.

For all metrics, the optimal sample size identified across the various population mortality rates (and thus size-frequency distributions) within the simulation study, were not significantly different from one another. This consistency across different population structures has important practical implications, suggesting that investigators can confidently apply our sampling recommendations without prior knowledge of the underlying population size structure. The robustness of the ~25 fish threshold across varying populations also suggests broad applicability across different fish species and ecosystems - a finding supported by our case study, where optimal sample sizes matched simulation predictions despite being collected in-situ with unknown population parameters. This universal applicability is particularly valuable for baseline surveys, stock assessments, and monitoring programs where population size structures may be unknown or changing over time.

The CV analysis revealed distinct patterns of precision across the three-population metrics (Figure 2.2 & 2.3-2.5). Initial CV values showed considerable variability, particularly for the proportion of juveniles, which exhibited both the highest starting CV and highest stabilization point compared to mean length and standard deviation metrics (Figure 2.2C & 2.5). This differential in metric stability has important implications for survey design and implementation. While our recommendation of 25 fish measurements provides a robust sampling threshold, researchers should account for these metric-specific variations in precision when establishing their sampling protocols and interpreting results. This consideration becomes especially relevant in multi-objective surveys where multiple population metrics are being assessed simultaneously. Furthermore, these findings suggest that studies primarily focused on juvenile proportions may benefit from additional sampling effort to achieve comparable levels of precision to other metrics.

While the findings indicate that ~25 fish measurements provide precise estimates of population metrics when using stereo-RUVs, several potential sources of bias need consideration. For example, when sampling schooling species, measuring all 25 fish from a single school may introduce significant bias due to size-specific schooling behaviour of fishes (Hoare et al. 2000; Hemelrijk and Kunz 2005). Additionally, deriving the mean lengths of a population based on the MaxN frame introduces its own biases, particularly in relation to field of view (FoV) constraints (Williams et al. 2022). As FoV decreases, length bias increases because the visible area can accommodate different numbers of fish depending on their size - more small fish can fit within the same FoV compared to larger individuals (Williams et al. 2022). Consequently, taking all 25 measurements from a single frame could skew the sample toward smaller size classes. These biases underscore the importance of sampling across multiple time points or schools to obtain representative population measurements. As such, to account for these potential biases, we recommend that the 25 measurements either come from 25 unique points within the video, or that - in the case that every fish in the video is a part of a school - that the measurements of fish come from 25 unique schools. Furthermore, as these findings focus on deriving these metrics at a species' population level, we suggest that investigators collect at least 25 measurements from the same species to get the most precise estimate of the fish demographic metrics for a particular site, whether from a single RUV deployment or multiple deployments at the same site.

When obtaining 25 measurements is not feasible due to low underlying fish abundance (less than 25 fish at a site for example) or visibility constraints, multiple pseudo-replicated deployments at the same site may be necessary. In the first case, assuming that most or every fish is measured within the population each deployment, additional deployments should not affect the estimate of the mean length and standard deviation of the lengths within the population. In the latter case, assuming each deployment captures a random and representative sample of the underlying population, additional deployments also should not affect the derived estimates. For situations where multiple deployments are not possible or when analysing pre-existing data with fewer than 25 measurements, researchers can use the CV curves presented in this study (Figure 2.2; See Data Availability Statement – Section 2.5) to estimate precision levels and make informed decisions about data inclusion based on their specific research requirements.

It is important to acknowledge that the specified precision cut-offs used in this study are ultimately arbitrarily defined unless there are *a priori* project requirements and/or the costs of sampling are defined and related to the trade-off in precision (Downing 1989). Here, a very conservative cutoff of 0.5% improvement in precision from the last point was selected to try to make the results and recommendations defined here as widely applicable as possible. However, this cut-off may not be appropriate for all studies and investigators may need to pick their precision cut-off in different ways and at different levels based on their different needs. Fisheries managers may determine their cut-off to give them the best chance at detecting significant differences within the population to trigger management decisions. Researchers on the other hand, should strive to optimize their sampling precision based on cost-effectiveness and statistical power requirements, ensuring their data can reliably detect both immediate patterns and subtle long-term trends in population structure.

These results have important implications for the use of stereo-RUVs in fish surveys. By optimising sampling effort, researchers can reduce the time and costs associated with video analysis—whether using manual annotation or computationally intensive machine learning techniques—while maintaining data precision. This increased efficiency is particularly valuable in the context of rapidly changing marine environments, where timely and cost-effective monitoring is essential to inform conservation efforts, fisheries management, and policy decisions.

Here we have provided the first empirical validation of optimal sampling requirements for stereo-RUV surveys, demonstrating that ~25 fish measurements consistently yield precise estimates of population metrics across diverse length-frequency distributions. Our simulation studies also uniquely demonstrate the robustness of this sampling threshold across varying population structures - a critical consideration when the underlying distribution is unknown (as is often the case with research of fisheries stock assessment). These findings provide an empirically validated framework for Stereo-RUV sampling that can enhance the precision and efficiency of fish population monitoring.

## 2.5 | Data Availability Statement

All data and code used in the analysis for this paper is available on a Zenodo Repository (10.5281/zenodo.14641960; Pine et al., 2025).

# Chapter 3 - Connectivity to artificial structures shapes fish communities in adjacent seagrass meadows

# Abstract

## *Context*

Estuaries are one of the most highly urbanised marine systems globally, with artificial structures like jetties representing one of the most common forms of marine infrastructure in these environments. As coastal development intensifies, natural habitats such as seagrass meadows increasingly find themselves adjacent to artificial structures like jetties, rockwalls, groynes, and revetments, creating novel ecological contexts with poorly understood implications for associated fish communities.

## *Objectives*

In this study, we aimed to understand how structural connectivity to artificial structures influenced (i) several fish assemblage metrics (abundance, species richness, diversity) and their behaviour, (ii) the proportion of juvenile fish within the assemblage (as a measure of nursery value), (iii) multivariate community composition, and (iv) the size structure of the abundant Yellowfin Bream (*Acanthopagrus australis*; a commercially and recreationally important species) within *Zostera capricorni* meadows in an urbanised estuary.

## *Methods*

Using a paired-block experimental design across 15 regions in Lake Macquarie, Australia (an estuary characterised by extensive waterfront development), we surveyed fish assemblages using unbaited stereo-remote underwater video in *Zostera capricorni* seagrass meadows adjacent to jetties (n=15) versus control areas without nearby artificial structures (n=15). We also characterised several focal-patch and seascape habitat characteristics for each sampling location to evaluate their role in explaining variation in the fish assemblages.

## *Results*

Fish total abundance and the proportion of juveniles was greater in *Zostera* meadows near jetties compared to meadows far from jetties, while species diversity, richness and community composition remained unchanged. Rates of feeding were lower in seagrass near jetties than seagrass far from jetties. We also saw that *A.* australis size-frequency structure shifted when seagrass was in close proximity to jetties, showing decreased size variance and decreased mean sizes. Notably, focal patch shape and the total amount of Zostera within the seascape influenced behavioural patterns of fish, with U-shaped relationships with the amount of feeding observed at each site – likely as a result of

shifts in resource distribution and foraging efficiency. However, no other focal-patch or seascape characteristics exhibited relationships with any of the assemblage metrics assessed.

## *Conclusions*

Our findings demonstrate that artificial structures influence fish communities well beyond their immediate footprint, with effects primarily driven by local proximity rather than focal-patch or other seascape characteristics such as seascape configuration. In substrate-limited systems, small jetties with low associated disturbances may provide localised ecological benefits to connected seagrass habitats through enhanced recruitment/larval settlement and resource provisioning, challenging conventional views of artificial structures as uniformly detrimental. However, these potential benefits must be considered alongside shifts toward smaller size structures and altered behaviour in jetty-adjacent areas. These results emphasise the need of considering both influence of artificial structures on habitats directly and adjacent habitats when assessing the impacts of coastal infrastructure.

## 3.1 | Introduction

Seagrass meadows are among the most productive marine ecosystems globally (Cullen-Unsworth and Unsworth 2013; Costanza et al. 2014), providing critical ecosystem services including carbon sequestration (Fourqurean et al. 2012), coastal protection (Reidenbach and Thomas 2018), nutrient cycling (Ziegler and Benner 1999), and habitat for fish and benthic communities (Jackson et al. 2001; Unsworth et al. 2019). These ecosystems support diverse fish assemblages through provision of food resources, shelter from predators, and spawning habitat, with many species exhibiting strong habitat associations during different life stages (Jackson et al. 2001; Gillanders 2006; Whitfield 2017). However, seagrass meadows are particularly vulnerable to coastal development, which has rapidly increased over the past century (Crossland et al. 2005; Nicholls et al. 2007; Firth et al. 2016), leading to the decline of seagrass extent by approximately 18% globally since the 1880s due to factors including reduced water quality, physical disturbance, and altered coastal processes (Waycott et al. 2009; Duarte et al. 2020; Dunic et al. 2021). This coastal urbanisation has resulted in the widespread installation of artificial structures, particularly jetties, which represent one of the most common forms of marine infrastructure in estuarine environments. As coastal development intensifies, seagrass meadows increasingly find themselves adjacent to artificial structures like jetties, creating novel ecological contexts with poorly understood implications for associated fish communities.

These structures alter local marine environments through multiple mechanisms, they can modify hydrodynamics and sediment transport patterns (Saengsupavanich et al. 2022), create shading that reduces light availability (Fitzpatrick and Kirkman 1995), and provide novel hard substrate habitat that supports distinct and abundant epibiotic communities (Connell and Glasby 1999; Dafforn et al. 2009; Bulleri and Chapman 2010; Firth et al. 2016). These structures can often support fish assemblages with diversity that is comparable or greater than on nearby natural reefs with similar multivariate fish community composition (Folpp et al. 2020; Paxton et al. 2020). Moreover, there is often a greater abundance of fish on artificial structures, with the greater resource availability associated with artificial structures often being cited as one of the mechanisms behind this (Bohnsack 1989; Munsch et al. 2014; Ferrario et al. 2016; Layman and Allgeier 2020). Though debate remains about whether this is simply an attractive effect or is associated with an increase in production as a result of the artificial structure (Layman and Allgeier 2020). Additionally, studies of piers and jetties have shown fish exhibit avoidance behaviour within the shaded regions directly underneath piers and jetties, with reduced abundance and feeding activity within these shaded areas

(Able et al. 2013; Grothues et al. 2013; Munsch et al. 2014; Grothues et al. 2016), while abundance and foraging/feeding activity increase along the edge of the jetties and within adjacent soft sediment habitat (Grothues et al. 2013; Munsch et al. 2014; Grothues et al. 2016).

Most research on artificial structures has focused on the ecological impacts on epibiotic and fish assemblages directly associated with the structures themselves, often comparing them to nearby natural habitats (Bulleri and Chapman 2010; Bishop et al. 2017; Scanlon et al. 2024). Despite strong theoretical foundations and documented local effects, we lack empirical understanding of how the proximity to these structures modifies fish assemblages, behaviour, and size-structure, and how habitat characteristics modify these relationships in adjacent seagrass meadows. This represents a critical knowledge gap in the current era of seascape ecology, where there is increasing recognition that the influence of an individual habitat patch may have impacts beyond its immediate surroundings (Pittman 2017b). There are several reasons to expect that the influence of jetties may extend into adjacent natural habitats. For example, three-dimensional complexity is important for larval settlement and fish recruitment, with some artificial structures supporting increased juvenile abundance compared to natural reefs with similar settlement success (Duffy-Anderson et al. 2003; Fowler and Booth 2013; Pastor et al. 2013). Juveniles recruiting to artificial structures may subsequently disperse to adjacent habitats as they grow and their habitat requirements change, extending the recruitment benefits beyond the structure itself. Additionally, jetties can modify seascape-level ecological processes by increasing habitat heterogeneity, disrupting or facilitating connectivity between natural habitat patches (Adams et al. 2014; Paxton et al. 2020; Lemasson et al. 2024), and altering environmental gradients through localised changes in conditions (Adams et al. 2014; Dafforn, Glasby, et al. 2015; Bishop et al. 2017). This is particularly important as the spatial arrangement of habitats within seascapes influences ecological processes including resource distribution and predator-prey dynamics and creating movement corridors (Dunning et al. 1992; Pulliam et al. 1992; Boström et al. 2011; Pittman 2017b). Consequently, the same seagrass patch may support different fish communities depending on its proximity to jetties and the broader seascape context. Considering the influences of nearby artificial structures is especially important for seagrass habitats, as seagrass meadows are often located immediately adjacent to jetties in estuarine environments, yet studies have not systematically examined how these structures influence fish communities in nearby natural habitats. Without understanding these adjacency effects, we cannot predict the cumulative impacts of coastal infrastructure on seagrass ecosystems or design sustainable infrastructure that minimises negative impacts while potentially enhancing local productivity (Dafforn, Mayer-Pinto, et al. 2015; Dafforn, Glasby, et al. 2015). This knowledge gap is particularly significant given that the effect of jetties may operate across multiple spatial scales, potentially modifying natural patch-scale habitat characteristics through altered resource distribution and connectivity.

In this study, we examined how the proximity to jetties influences fish assemblages in *Zostera capricorni* (hereafter referred to as *Zostera*) seagrass meadows within an urbanised temperate estuary. We considered the influence of the local and seascape context of seagrass patches on these relationships. We employed a paired-block experimental design, sampling across 15 sites using unbaited stereo-remote underwater video systems, with each site containing both jetty-adjacent treatment and control treatments (30 samples total) within 300m of each other to control for broad estuarine gradients while isolating specific effects of jetty proximity. We quantified fish behaviour, assemblage structure, focal-patch characteristics, and seascape context at each sample to assess how proximity to jetties modifies ecological relationships across multiple spatial scales. Based on the mechanisms outlined above, we developed four specific hypotheses associated with different aspects of the surveyed fish community: 1) jetty-adjacent seagrass will support higher fish abundance but with altered species composition and richness, while maintaining similar diversity compared to distant seagrass; 2) given the documented increases in foraging and feeding activity along the edges and in the matrix next to artificial structure (Grothues et al. 2013; 2016), we predict that feeding and foraging behaviour will be elevated in jetty-adjacent seagrass compared to seagrass far from jetties; 3) as artificial structures have been shown to have a greater number of juveniles on them compared to some natural habitats (Duffy-Anderson et al. 2003; Fowler and Booth 2013; Pastor et al. 2013), and that juveniles often utilise/move to connected habitats, we predict that jetty-adjacent seagrass would support smaller mean sizes of fish and greater proportions of juvenile fish; 4) recognising that seascape connectivity and context can modify habitat-species relationships (Pittman 2017b), we predicted that relationships between focal-patch characteristics (e.g. patch shape and total fish abundance) and seascape characteristics would differ between jetty-adjacent and control seagrass.

# 3.2 | Methods

## *3.2.1 Study site*

This study was conducted over three days during Austral summer 2023 in Lake Macquarie, an urbanised temperate estuary in New South Wales, Australia (Figure 3.1). Lake Macquarie is characterised by extensive waterfront development with a large number of domestic jetties extending from residential properties into the estuary. Extensive *Z. capricorni* meadows occur throughout the estuary, creating diverse seascape conditions ideal for examining the impacts of jetties on seagrass fish communities. There are several definitions of what constitutes a jetty particularly between American and British English  and it is often used synonymously to describe breakwaters, groynes, piers, wharfs (Collins Dictionary 2025; Cambridge Dictionary 2025). Here we define a jetty as a structure that extends from the shore into the water that is not filled in (with stone or concrete) underneath that allows docking, recreation, or pedestrian access.

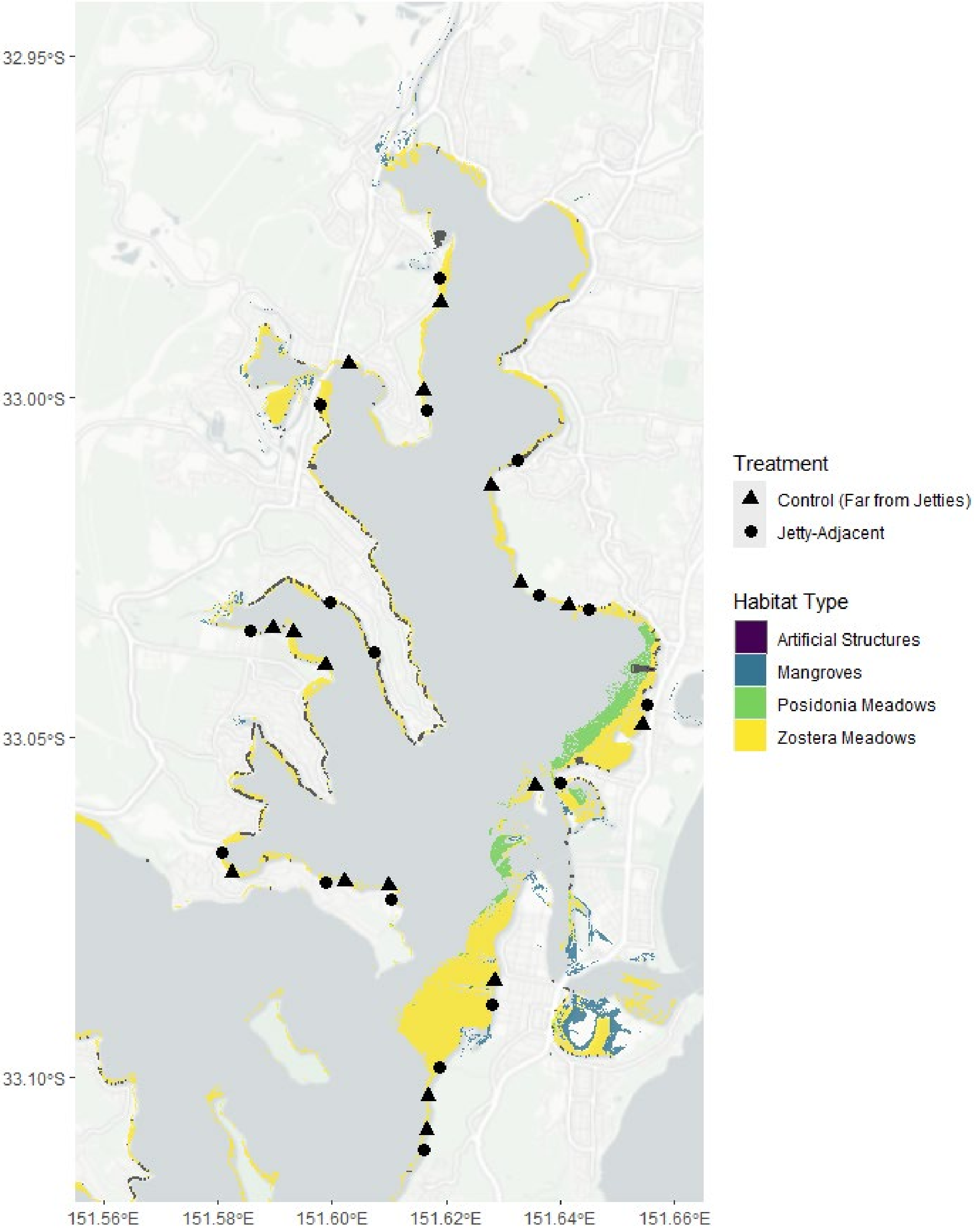


**Figure 3.1** – Map of the northern section of Lake Macquarie (New South Wales, Eastern Australia: 33°06'33.07"S, 151°61'83.66"E) highlighting key estuarine habitats, distribution of jetties, and locations sampled. Dots represent locations sampled.

### *3.2.2 Experimental Design and Site Selection*

Due to the irregular distribution of jetties throughout the estuary, systematic spatial sampling methods were not feasible. Instead, we employed a paired-block experimental design to isolate the effects of jetties from other sources of spatial variation such as varying estuarine position, sampling fish communities using unbaited stereo-remote underwater videos (stereo-RUVs). Within each block, sites were selected that were at similar depths and had similar shoreline habitat to reduce confounding factors.

We established two different treatments within each block, jetty-adjacent seagrass meadows where the meadow occurs within 10-20m of a jetty, and a control seagrass meadows positioned far from jetties (>300m). We were unable to include a treatment that consisted of jetties only (e.g., jetties without any seagrass nearby), as there were not enough instances of this occurring within our study site to have sufficient replication (Figure 3.1). The 300m distance was selected to ensure control sites were functionally disconnected from jetty habitats, based on home range estimates for the fish species observed in our pilot study. Specifically, a buffer zone of 300m around a point corresponds to the 95% home range area of Yellowfin Bream (*Acanthopagrus australis*; (Swadling et al. 2024) observed in our pilot study. This buffer zone also encompasses typical home range estimates for other common species in this system, including Luderick *(Girella* tricuspidata)*,* Australasian Snapper (*Chrysophrys auratus)*, Eastern Blue Grouper (*Achoerodus viridis*), and various other Labrids, which demonstrate notable site fidelity in similar habitats (Curley et al. 2013; Ferguson et al. 2013; Harasti et al. 2015; Lee et al. 2015; Ferguson et al. 2016; Fetterplace et al. 2016; Taylor et al. 2017; 2018; Becker et al. 2023). By positioning control sites at least 300m from any jetty, the majority of the fish communities there should be unable to routinely utilise jetty resources as a part of their daily activity patterns, as jetties fall outside their typical home range. For the purpose of this study, we also define this 300m buffer zone around our sampling point as our seascape sampling unit (SSU) from which our seascape characteristics are derived.

Sites were distributed as evenly as possible throughout the upper half of Lake Macquarie, with the lower estuary excluded due to thermal discharge from a coal-fired power plant creating atypical conditions (Ingleton and McMinn 2012). Overall, a total of 15 paired sites were established with a minimum separation distance of 600m between sites to ensure spatial independence. This resulted in 30 total sampling locations (15 jetty-adjacent, 15 control).

## *3.2.3 Fish video surveys*

### 3.2.3.1 Data collection

We used stereo-remote underwater video systems (stereo-RUVs comprised of two GoPro Hero 12 cameras set to a wide field of view at 60 fps, with 800mm spacing, 4° inward rotation) to conduct fish surveys at each site. To minimise potential confounding effects from bait plumes attracting species from surrounding habitats or nearby sites (Cappo 2006; Dorman et al. 2012; Hardinge et al. 2013), we used unbaited RUVs rather than baited systems, as our study focused on fish assemblages naturally associated with *Z. capricorni* meadows and the influence of connectivity and seascape characteristics on the community within the patch. Prior to deployment, each stereo-RUV system was calibrated using a standard 1x1x1m SeaGIS Calibration cube using the CamCal Software (v4.1; SeaGIS 2024a) to the standards outlined in the SeaGIS CamCal manual (SeaGIS 2024a). The systems were deployed for one hour during the tidal slack period (within 1.5 hours either side of high tide) at all sites, minimising potential confounding effects from incoming or outgoing tides. Paired sites within the same block were sampled on the same day at the same time to reduce potential confounding factors.

### 3.2.3.2 Video processing and analysis

Of the 30 videos collected, four videos were excluded due to technical errors (n=2) or poor visibility (n = 2). We set the minimum visibility threshold at 2m as visibility below this level (well below our average visibility of ~5m) limited fish detection and prevented accurate length measurements, as our stereo-RUVs had an optimal measuring distance of 3-8m. This resulted in 11 complete site pairs (22 videos), and 4 videos from sites with only one usable treatment (incomplete site pairs), resulting in a total sample size of 26 videos across 15 sites. We analysed a 60-minute interval for each video, beginning five minutes after the cessation of human activity to minimise the effects of deployment disturbance on fish behaviour.

We used EventMeasure software (v6.23; SeaGIS 2024b) to annotate fish generating data for three primary fish assemblage metrics: MeanCount (average of a series of instantaneous fish counts throughout the video (Schobernd et al. 2013), species richness, and Shannon's H diversity index (using MeanCount as the index of abundance). We systematically sampled MeanCount every 30 seconds and calculated species richness across the entire video duration as per Erickson et al. (2023).

Given its linear association with true abundance (Conn 2011; Schobernd et al. 2013), we refer to MeanCount as abundance throughout our analysis.

Each fish counted and measured during the systematic sampling for MeanCount was monitored for 10 seconds prior and 10 seconds after the systematic sampling period and classified into one of five different categories: passing - swimming through the frame without stopping; foraging - actively searching for food; feeding - consuming prey items (e.g., crabs, epiphytes, algae off of seagrass blades, or plankton); aggressive behaviour - inter- or intra-specific chasing; or resting – remaining stationary without exhibiting other behaviours.

### 3.2.3.3 Fish measurements and classification

We measured fish fork-length during systematic sampling within EventMeasure (SeaGIS 2024b), excluding measurements with RMS values exceeding 10mm to maintain measurement accuracy (as per guidelines set out by SeaGIS, 2024b). We classified fish as juvenile,or adult based on their fork length relative to species-specific FL50 values (the fork length at which 50% of fish in the population reach sexual maturity) obtained from published studies (Appendix A). For species lacking established FL50 values, we used a conservative estimate of 33% of total length derived from FishBase (Froese and Pauly 2021; Piggott et al. 2020). To ensure robust estimates of juvenile proportions and length statistics within assemblages, we extended video analysis beyond the systematic sampling period (60 minutes) when fewer than 25 fish were measured, as previous research has demonstrated this as the minimum threshold for precise estimates of juvenile proportions and length statistics using stereo-RUVs (**Chapter 2**). This approach allowed us to calculate reliable juvenile proportion values across the entire assemblage. However, these additional observations beyond the standard systematic sampling period were not used for the calculation of total abundance, species richness, and diversity – they were only used for the proportion of juveniles and length-frequency analysis.

## *3.2.4 Habitat characteristics covariates*

We measured both seascape and focal patch characteristics across sampling locations. Aspects of the seascape measured included structural connectivity to other estuarine habitats and seascape configuration (see Table 3.1 for metrics used and how each of the measures were derived). Measures of seascape configuration were calculated based off our seascape sampling unit (SSU; 300m buffer around the sampling point; outlined in **Chapter 1** – Section 1.3.2.2.1). All spatial analyses were conducted using habitat maps from the NSW Department of Primary Industries Spatial Data Portal (2025).

For structural connectivity, only connectivity to *Posidonia* meadows was measured as there were no other habitat types occurring throughout the estuary beside the *Zostera* we sampled itself (Table 3.1; Figure 3.1). Although a small section of mangrove habitat exists near the estuarine mouth, distance to mangrove was highly spatially correlated with distance from the estuary mouth (which was already accounted for with the paired-block design).

**Table 3.1** – Focal patch-level and seascape characteristics measured at each sampling site, including units of measurement and data sources

| Predictor Variable | Unit | Description and Methods |
|---|---|---|
| | | **Focal Patch Characteristics** |
| Focal Patch Area | ha | Measurement of the focal patch size.<br>Derived from the R package *landscapemetrics.* |
| Focal Patch Shape | Index | Measurement of patch shape complexity compared to a standard square of the same size.<br>Derived from the R package *landscapemetrics.* |
| Focal Patch Radius of Gyration | m | Measurement that characterises patch area and compactness.<br>Derived from the R package *landscapemetrics.* |
| Mean Seagrass Density | %Cover | Metric of Seagrass Density within a meadow measured as percent cover.<br>Derived from three replicate in-situ photo 1x1m photo quadrats with a 50x50 point intercept method within the focal patch for each site (**Appendix E**) |
| | | **Seascape Configuration** |
| Total Area of X Habitat within the functional Seascape | ha | The sum total area of all patches grouped by habitat type. Habitat types included: *Z. capricorni*, *P. australis*, and jetties.<br>The total area of jetties within the seascape was used only used in models using data that was subsetted to only include the jetty-adjacent sites to see if the amount of jetties in the seascape influenced the response variable.<br>Derived from the R package *landscape metrics.* |
| Number of jetties within the Seascape | Count | The number of jetties within the seascape.<br>This metric was used only used in models using data that was subsetted to only include the jetty-adjacent sites to see if the number of jetties in the seascape influenced the response variable.<br>Derived from the R package *landscapemetrics* |
| Total Area of Habitat Overall within the functional seascape | ha | The sum total area of all habitats (not including sandy matrix)<br>Derived from the R package *landscapemetrics.* |
| Overall Landscape Fragmentation Index | Index | Index characterising the degree that a landscape is broken up into smaller and more isolated patches.<br>Components derived from the R package *landscape metrics,* calculated using the formula:<br>$Landsacpe\ Fragmentation = \sqrt[4]{\frac{Patch\ Density * Landscape\ Division * Area\ Weighted\ Mean\ Perimeter\ Area\ Ratio * 1}{Mean\ Radius\ of\ Gyration}}$ |
| | | **Seascape Structural Connectivity** |
| Distance to Posidonia Meadows | m | Cost Distance Analysis through the water to the nearest *Posidonia australis meadow*.<br>Derived from the R package *gdistance* |

### *3.2.5 Statistical modelling process*

We assessed the influence of the explanatory variables on the composition of the multivariate fish assemblage using PERMANOVA in Primer7 software (Clarke and Gorley 2006). We conducted two PERMANOVA analyses, one using the raw abundance data and another with a 4th root transformation to weight the contributions of common and rare species more evenly (Clarke and Warwick 2001).

All univariate analyses of the four key fish assemblage metrics (abundance, species richness, Shannon H diversity, and the proportion of juveniles) were done in R (R v4.4.2; R Core Team 2025). Prior to analysis, we removed highly colinear variables using a conservative Pearson correlation coefficient threshold of 0.65 (Dorman et al. 2012). For correlated variable pairs, we retained the variable that captured the greatest variation and demonstrated the strongest ecological relevance based on domain knowledge and established literature (as per best practice outlined in Dorman et al. 2012). We excluded variables with substantial missing values or with fewer than five unique observations to minimise model instability and reduce the risk of Type I/II error. Initial univariate models were fit as generalised additive mixed models (GAMMs) to test for the presence of non-linear relationships which are known to be common throughout seascape/landscape ecology (Levin 1992; Wu and Hobbs 2002; Boström et al. 2011). However, in these initial analyses we did not observe any non-linear relationships and as such the models were fit as generalised linear mixed models (GLMMs) using the R package *glmmTMB* (Brooks et al. 2017) with the structure outlined by *Formula 1*. This approach allowed assessment of both the main effects of habitat characteristics and the treatment (jetty-adjacent vs control) and their interactions, while accounting for block-level variation through random effects (*Formula 1*). Distribution families for the models were selected based off model fit and Akaike's Information Criterion (AIC) analysis (Sakamoto, et al., 1986). Final models were constructed using AIC stepwise selection to ensure model parsimony and final model fit was assessed by inspection of residual and QQ-plots in the *DHARMa* package (Hartig 2017). We assessed the significance of the predictors in the final models using Type II Wald chi-squared tests implemented in the *car* package (Fox et al. 2012).

**Formula 1**:

$$Fish\ Assemblage\ Metric \sim Treatment + \ Treatment * Predictors + Random\ Factor(Block)$$

For behavioural analysis, we used the proportion of each behaviour type observed at each site (calculated as the number of observations of a given behaviour divided by the total number of behavioural observations at that site) as our response variable for the statistical models. Due to initial data analysis indicating the potential presence of non-linear relationships, we used GAMs to assess if there were any differences in behaviour between treatments and if there were any relationships with focal patch or seascape characteristics using a model structure outlined by *Formula 2*. Continuous Predictors were set as thin plate spline smooths. For variable selection, we employed a double-penalty selection approach, which penalises the null-space of the predictors based off their model contribution with variables not contributing to the model being penalised out of the model entirely. This can be a preferred methods of variable selection when using GAMs, when the number of variables is small or the sample size is large (Marra &Wood, 2011). Initial models fitted all predictors with a basis function (k=3) to prevent overfitting. We evaluated and adjusted basis functions using the *gam.check()* function in the *mgcv* package (Wood 2015). To minimize overfitting and reduce small-sample-size bias, we used Restricted Maximum Likelihood (REML) estimation. As the PERMANOVA analysis both using the raw abundance and 4th root transformations showed no significant differences in the community structure between the treatments, we pooled the behavioural observations across the full assemblage for this analysis. Furthermore, as aggressive and resting behaviours were not frequently observed (most observations at most sites were 0 or 1), these observations were filtered from the analysis prior to the calculation of the proportion of behaviours observed. Three-way interactions between habitat characteristics, treatment, and behaviour were unable to be modelled due to insufficient degrees of freedom given the model complexity.

**Formula 2**:

$$\begin{aligned} &Proportion\ of\ Observed\ Behaviours \sim Behaviour * Treatment \\ &\qquad + s(Habitat\ Characteristics, by\ Behaviour) + Random\ Factor(Site|Block) \end{aligned}$$

Length-frequency distributions of the fish *Acanthopagrus australis* (Yellowfin Bream) were modelled using Generalized Additive Mixed Models for Location, Scale, and Shape (GAMMLSS) using the R package *gamlss* (Stasinopoulos and Rigby 2008) following the same basic structure and variable selection procedure as outlined above in the GAMM analysis. Standard GAMM approaches model only the mean response, assuming constant variance. However, the predictors measured here may affect not only average length but also the spread of the size distribution through differential effects on recruitment, growth rates, or size-selective mortality. GAMMLLSS allows simultaneous modelling of both the mean and variance as functions of the predictors (Stasinopoulos et al. 2018), allowing us to detect whether predictors influence the entire length-frequency distribution rather than mean length alone. *A. australis* was selected as it was the only species to be observed in sufficient enough amounts across all sites sampled (as per guidelines set in **Chapter 2**). This estuarine dependent-species is commercially and recreationally relevant throughout eastern Australia (Curley et al. 2013), is commonly found in a broad range of habitats (Curley et al. 2013; Gannon et al. 2015) and are often associated with artificial structures (Taylor et al. 2018). Given their occurrence across multiple habitat types, understanding how their length-frequency distributions relate to jetties and seascape is important to potentially facilitate future comparisons with relationships observed in non-seagrass habitats.

When a significant treatment effect was observed, a “dosage” analysis was undertaken to see if the results in the jetty-adjacent sites were associated with the number of or the total area of jetties within the seascape. This involved the same modelling processes described above, however only using the subset of the data that comprised of jetty-adjacent sites. Complete model specifications and model diagnostics for all the statistical analysis are provided in **Appendix B2**. All figures were created in R, using the package ggplot2 (Wickham 2016) to enable reproducibility.

## 3.3 | Results

### *3.3.1 Influence of jetty proximity on key fish assemblage metrics*

Diversity and richness did not differ between *Zostera* meadows near and far from jetties ($p>0.05$; Figure 3.2B & C; **Appendix B1** – Table B2). Fish abundance ($\chi^2 = 9.77$, df = 1, $p = 0.0017$) and the proportion of juveniles ($\chi^2 = 5.429$, df = 1, $p = 0.0198$) was higher in seagrass meadows near jetties compared to seagrass meadows far from jetties (Figure 3.2A & D). For all fish assemblage metrics, focal patch or seascape characteristics did not significantly improve model fit and were removed during variable selection (**Appendix B1** - Table B1). For both abundance and the proportion of juveniles, there was no significant relationship observed with jetty in the subsequent dosage analysis ($p > 0.05$; **Appendix B** - Table B6)

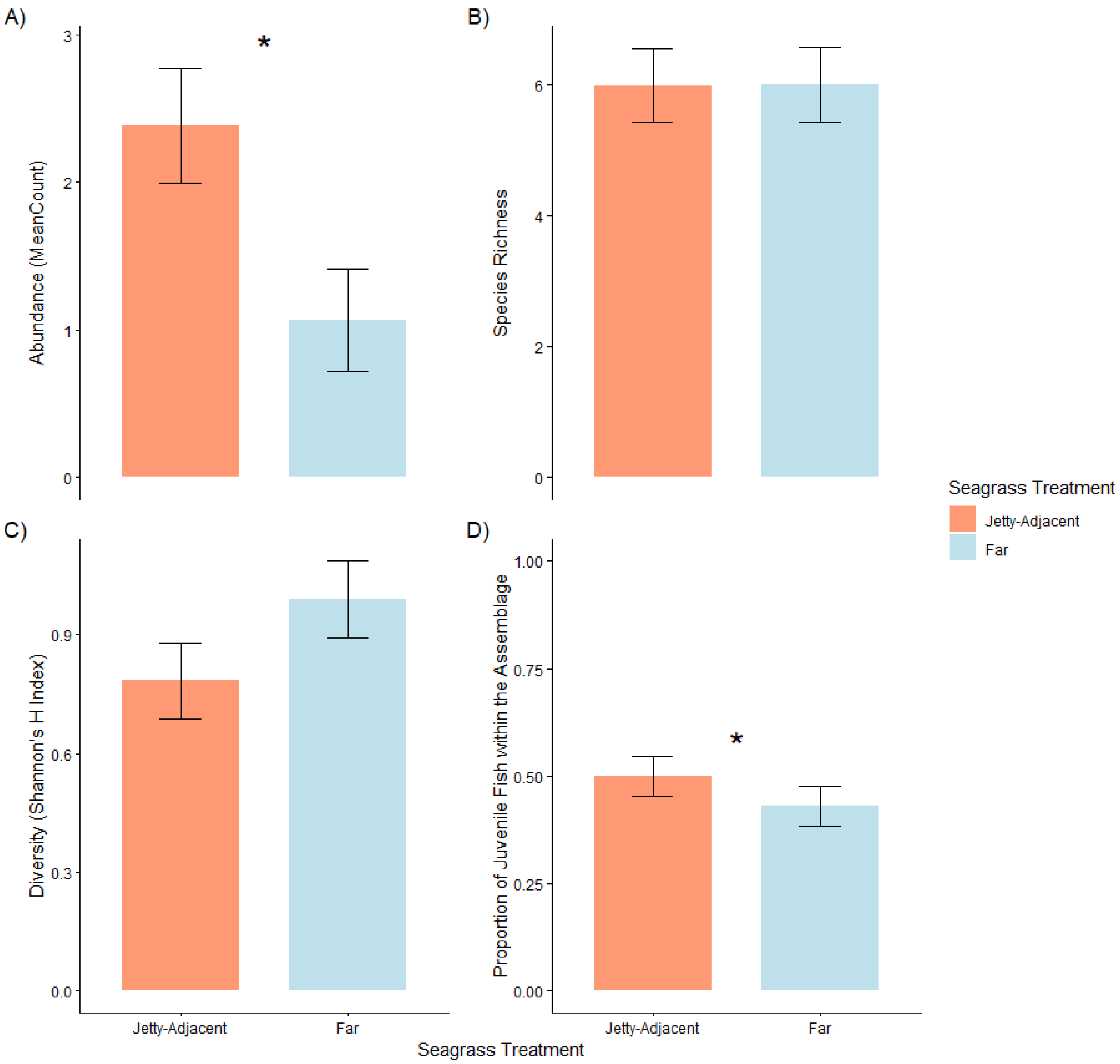


**Figure 3.2** – Predicted estimated marginal means (± standard error) of each of the four key fish assemblage metrics for each treatment - Jetty-adjacent seagrass or control seagrass (seagrass away from jetties). A) Fish abundance; B) Species richness; C) Diversity (Shannon H); D) Proportion of juveniles within the fish assemblage. Asterisks (*) indicate significant differences between seagrass treatments.

### *3.3.2 Influence of jetty proximity and habitat characteristics on fish behaviour*

Fish behaviour was significantly influenced by both jetty proximity (Figure 3.3A) and habitat characteristics (Figure 3.3B-C), with distinct patterns emerging for different behaviour types. Comparing the proportions of each observed behaviours between treatments, feeding behaviour was significantly more frequent in seagrass areas (10.29 ± 2.8%) compared to jetty-adjacent locations (5.24% ± 1.77%; estimate = -0.7289, t.ratio = -1.99, $p = 0.0495$) – though this was only marginally significant, while passing and scavenging behaviours showed no significant differences between treatments ($p > 0.05$). At jetty-adjacent sites, the proportion of feeding behaviour (5.24% ± 1.77%), was significantly lower ($p < 0.001$; Appendix B1 – Table B3) than both foraging (46.31% ± 5.29%) and passing (42.77% ± 6.16%), which had similar proportions ($p >0.05$; Appendix B1 – Table B3). This trend was also observed amongst the behaviours for the seagrass far from jetties: foraging (42.55% ± 5.23%), passing (41.21% ± 5.66%), and feeding (10.29% ± 2.81%).

Among habitat characteristics, Zostera meadow area had a significant U-shaped relationship with feeding behaviour ($F = 1.651$, $p = 0.042$; Figure 3.3B) but showed no significant relationships with passing or scavenging behaviours ($p > 0.05$). Focal patch shape significantly influenced only feeding behaviour ($F = 2.773$, $p = 0.032$; Figure 3.3A) in a similarly U-shaped relationship.

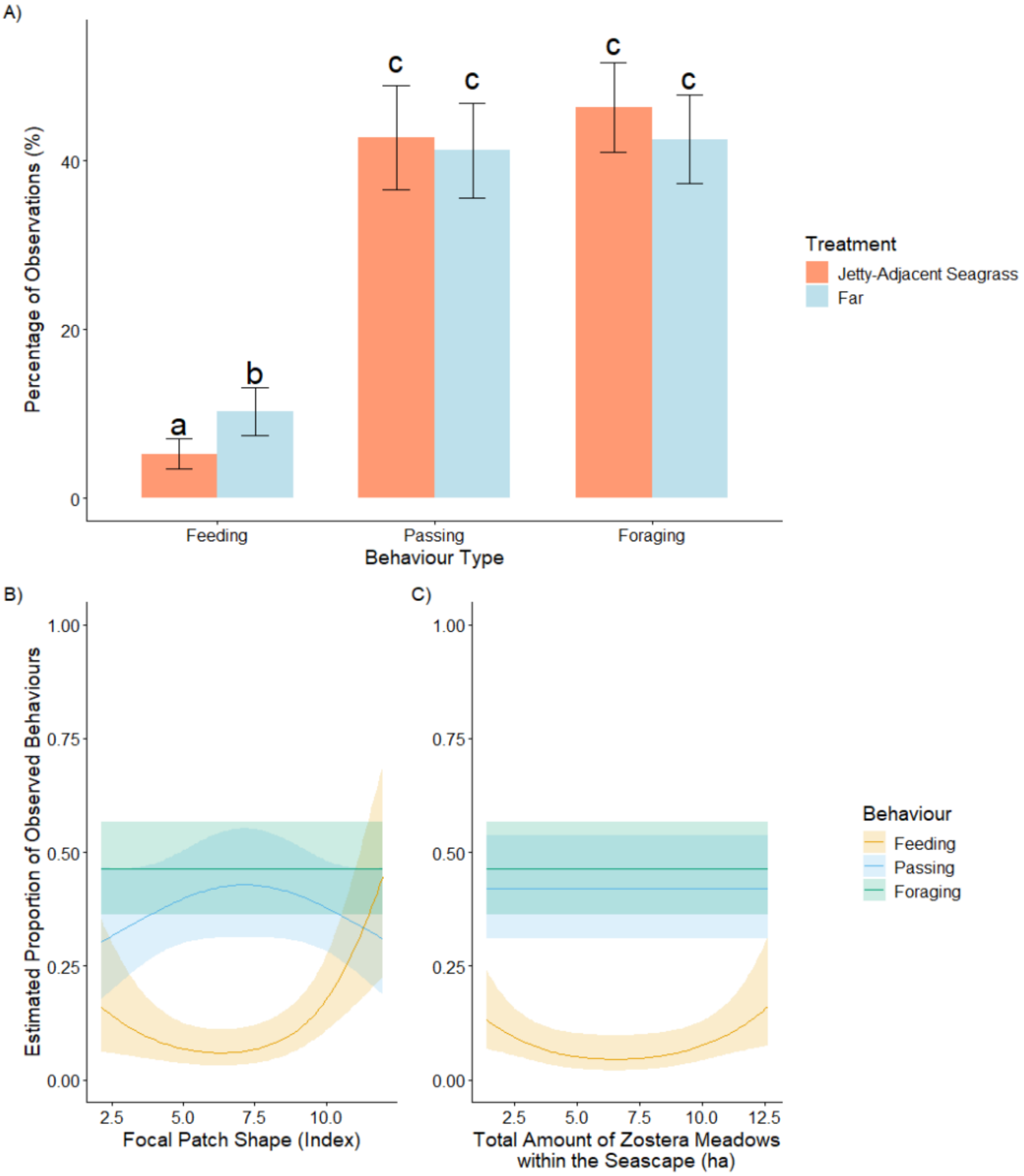


**Figure 3.3** – Effects of jetties on fish behavioural patterns and relationships with habitat characteristics. A) Percentage of observations for three behavioural types (feeding, passing, scavenging) comparing jetty-adjacent seagrass treatment (orange bars) with control seagrass areas (blue bars). Error bars represent 95% confidence intervals. Letters represent significance codes, where different letters represent significant differences between groups and the same letters represent no significant difference. B-C) Relationships between the proportion of behaviours observed and various patch and seascape-scale habitat characteristics: B) Focal patch shape (Index); C) Total amount of *Zostera* meadows within the seascape (hectares). Coloured bands represent 95% confidence intervals around fitted curves. Lines represent relationships from the generalised additive model.

### *3.3.3 Influence of jetties on community composition*

The multivariate community composition did not differ between jetty-adjacent seagrass and the control seagrass meadows (raw abundances: pseudo-F = 0.8831, p = 0.563; 4th root transformation: pseudo-F = 0.4389, p = 0.824; Figure 3.4). None of the seascape or focal-patch characteristics significantly influenced the multivariate composition of the communities ($p > 0.05$; **Appendix B1** – Table B5).

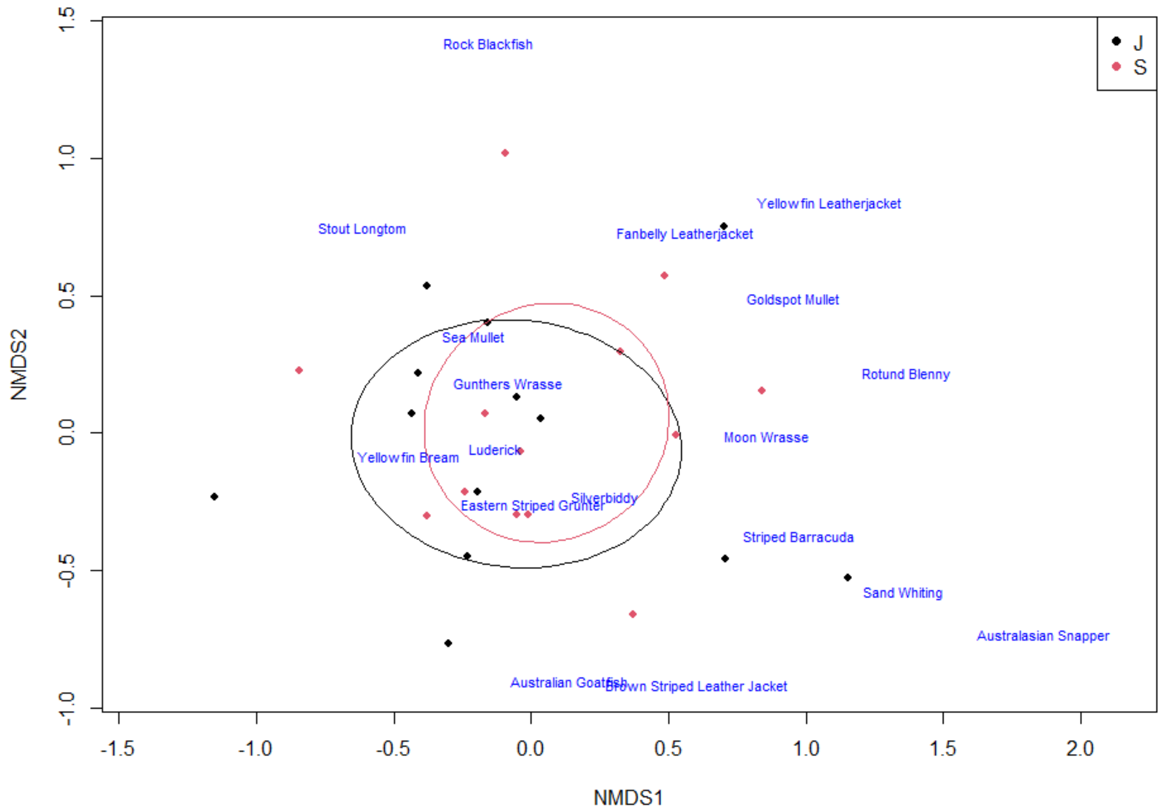


**Figure 3.4** – Non-metric multidimensional scaling (NMDS) ordination of fish assemblage composition (using raw abundance) in *Zostera* meadows adjacent to jetties (J) or away from jetties (S). 2D-stress = 0.184.

### *3.3.4 Influence of jetties on the length-frequency distribution of Yellowfin Bream*

The GAMMLSS model revealed significant effect of jetty-proximity on both the mean (μ; estimate = 0.407, SE = 0.0189, p < 0.0001) and variance (σ; estimate = 0.4, SE = 0.0406, p > 0.0001) of fish lengths, indicating that proximity to jetties effects not only average fish size but also the variability in size distributions. *A. australis* had smaller mean-lengths in the *Zostera* meadows adjacent to jetties with lower variance in lengths, leading to a narrower distribution compared to the length-frequency distribution observed in seagrass meadows far from jetties (Figure 3.5). No focal patch or seascape characteristics significantly improved model fit enough and thus were excluded from the final GAMMLSS model during variable selection.

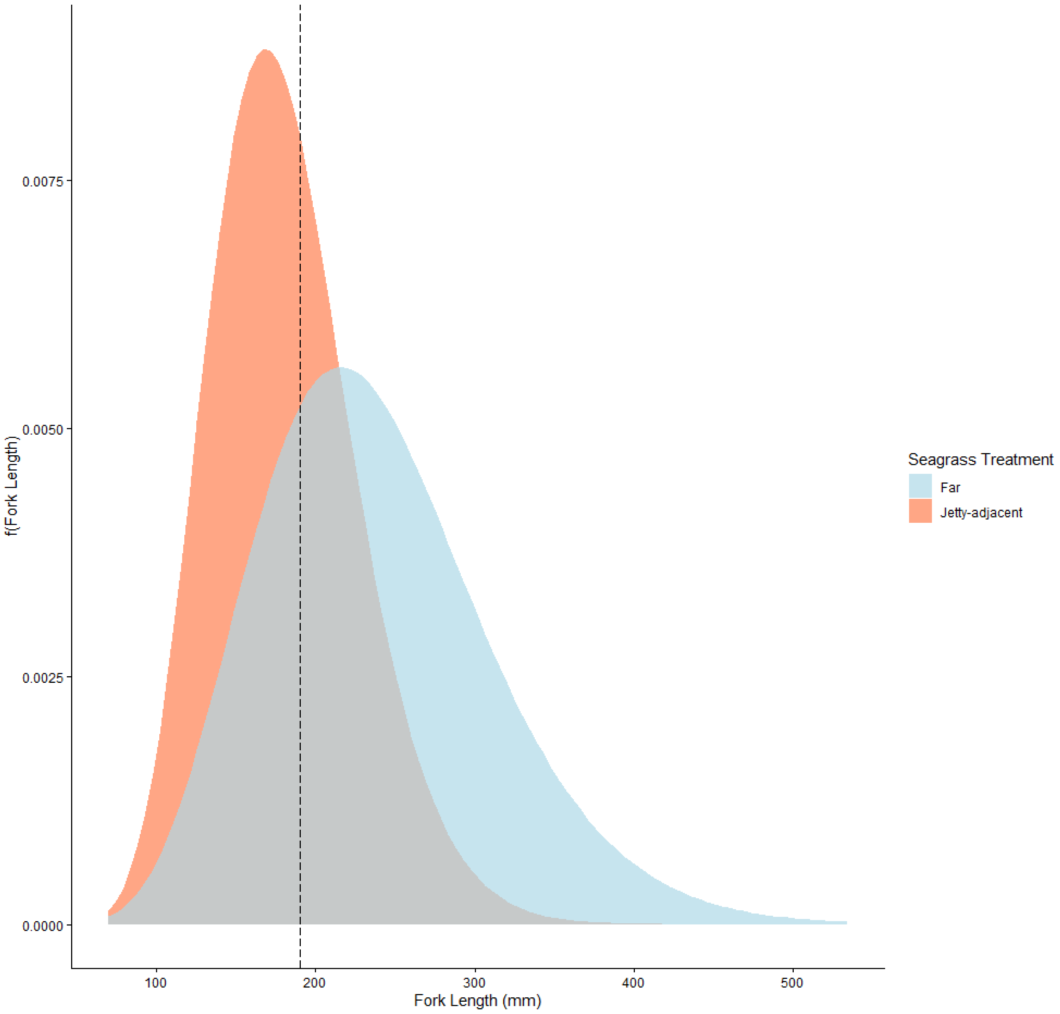


**Figure 3.5** – Influence of jetty adjacency on the length-frequency distribution and mean-variance relationship of Yellowfin Bream length in *Zostera* meadows. Dotted line represents the juvenile-adult cutoff (FL50 – 185mm) for Yellowfin Bream, where individuals smaller are classified as juveniles.

## 3.4 | Discussion

As coastal sprawl of artificial structures continues into marine and coastal areas (Crossland et al. 2005; Nicholls et al. 2007; Firth et al. 2016) seagrass meadows often find themselves in close proximity to these structures. Most research on artificial structures has focused on the ecological impacts on epibiotic and fish assemblages directly associated with the structures themselves (Bulleri and Chapman 2010; Bishop et al. 2017; Scanlon et al. 2024), however the understanding of their influence on nearby connected habitats remains limited. This study provides one of the first quantitative assessments of how jetties influence fish assemblages in adjacent seagrass meadows, revealing that the ecological impacts of artificial structures on fish communities can influence connected seagrass meadows. Our findings provide mixed support for our initial hypotheses and highlight the complexity of jetty-seagrass interactions. Consistent with our hypothesis, fish abundance was significantly greater in jetty-adjacent seagrass meadows compared to control sites (Figure 3.2). However, contrary to our predictions, species diversity, richness, and community composition remained unchanged between treatments (Figure 3.2B & C; Figure 3.4), suggesting that jetties may enhance abundance in closely connected seagrass habitats without altering the taxonomic structure of the communities. Behavioural patterns varied from our hypothesis, showing greater proportion of feeding behaviours in seagrass far from jetties (Figure 3.3) rather than seagrass close to jetties as expected. We also observed no changes in the proportions of foraging and passing behaviour across treatments. Jetty-adjacent seagrass supported a greater proportion of juvenile fish (Figure 3.2D) and also shifted Yellowfin Bream length-frequency distribution toward smaller individuals with reduced variance compared to seagrass far away from jetties (Figure 3.5). This supports our hypothesis and aligns with the proposed mechanism of juveniles recruiting to artificial structures and subsequently dispersing to adjacent habitats. Generally, our results did not support our hypothesis that we would see relationships with focal and seascape characteristics alongside the influence of connectivity to jetties, as for all responses except for behaviour, there were no significant relationships with any focal patch characteristics or measure of structural connectivity or seascape configuration (Table 3.1). These results highlight the importance of seascape connectivity and context in understanding how coastal infrastructure influences marine ecosystems and support the growing consensus that habitat patches cannot be assessed in isolation from their surrounding seascape/landscape context (Boström et al. 2011; Pittman 2017b; Pittman et al. 2021; Wedding et al. 2025).

### *3.4.1 Connectivity to jetties may aggregate or produce fish*

The connectivity between jetty and seagrass habitats may facilitate resource supplementation through landscape complementation - where fish access prey resources across multiple habitat types, or through spillover of mobile prey from jetty to seagrass environments (Pulliam et al. 1992; Dunning et al. 1992). This is particularly relevant in estuarine and coastal systems where artificial structures commonly support greater abundances of benthic invertebrates and encrusting organisms that serve as prey for many fish species (Connell and Glasby 1999; Dafforn et al. 2009; Bulleri and Chapman 2010; Firth et al. 2016). Within this context of resource supplementation, two primary mechanisms may explain the increase in both fish abundance and the proportion of juveniles in adjacent seagrass meadows: 1) aggregation of existing fish from the broader system to resource-rich areas, or 2) genuine productivity enhancement leading to local population increases (Layman and Allgeier 2020). Distinguishing between these mechanisms is challenging with observational data alone (Brickhill et al. 2005), but the wider ecological and seascape context of Lack Macquarie provides some important insights that allow us to potentially understand which process is occurring. Lake Macquarie has experienced extensive waterfront development and urbanisation that has led to the elimination of most natural hard substrates, including rocky shores and oyster reefs (Figure 3.1; Simmons & Trengove 1989; Lake Macquarie City Council 2018). In such substrate-limited environments, artificial structures have been shown to enhance recruitment, increase food availability, and provide refuge from predation, thus enhancing productivity rather than simply redistributing it (Layman and Allgeier 2020). Given this context, the elevated fish abundance in jetty-adjacent seagrass meadows may reflect enhanced local productivity rather than a redistribution of existing fish populations, with artificial structures providing critical hard substrate habitat and resources that otherwise would be scarce in the system.

### *3.4.2 Community structure remains stable despite abundance changes*

The absence of significant relationships with jetty proximity with species diversity, richness, and community composition provides important insights into how jetties influence fish assemblages. While jetty adjacency increased fish abundance in seagrass meadows, the lack of change in community composition, diversity, and richness metrics suggest that connectivity to jetties does not alter the pool of species utilising connected seagrass habitats or change the niches available to the population but rather enhances the density of the existing community. This pattern further supports the notion that these changes in density may be driven by resource enhancement, where connectivity to jetties provides supplementary resources that benefit the established seagrass community without attracting novel species or excluding existing ones.

An alternative explanation for these observations may be that due to the extensive waterfront development and ubiquity of jetties throughout Lake Macquarie, the entire estuarine system has been modified to the point that no truly “natural” seagrass fish communities remain – including those that are far from jetties. In such a heavily modified system, all seagrass patches may already reflect some degree of artificial structure influence, making it difficult to detect compositional differences that might be apparent in less developed estuaries. This highlights the challenge of establishing appropriate reference conditions in urbanised coastal systems where historical baselines may have been fundamentally altered (Atmore et al. 2021)

The similar community composition across treatments indicates that connectivity to jetties do not create strong environmental filters that would favour particular species over others. This finding is particularly significant because our study examines the effects of jetty connectivity on adjacent seagrass meadows, rather than direct impacts within the jetty footprint itself. In contrast to studies examining fish communities directly associated with artificial structures - which often show shifts in fish community composition (Clynick et al. 2008; Duffy-Anderson et al. 2003; Pereira et al. 2016; Scanlon et al. 2024) - our results suggest that the spillover effects of jetties into connected natural habitats may be more subtle, enhancing existing communities rather than fundamentally restructuring them. This distinction between direct structural impacts and connectivity-mediated effects has important implications for understanding the broader seascape-scale influences of coastal infrastructure.

### *3.4.3 Size structure shifts with jetty proximity*

A key finding of this study is that connectivity to jetties significantly alters the size structure of Yellowfin Bream populations in seagrass meadows, with jetty-adjacent areas supporting smaller mean fish lengths and narrower variance in lengths compared to control sites far from jetties (Figure 3.5). This shift towards smaller individuals coincides with elevated juvenile proportion overall in jetty-adjacent seagrass, suggesting that proximity to hard substrate structure may enhance recruitment and early life stage settlement into adjacent seagrass habitats.

The shift towards smaller fish in areas seagrass highly connected to jetties may reflect several potential mechanisms. One explanation is that adjacency to jetties enhances juvenile recruitment and larval settlement. In substrate-limited systems, extensive hard substrate availability may create settlement hotspots that subsequently supply adjacent seagrass meadows with newly recruited juveniles. Additionally, altered hydrodynamic conditions around jetty infrastructure may enhance larval retention and settlement directly into seagrass habitats by creating favourable flow conditions. Indeed, there are studies showing that jetties increase sedimentation rates by slowing down hydrodynamic flows, facilitating particle settlement (Saengsupavanich et al. 2022), suggesting they may have a similar influences on larvae. However, alternative or complimentary mechanism may also contribute to these patterns. The concentration of smaller size classes in jetty-adjacent seagrass may reflect size-selective fishing pressure, as these locations provide greater access for recreational fishers from the shoreline. The notable lack of Yellowfin Bream larger than the minimum recreational fishing size limit (Figure 3.5; 250mm; NSW Department of Primary Industries 2025b) in these areas supports this idea of potential size-selective fishing pressures. Though we have not quantified fishing intensity across sites, if fishing pressure is indeed greater near jetties, the combination of enhanced juvenile recruitment and size-selective removal/mortality of larger individuals above the legal limit would produce the observed pattern.

Variance in Yellowfin Bream lengths followed similar patterns to the mean, generally conforming to the expected mean-variance relationship (Figure 3.5). However, a significant treatment effect on variance indicates that jetty presence introduces additional sources of size heterogeneity beyond what would be expected from mean size alone. This increased variability may stem from the combined influences of enhanced juvenile recruitment, size-selective mortality processes, temporal variation in recruitment patterns, or anthropogenic disturbances associated with jetty infrastructure creating more variable growth or survival conditions.

However, despite these plausible explanations for this observed shift in length-frequency distribution, we cannot determine the exact mechanisms driving these shifts in mean length and variance without direct measurements of recruitment rates, larval settlement, fishing pressure, prey abundance assessments, and longer-term monitoring to distinguish between transient aggregation or sustained demographic changes.

### *3.4.4 Behavioural responses to jetties and habitat characteristics*

Fish behavioural patterns varied with proximity to jetties (treatment effect), with fish exhibiting significantly more feeding behaviour in control seagrass meadows compared to jetty-adjacent sites

(Figure 3.3A). This reduced feeding activity in jetty-adjacent areas may reflect increased satiation due to increased connectivity to prey-rich jetty habitats, or alternatively, reduced resource availability within seagrass meadows due to increased competition from greater fish abundance within jetty-adjacent meadows (Figure 3.2A).

Feeding behaviour showed significant relationship with focal patch shape and the total amount of *Zostera* meadows within the seascape, indicating that this behaviour is related to both focal patch and seascape characteristics. Feeding was relatively the same across the lower value of observed patch shape index, before increasing sharply around a shape index of 10 (Figure 3.3B). Increasing patch shape index is associated with an increase in the complexity of the shape of the patch, increasing the proportion of edge habitat within the patch. Edge habitats have been shown to be an important micro-habitat (Ries et al. 2004; Carroll et al. 2019), particularly in seagrass habitats (Smith et al. 2008; 2011; 2012), that often contain an increased diversity and abundance of resources due to the mixture of resources from the habitat patch itself as well as the habitat or matrix adjacent to the edge (Bologna and Heck 2002; Ries et al. 2004; Ries and Sisk 2004). This may provide one explanation as to why feeding rates were greater at more complex patch shapes.

Feeding also exhibited a slight U-shaped relationship with the total area of *Zostera* within the seascape (Figure 3.3C), implying that there may be two different processes occurring that create this shape. This pattern may be explained my optimal foraging theory (Charnov 1976; Pyke 1984). At smaller amounts of *Zostera* within the seascape, foraging efficiency is increased as there is minimal area to cover and the concentration of resources is often higher (Ritchie and Olff 1999), often leading to increased instantaneous feeding rates (Charnov 1976; Brown 1988). At large amounts of *Zostera* within the seascape, even though there is a greater area to forage over - reducing foraging efficiency (Ritchie and Olff 1999) - greater amounts of habitats will have a greater overall abundance of resources (Connor et al. 2000), potentially leading to increased observed feeding rates. However, these behavioural observations represent instantaneous samples and may not capture temporal variation in activity patterns. Without direct assessment of prey abundance, quantification of competitive interactions, or controlled experiments examining risk perception, we cannot definitively determine the mechanisms behind these behavioural responses. Future studies incorporating prey/resource surveys, giving-up density experiments, or acoustic telemetry would provide more robust insights into the underlying drivers of these behavioural responses.

### *3.4.4 Limitations and caveats*

There are several important caveats with this study that are worth noting. Firstly, the jetties surveyed here are primarily small residential or public jetties with a small footprint (~1-4m wide, ~3-8m long) rather than large commercial infrastructure (e.g. piers, docks, wharfs). The ecological impacts of larger structures may differ substantially due to greater shading, disturbance, and different associated activities. This context is critical as the jetties sampled here would be relatively less disruptive than these larger structures, with less consistent shading (due to small width and the movement of the sun), and less anthropogenic disturbances that may be associated with marinas, ports, or refuelling stations. However, the level of disturbance/activity around these jetties is unable to be quantified without data on the frequency and density of activities surrounding them.

Secondly, our study site (Lake Macquarie) represents a particularly substrate-limited system due to extensive urbanisation, shoreline development, and historical habitat loss (Simmons and Trengove 1989; Lake Macquarie City Council 2018). In these systems, some of the potential negatives of being highly connected to jetties may be outweighed by the fact that these structures provide hard substrate that facilitates increased larval recruitment/settlement, increases resource availability, and increases productivity (Layman and Allgeier 2020). As such, the relationships observed here may not occur in different estuarine systems with more abundant natural hard substrate/habitats, where artificial structures may simply redistribute rather than enhance overall productivity and have a greater negative impact on connected natural habitats. This further highlights the importance of the wider seascape context when assessing and characterising benthic and fish community responses in marine habitats.

Thirdly, we could not quantify the frequency or intensity of anthropogenic disturbances (boat traffic, fishing pressure, maintenance activities) associated with different jetties and areas, introducing unmeasured variation that may influence fish community responses. We tried to account for this by including estuarine region (block) as a random factor within the models (*Formula 1* & *2*). However, future studies should quantify these measures to disentangle the influence of infrastructure effects from the effects of associated disturbances.

The temporal resolution of the survey also needs to be highlighted, as the lack of temporal replication does not allow us to causally distinguish between transient aggregation and sustained population enhancement. Longer-term monitoring programs, ideally spanning multiple different seasons and recruitment events, is needed to confirm the productive or attractive nature of the effects observed - despite evidence supporting the production in substrate limited systems (Layman and

Allgeier 2020). Furthermore, tagging, acoustic tracking, or otolith microchemistry could provide direct evidence of movement patterns and settlement sources.

An important limitation of our design is that we did not assess the influence of various gradients of connectivity to jetties and how that influences the responses examined here. This was due to extensive waterfront development and the ubiquity of jetties throughout Lake Macquarie (Figure 3.1), which meant that we could not established sampling locations at intermediate distances/along the gradient of connectivity to artificial structures while maintaining adequate site replication (paired block). This constraint meant we were only able to compare immediately adjacent (and thus highly connected) versus distant seagrass meadows, which precludes us from assessing how the influence of jetties changes across distance. Further studies, in less urbanised estuaries with sampling designs that specifically attempt to sample across a gradient of connectivity to artificial structures could provide insight into the spatial scale over which these influences operate.

### 3.4.5 Ecological and management implications

Our findings contribute to the growing evidence and consensus that marine ecosystems function as interconnected seascapes rather than isolated habitat patches, with a combination of seascape level factors and focal patch characteristics influencing relationships with various aspects of fish communities. Additionally, the enhanced fish abundance, elevated juvenile proportion, and altered size structure in jetty-adjacent seagrass meadows may have cascading implications for broader ecosystem functioning. Increased fish densities may alter grazing pressuring on epiphytes, predation pressure on invertebrates, and nutrient cycling via bioturbation and excretions. The behavioural changes observed, particularly altered feeding patterns (Figure 3.3), suggest potential modifications to energy transfer pathways that may cascade through the food web.

The size structure changes, particularly the increased representation of smaller size classes of Yellowfin Bream within seagrass meadows with high connectivity to jetties, may influence the nursery function of seagrass habitats. If these patterns represent a genuine enhancement of recruitment and settlement, rather than simply aggregation of existing individuals, seagrass meadows adjacent to jetties/hard substrate habitats may provide disproportionate contributions to fisheries production. However, this potential benefit must be weighed against the reduced representation of larger, reproductively mature individuals in these areas, which may result from either size-selective fishing pressures or demographic processes.

From a management perspective, these findings have immediate relevance for the planning of coastal development and management of these systems. In substrate-limited systems like Lake Macquarie, the results suggest that small residential jetties may provide some benefit when their footprint and associated disturbances are minimised. This supports the strategic placement of artificial reefs/structures as potential strategies to improve estuarine ecosystems for fish communities. This alongside further nature-based enhancement of these structures (such as OzFish's "Pimp my Jetty" programme; OzFish 2023) may help amplify positive effects while supporting broader conservation goals (Dafforn, Mayer-Pinto, et al. 2015). It is important to note that we don't want to imply that jetties are uniformly beneficial, as purpose-built artificial reefs or restored natural habitats like oyster reefs would likely provide greater ecological benefits than incidental infrastructure. Additionally, these findings surrounding the influence of connectivity to jetties highlights that traditional assessments that focus on the direct impacts associated with the footprint of artificial structures may significantly underestimate the influence of coastal infrastructure, as they do not account for potential impacts to connected habitats.

## 3.5 | Conclusion

This study demonstrates that the ecological influence of coastal infrastructure extends beyond the impact of their immediate footprint, with fish abundance, juvenile proportion, behaviour, and size structure, significantly altered in seagrass meadows adjacent to jetties compared to seagrass far from jetties. While high connectivity to jetties was associated with these observed changes, we did not detect a significant influence of cumulative jetty area within the seascape (defined as our 300m buffer seascape sampling unit) on the jetty-adjacent sites, suggesting that these influences may operate primarily at local scales in this highly urbanised system studied here. The observed responses were driven primarily by being highly connected (directly adjacent) to jetties rather than focal-patch or seascape characteristics such as measures of seascape configuration, highlighting the importance of connected habitats and seascape context when assessing the impacts of marine infrastructure. The results suggest that in more substrate-limited estuarine systems like Lake Macquarie, small-scale artificial structures may provide localised ecological benefits to connected seagrass habitats via enhanced recruitment and resource provisioning, challenging conventional views of artificial structures as uniformly detrimental. However, these benefits must be weighed against potential negative effects on the area directly associated with the structures and other as aspects of the community (such as the benthic and epifaunal communities) as highlighted throughout the literature.

As coastal urbanisation and development continue to accelerate globally, understanding how artificial structures interact with natural habitats at a seascape scale is increasingly critical for sustainable development and ecosystem management. Our findings provide a foundation for more nuanced approaches to coastal infrastructure planning that consider both direct and indirect ecological effects across connected seascapes. Furthermore, these findings will aid in predicting local impacts of small-scale local marine infrastructure on seagrass-associated fish communities alongside informing sustainable development and management of these systems into the future.

# Chapter 4 - Seascape connectivity and configuration often outweigh focal patch characteristics in structuring temperate estuarine seagrass fish assemblages

# Abstract

## *Context*

The role of the seascape and its various components including structural connectivity and seascape configuration in structuring fish assemblages alongside characteristics of the focal patch itself is increasingly recognised in marine ecology. Despite recognition of the impact of multi-scale processes on fish assemblages, we lack quantitative understanding of how the interplay between structural connectivity, seascape configuration, and focal patch characteristics collectively shapes fish assemblages in general, and the juvenile fish assemblage specifically, in estuarine seagrass systems.

## *Objectives*

We aimed to understand (i) how seascape characteristics – including different measures of: seascape configuration (inclusive of composition) and structural connectivity - as well as different focal patch characteristics influence the abundance, species richness, and diversity of fish assemblages in *Zostera capricorni (Z.capricorni)* seagrass meadows, (ii) the relative importance of these predictor categories (measures of structural connectivity, seascape configuration, and the focal patch) for each fish assemblage metric individually and overall, and (iii) which of these characteristics may be more important for juvenile fishes versus the full assemblage..

## *Methods*

We surveyed fish assemblage using unbaited stereo-remote underwater video at 50 *Zostera capricorni* meadows sites across Port Stephens, New South Wales, Australia (Austral summer of 2024). Sites were spatially balanced and selected using a methodology which maximised overlapping variation of all seascape and patch-level characteristics. Full-subsets GAM analyses were conducted to assess the degree to which fish assemblage metrics could be explained by variation in characteristics of the focal patch and its seascape (structural connectivity, seascape configuration).

## *Results*

Measures of structural connectivity to other habitats were the most important category of predictor overall, followed by measures of seascape configuration, and then focal patch characteristics. However, the relative importance of these categories varied among the different assemblage metrics. Juveniles comprised 57% of the fish assemblage in *Z. capricorni* meadows, and juvenile abundance

patterns largely mirrored overall fish abundance patterns, indicating that seascape characteristics shaping overall fish abundance may simultaneously influence nursery habitat quality in these juvenile-dominated systems. Notably, 40% of the relationships observed within the most parsimonious models were non-linear, often with unimodal or U-shaped relationships.

## *Conclusions*

These findings highlight the importance of structural connectivity and seascape configuration in shaping fish assemblages alongside focal patch characteristics. The predominance of non-linear relationships – likely driven by landscape supplementation, edge effects, and competitive dynamics – reveals complex spatial ecological relationships with potential thresholds in fish community responses to seascape characteristics. This complexity reinforces the need for seascape-scale management that maintains diverse habitat configurations throughout estuarine systems rather than focusing solely on individual patches, providing an evidence-based foundation for seagrass restoration and conservation that supports both biodiversity and fisheries goals.

# 4.1| Introduction

Marine habitats have faced unprecedented global degradation, with approximately 50 % of coral reefs (Hughes et al. 2017), 35% of mangroves (Valiela et al. 2001), 85 % of oyster reefs (Beck et al. 2011), and 30 % of seagrass meadows lost or severely degraded worldwide (Waycott et al. 2009; Duarte et al. 2020; Dunic et al. 2021). These critical habitats experience ongoing anthropogenic pressures from climate change, degraded water quality, disease, and direct habitat destruction through coastal development and destructive fishing practices (Duarte et al. 2020). The loss of these critical marine habitats disrupts fish population dynamics, food web stability, and the resilience of coastal ecosystems to environmental change (Lotze et al. 2019; Smale et al. 2019; Duarte et al. 2020), with substantial socio-economic impacts on fisheries that contribute US$363 billion annually to the global economy (Sumaila et al. 2019; Food and Agriculture Organisation 2022).

Among marine habitats, seagrass meadows have experienced particularly significant degradation and loss, with more than 19% of the known extent lost since 1880 and continuing losses at approximately 1-2% per year (Dunic et al. 2021). This loss of seagrass has resulted in the loss of key ecosystem functions and services they provide such as nutrient cycling, sediment stabilisation, dissipation of wave energy, and carbon production and export (Fourqurean et al. 2012), which are valued at approximately US$28,916 per hectare per year (Costanza et al. 2014). Seagrass loss also further undermines their increasingly recognized value in supporting productive fisheries (Nordlund et al. 2018; Unsworth et al. 2019).

Seagrass meadows serve as critical structured habitat for marine fishes and invertebrates (Jackson et al. 2001; Boström et al. 2006; Gillanders 2006; Boström et al. 2017). For fish populations, seagrass meadows function as foraging grounds with abundant and diverse resources (Jackson et al. 2001; Waycott et al. 2009; Fourqurean et al. 2012). These habitats provide refuge from predation and are often cited as a nursery habitat, supporting a greater density of juveniles that subsequently recruit into adult populations (Jackson et al. 2001; Heck et al. 2003; Gillanders 2006; McDevitt-Irwin et al. 2016; Whitfield 2017). These attributes make seagrass meadows critical in estuarine and coastal systems for maintaining fish diversity and supporting fisheries globally (Waycott et al. 2009; Unsworth et al. 2019). Fish assemblages in seagrass meadows respond to habitat characteristics across multiple spatial scales, from individual patch features to broader seascape patterns. At the patch scale, seagrass structural complexity (the 3-dimensional structure of the seagrass) significantly influences assemblages and ecological processes by influencing predator-prey dynamics by providing refugia from visual predators (Edgar and Shaw 1995; Jackson et al.

2001) and attenuating wave energy (Fonseca and Cahalan 1992; Reidenbach and Thomas 2018; Vettori et al. 2024). Furthermore, patch size and shape determine the ratio of edge to interior habitat, influencing the dynamics of edge effects within seagrass patches and creating distinct zones with different ecological functions – with edges of patches often supporting greater fish densities and species richness due to altered predator-prey interactions (Smith et al. 2008; Macreadie et al. 2009; 2010; Smith et al. 2010; 2012). However, most studies examining these patch-scale relationships have ignored the broader seascape context (Smith et al. 2008; Sheaves 2009; Smith et al. 2010; 2012).

At the seascape scale, the spatial arrangement of habitat patches significantly influences various ecological processes such as landscape complementation/supplementation, niche-partitioning, availability of resources, foraging, and predator-prey interactions (Grober-Dunsmore et al. 2007; Boström et al. 2011). For example, habitat fragmentation alters connectivity between patches, potentially increasing mortality and energy expenditure as fish travel between habitats with complimentary and supplementary resources (Laurance 2008; Fahrig 2017). Additionally, proximity to other habitat types (e.g., mangroves, coral reefs) creates connectivity corridors that support ontogenetic habitat shifts and access to complementary resources (Nagelkerken et al. 2015; Sheaves et al. 2015). These multi-scale habitat relationships can create complex, often non-linear, responses in fish assemblages that cannot be understood by examining patch characteristics in isolation. Recent advances in seascape ecology have shifted our understanding of nursery habitats from isolated patches to interconnected seascapes (Nagelkerken et al. 2015; Litvin et al. 2018). The "seascape nursery" concept recognises that the nursery function of a patch depends not only on the quality of individual habitat patches, but on connectivity between complimentary and supplementary habitats across the seascape and throughout fish ontogeny (Nagelkerken et al. 2015; Litvin et al. 2018). However, empirical understanding of the relationships between juvenile fish and seascape characteristics remains limited, with few studies directly assessing these relationships (Gilby, Olds, Connolly, Henderson, et al. 2018; Pittman et al. 2021). This ecological understanding is critical, as without it, it is difficult to predict how changes in the seascape will affect nursery function and difficult to inform evidenced based conservation, restoration, and management targeted around increasing nursery function within the seascape.

These management challenges are particularly nuanced in estuarine systems, where environmental gradients add another layer of complexity, and applying seascape ecology in estuaries requires considering their unique environmental context. Estuaries feature complex gradients from the mouth to the upper regions, creating ecotones that significantly influence habitat function and fish assemblages (Mateus et al. 2008; Whitfield, Elliott, et al. 2012; Basset et al. 2013; Baillie et al. 2015). These gradients encompass changes in salinity, temperature, pH, depth, wave energy, and turbidity, often producing distinct environmental conditions that may mediate the effects of seascape characteristics on fish communities and create context-dependent relationships (Mateus et al. 2008; Sheaves 2009; Whitfield, Elliott, et al. 2012; Bradley et al. 2019; 2020). Despite growing recognition of these multi-scale processes, most existing studies examine either patch-level characteristics, broad connectivity patterns, or estuarine gradient in isolation (Gilby, Olds, Connolly, Henderson, et al. 2018; Pittman et al. 2021). This creates a critical knowledge gap where we lack quantitative understanding of how the interplay between seascape connectivity, habitat composition, and focal patch characteristics collectively shapes juvenile fish assemblages and fish assemblage more broadly in these systems (Nagelkerken et al. 2015; Whitfield 2017; Olds et al. 2017). Without this integrated understanding, we are unable to understand how habitat modification affects nursery function or design effective restoration strategies for fish assemblages that optimise both patch quality and seascape configuration.

In this study, we examined how both focal patch and broader seascape characteristics influence fish assemblages and juvenile fish populations in *Zostera capricorni* seagrass meadows within a temperate estuary, employing spatially balanced sampling across 50 sites using unbaited stereo-remote underwater video. We hypothesized that fish abundance, richness, and diversity would be significantly influenced by: (i) connectivity to key estuarine habitats, (ii) seascape configuration, and (iii) focal patch characteristics. We predicted these relationships would vary, differ between juvenile and full assemblages, and exhibit non-linear patterns reflecting threshold effects and ecological trade-offs common throughout landscape/seascape ecology (Tischendorf 2001; Maxwell et al. 2017; Pittman 2017b). Our findings aim to advance the understanding of fish seascape ecology in estuarine seagrass meadows while providing quantitative foundations for restoration and management strategies focused on fish community outcomes that consider both patch-level and broader seascape characteristics.

# 4.2| Methods

## 4.2.1 Study site

This study was conducted during Austral summer 2024 (between February 8th – February 13th) in Port Stephens, a temperate tide-dominated drowned-valley estuary in New South Wales, Australia located within the Port Stephens – Great Lakes Marine Park (Figure 4.1). We selected this location for several key reasons. In Port Stephens, *Zostera capricorni* (*Z. capricorni*) meadows occur throughout the entire estuarine gradient, allowing for a range of different conditions at the seascape and patch level to be assessed while minimising confounding effects of the gradient itself. Additionally, the estuary contains diverse habitats, providing an ideal system for examining the influence of habitat connectivity and seascape arrangement on fish assemblages.

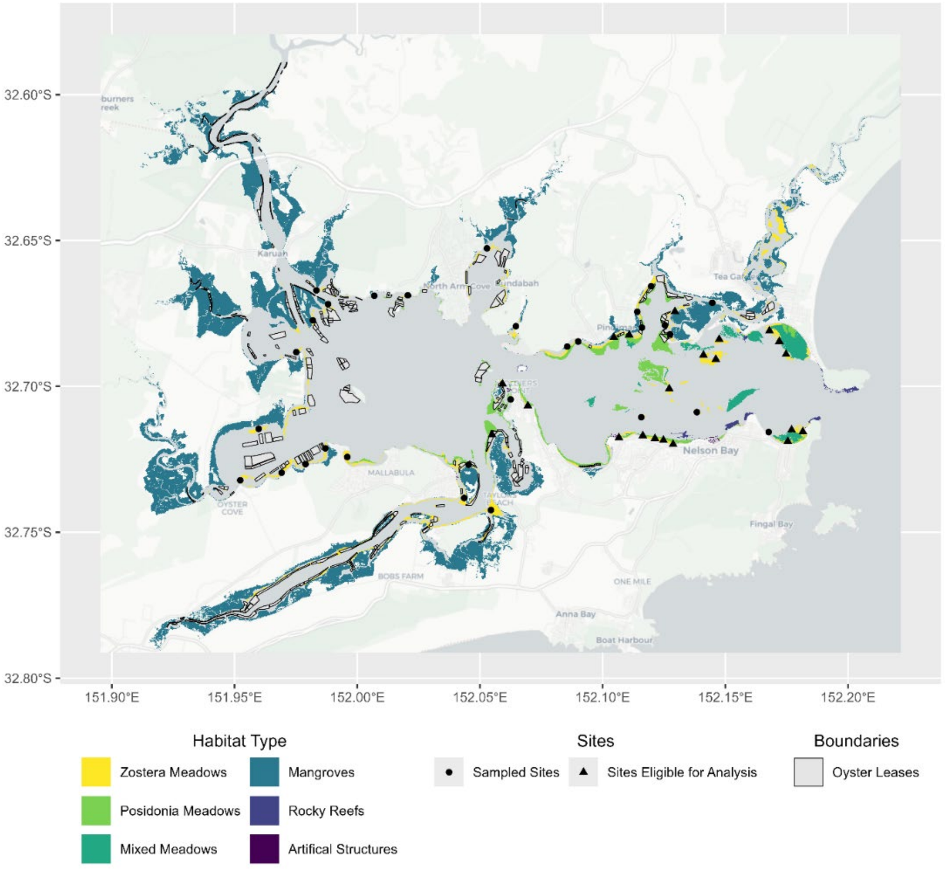


**Figure 4.1 -** Key estuary habitats within the Port Stephens Estuary (New South Wales, Eastern Australia; 32°41'44.0"S 152°04'18.2"E). Habitats mapped include *Zostera capricorni* meadows, mixed meadows, rocky reefs, *Posidonia australis* meadows, mangroves, artificial structures, and oyster leases. Black dots represent our 50 sites sampled. Triangles represent sites eligible for analysis after video quality control (22 sites).

### *4.2.2 Study design and site selection*

We employed a novel systematic sampling design to capture the full range of seascape and patch-level variation across our study area, while maintaining spatial independence between sites. Our approach involved first identifying a large number of spatially balanced potential sites within the estuary, then selecting from this initial set, the subset of 50 sites which simultaneously captured the maximum range for all local and seascape variables considered. This approach is explained in greater detail below.

We first identified the maximum number of spatially balanced sites that could fit within the estuary with a minimum spacing of 300m (~150 potential sites), excluding areas known to consistently have poor visibility that would prevent video sampling, using the spatially balanced algorithm (BAS) in the *MBHdesign* R package (Foster 2021). 300m spacing was chosen as it represents the 95th percentile of home ranges sizes estimated for the most common species (Yellowfin Bream; Swadling et al. 2024) observed in this system. This radius also encompasses typical home range estimates for other common species in this system, including Luderick *(Girella* tricuspidata)*,* Australasian Snapper (*Chrysophrys auratus)*, Eastern Blue Grouper (*Achoerodus viridis*), and various other Labrids which demonstrate notable site fidelity in similar habitats (Curley et al. 2013; Ferguson et al. 2013; Lee et al. 2015; Harasti et al. 2015; Fetterplace et al. 2016; Ferguson et al. 2016; Taylor et al. 2017; 2018; Becker et al. 2023). Using this *a priori* knowledge, we took an organism-based approach to setting the scale of our seascape (following best practice principles outlined by Pittman 2017) and define a 300m buffer around each sampling point as our seascape sampling unit (SSU), representing the seascape which is accessible and used by the majority of fish within these areas.

To select the final 50 sites from the 150 potential locations, we calculated all spatial metrics (seascape and focal patch, see below) for each potential site and conducted a Non-metric Multidimensional Scaling (NMDS) analysis using Bray-Curtis dissimilarity. The resulting ordination was divided into 50 clusters via a hierarchical clustering algorithm (using the *hclust* function from the R package *vegan* (Oksanen et al. 2013), and we selected one site randomly from each cluster to get the final 50 sites. We validated the spatial balance of our final 50 sites using a Kolmogorov-Smirnov (KS) clustering algorithm. The resulting 50 sites (Figure 4.1) capture the fullest spectrum of variation possible for our seascape and focal patch predictors.

### *4.2.3 Habitat characteristics*

To characterise the complex estuarine environment, we measured habitat characteristics at multiple spatial scales. Specifically, we measured: focal patch-level characteristics of the *Z. capricorni* meadows in which we sampled, the local seascape configuration within our defined SSU (300m buffer around the sampling point), and structural connectivity to surrounding habitats and estuary mouth (see Table 4.1 for metrics used). We use the term "seascape characteristics" throughout this paper to encompass all habitat characteristics beyond the focal-patch level. We further categorise seascape characteristics into measures of structural connectivity (characteristics that measure the distances between various different estuarine habitats; e.g., distance to *Posidonia* meadows & distance to mixed seagrass meadows; hereafter referred to as connectivity; Table 4.1) or seascape configuration (inclusive of seascape composition; e.g., total area of habitat within the seascape & total area of *Posidonia* meadows within the seascape; Table 4.1). All spatial analyses were conducted using habitat maps from the NSW Department of Primary Industries Spatial Data Portal (2023), which identified seven habitat types: *Z. capricorni* meadows, *P. australis* meadows, mixed meadows (comprised of *Z. capricorni* and *P. australis*), mangroves, rocky reefs, oyster leases, and artificial structures (artificial breakwaters and jetties).

**Table 4.1** – Focal patch and seascape characteristics measured at each sampling site, including units of measurement, how they were derived, and data sources. All seascape configuration measures were calculated within the seascape sampling unit (300m buffer around each sampling point).

| Predictor Variable | Unit | Description and Methods |
|---|---|---|
| **Focal Patch Characteristics** | | |
| Depth | m | Sourced from Bathymetry Data Layer (NSW Department of Climate Change, Energy, the Environment and Water 2025; NSW Office of Environment and Heritage (OEH) 2025) |
| Focal Patch Area | ha | Measurement of the focal patch size.<br>Derived from the R package *landscape metrics.* |
| Focal Patch Shape | Index | Measurement of patch shape complexity compared to a standard square of the same size.<br>Derived from the R package *landscape metrics.* |
| Focal Patch Radius of Gyration | m | Measurement that characterises patch area and compactness.<br>Derived from the R package *landscape metrics.* |
| Mean Seagrass Density | %Cover | Metric of Seagrass Density within a meadow measured as percent cover.<br>Derived from three replicate in-situ photo 1x1m photo quadrats with a 50x50 point intercept method within the focal patch for each site (See **Appendix E** for Further Details) |
| **Seascape Configuration Measures** | | |
| Total Area of X Habitat within the functional Seascape | ha | The sum total area of all patches grouped by habitat type. Habitat types included: *Z. capricorni*, Mixed Seagrass Meadows, *P. australis*, Rocky Reefs, Artificial Structures, Mangroves and Oyster Leases.<br>Derived from the R package *landscape metrics.* |
| Total Area of Habitat Overall within the functional seascape | ha | The sum total area of all habitats (not including sandy matrix)<br>Derived from the R package *landscape metrics.* |
| Mean patch area of X Habitats | ha | The mean area of patches within the functional seascape grouped by habitat type. Habitat types included: *Z. capricorni*, Mixed Seagrass Meadows, *P. australis*, Rocky Reefs, Artificial Structures, Mangroves, and Oyster Leases.<br>Derived from the R package *landscape metrics.* |
| Variation of X habitat patch area | Coefficient of Variation (CV) | Variation of patch areas within the functional seascape grouped by habitat type. Habitat types included: *Z. capricorni*, Mixed Seagrass Meadows, *P. australis*, Rocky Reefs, Artificial Structures, Mangroves, and Oyster Leases.<br>Derived from the R package *landscape metrics.* |
| Overall Landscape Fragmentation Index | Index | Index characterising the degree that a landscape is broken up into smaller and more isolated patches.<br>Components derived from the R package *landscape metrics,* calculated using the formula:<br>$Landsacpe\ Fragmentation = \sqrt[4]{\frac{Patch\ Density * Landscape\ Division * Area\ Weighted\ Mean\ Perimeter\ Area\ Ratio * 1}{Mean\ Radius\ of\ Gyration}}$ |
| **Structural Connectivity Measures** | | |

| | | |
|---|---|---|
| Distance to X Habitat | m | Cost Distance Analysis through the water to the nearest habitat type. Habitat types included: *Z. capricorni*, Mixed Seagrass Meadows, *P. australis*, Rocky Reefs, Artificial Structures, Mangroves, and Oyster Leases.<br>Derived from the R package *gdistance* |
| Distance from the Estuary Mouth | m | Cost Distance Analysis through the water to the mouth of the estuary<br>Derived from the R package *gdistance* |
| | | **In-situ Environmental Parameters** |
| Temperature | ºC | YSI Professional Plus positioned near the seagrass canopy |
| Salinity | PSU | YSI Professional Plus positioned near the seagrass canopy |
| pH | Unitless | YSI Professional Plus positioned near the seagrass canopy |

## *4.2.4 Fish video surveys*

### 4.2.4.1 Data collection

We used stereo-remote underwater video systems (Stereo-RUVs comprised of two GoPro Hero 12 cameras set to a wide field of view at 60 fps, with 800mm spacing, 4° inward rotation) to conduct fish surveys at each site. To minimise potential confounding effects from bait plumes attracting species from surrounding habitats or nearby sites (Cappo 2006; Dorman et al. 2012; Hardinge et al. 2013), we used unbaited RUVs rather than baited systems because our study focused on fish assemblages naturally associated with *Z. capricorni* meadows. Prior to deployment, each stereo-RUV system was calibrated using a standard 1x1x1m SeaGIS Calibration cube and CamCal software (v4.1; SeaGIS 2024a) to the standards outlined in the SeaGIS CamCal manual (SeaGIS 2024a). The systems were deployed for one hour during the tidal slack period (within 1.5 hours either side of high tide) at all sites. At each site, Stereo-RUV systems were placed within the *Zostera* meadow equidistant from both edges of the meadow facing in a random direction.

### 4.2.4.2 Video processing and analysis

Of the videos collected across our 50 sampling sites only 22 were suitable for analysis, with 2 videos excluded due to technical errors (camera failure during recording) and 26 for poor visibility (videos with less than 2m visibility). Eligible videos were predominantly from the lower estuary (Figure 4.1). We set the minimum visibility threshold to 2m as visibility below this level (well below our average visibility of ~5m) limited fish detection and prevented accurate length measurements, as our stereo-RUVs had an optimal measuring distance of 3-8m. We analysed a 60-minute interval for each video, beginning five minutes after the cessation of human activity to minimize the effects of deployment disturbance on fish behaviour.

We used EventMeasure software (v6.23; SeaGIS 2024b) to annotate fish, generating data for three primary fish assemblage metrics: MeanCount (average of a series of instantaneous fish counts throughout the video), species richness, and Shannon's H diversity index (using MeanCount as the index of abundance). We systematically sampled MeanCount every 30 seconds and calculated species richness across the entire video duration (Erickson et al. 2023). Given its linear association with true abundance (Conn 2011; Schobernd et al. 2013), we refer to MeanCount as abundance throughout our analysis.

### 4.2.4.3 Fish measurements and classification

We measured fish fork-length during systematic sampling within EventMeasure (SeaGIS 2024b), excluding measurements with RMS values exceeding 10mm to maintain measurement accuracy (as per guidelines set out by (SeaGIS 2024b). We classified fish as juvenile or adult based on their fork length relative to species-specific FL50 values (the fork length at which 50% of fish in the population reach sexual maturity) obtained from published studies (**Appendix A**). For species lacking established FL50 values, we used a conservative estimate of 33% of total length derived from FishBase (Piggott et al. 2020; Froese and Pauly 2021).

To ensure robust estimates of juvenile proportions and length statistics within assemblages, we extended video analysis beyond the systematic sampling period when fewer than 25 fish were measured, as previous research has demonstrated this as the minimum number of fish required for precise estimates of juvenile proportions and length statistics using stereo-RUVs (**Chapter 2**). This approach allowed us to calculate reliable juvenile proportion values across the entire assemblage.

## *4.2.5 Statistical analyses*

### 4.2.5.1 Univariate analysis of key fish assemblage metrics

We used generalized additive models (GAMs) to account for potential non-linear relationships between predictors and fish community metrics (abundance, species richness, Shannon H diversity index, proportion of juveniles). Prior to analysis, we excluded variables with substantial missing values or with fewer than five unique observations to minimise model instability and reduce the risk of Type I/II error (**Appendix C** – Table C1). Given the large number of potential explanatory variables an information-theoretic full subsets approach (Fisher et al. 2018) was used to identify parsimonious candidate GAMs using the R package *FSSgam* (Fisher et al. 2018). This approach is widely used in ecological studies, particularly seascape and landscape studies with a large number of potential predictors, due to its ability to guide the creation of conservative, ecologically interpretable models (Cowan et al. 2023; Goetze et al. 2024; Moustaka, Evans, et al. 2024; Moustaka, Robbins, et al. 2024). The maximum number of predictor variables for each model was limited to three to prevent overparameterisation. We used a conservative collinearity cut-off of 0.28 and assessed both collinearity (using Pearson correlation coefficient) and non-linear collinearity (concurvity), ensuring that the correlated predictors were not included in the same candidate model to minimise the potentially of spurious relationships (Graham 2003). All continuous variables were fit with a thin plate spline basis function, with three knots (k=3) to further prevent overfitting. Given the small sample size, we were unable to assess interactions between the predictors without over-parametrising and overfitting the models.

Candidate models were compared using Akaike Information Criterion corrected for small sample sizes (AICc; Sakamoto, Ishiguro & Kitagawa 1986). When multiple candidate models occurred within +/- 2 AICc of the best model, the most parsimonious model(s) was selected for further interpretation and analysis. The final models were examined for goodness of fit through QQ and residual plots. We further assessed the suitability of the number of selected knots of the final models using the *gam.check()* function in the *mgcv* package, as per best practice (Wood 2015).

The relative importance of all the predictor variables examined was determined by summing the weighted AICc of all models containing the associated predictor identified during the full-subsets analysis (Burnham and Anderson 2004). To examine the relative variable importance of each category of predictor (focal patch characteristics, structural connectivity, seascape configuration) across all fish assemblage metrics and visualise them, the raw variable importance scores were scaled within each model from 0-1, where 0 represented the least important variable and 1 was the most important variable for that metric. This was necessary because the raw relative variable importance score for each fish assemblage metric occur on different scales and thus were not comparable across models. All figures were created in R, using the package *ggplot2* (Wickham 2016).

### 4.2.5.2 Assessing fish community composition

To examine how habitat characteristics influenced fish community composition, we performed non-metric multidimensional scaling (NMDS) using the Bray-Curtis dissimilarity index using the *metaMDS* function from the *vegan* package (Oksanen et al. 2013). The optimal number of dimensions used were selected based on achieving a 2D-stress less than 0.2, which is considered acceptable for ecological interpretation (Clarke 1993). To identify how habitat characteristics related to community structure, we fit environmental vectors to the ordination space using the *envfit()* function.

# 4.3 | Results

## *4.3.1 Univariate fish assemblage metrics*

Distance from *Posidonia* meadows was the most common predictor that significantly explained variations among the four key fish assemblage metrics, appearing as a significant predictor for both abundance and species richness (Figure 4.2). Grouping across all models, measures of structural connectivity was the most important category of predictor, followed by seascape configuration measures, and focal patch characteristics (Figure 4.3A). Despite this overall result, looking at the relative variable importance within each assemblage metric we saw distinct patterns (Figure 4.2 & 4.3B). However, for all assemblage metrics except fish abundance and diversity, structural connectivity was the most important category on average (though for diversity it was only marginally lower than the top category; Figure 4.3B). For total fish abundance seascape configuration had the greatest mean variable importance - which was primarily driven by one predictor (total area of *Posidonia* within the seascape; Figure 4.2) - followed by focal patch characteristics and finally followed by structural connectivity (Figure 4.3B). For species richness, measures of structural connectivity were most important on average, followed by seascape configuration, with focal patch characteristics exhibiting the lowest mean importance. This pattern was driven by two variables with high importance in the structural connectivity (distance from *Posidonia* meadows; Figure 4.2) and configuration categories (total amount of habitat within the seascape; Figure 4.2). For diversity (Shannon H index), focal patch characteristics and measures of structural connectivity had similar mean variable importance, followed by measures of seascape configuration (Figure 4.3B). For the proportion of juvenile fish within the assemblage, measures of structural connectivity had the greatest mean importance, followed by focal patch characteristics, and then seascape configuration (with only small differences between the latter two; Figure 4.3B). The larger mean in the structural connectivity category was driven by the high importance of distance from mixed seagrass meadows (Figure 4.2)

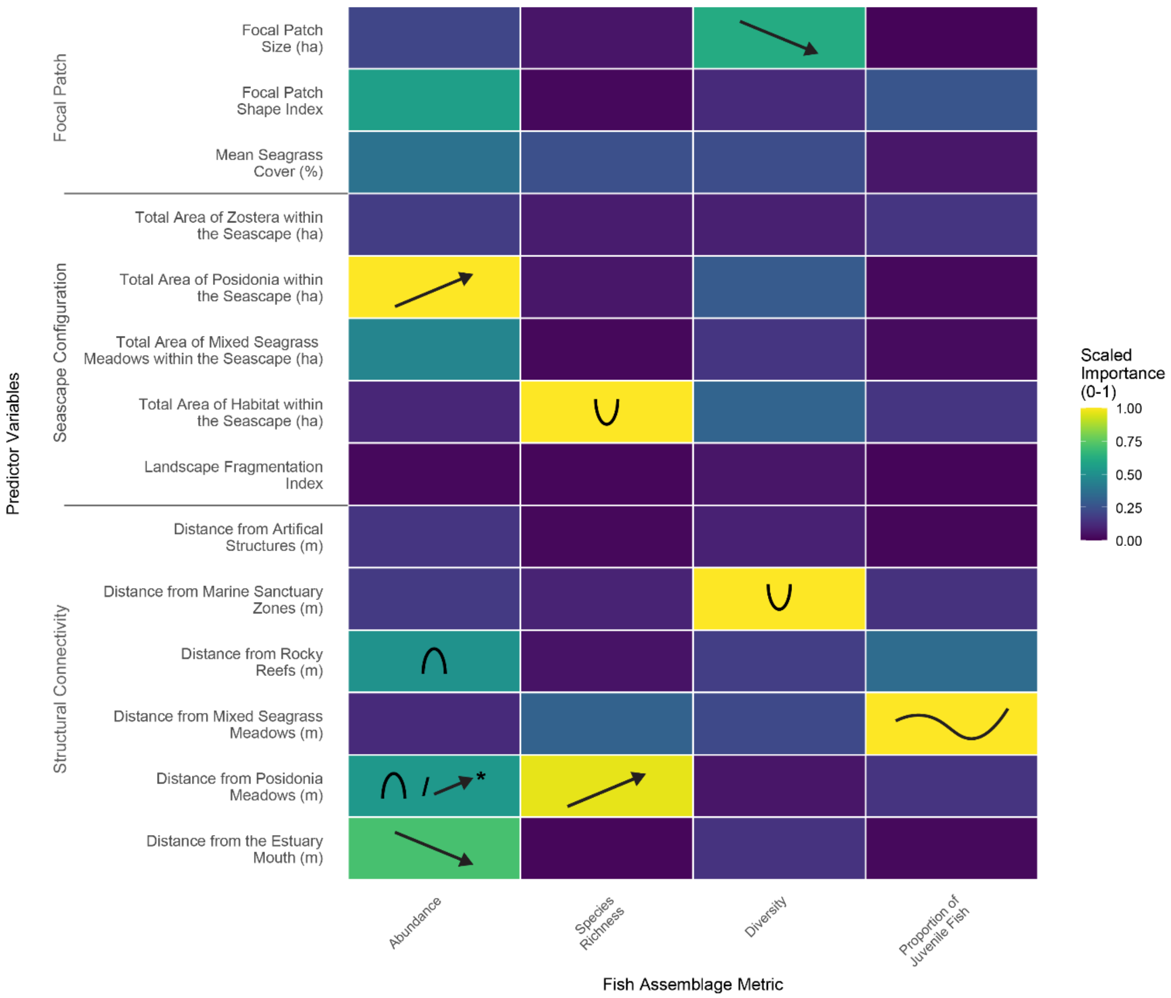


**Figure 4.2** - Heat-map of the relative importance for each predictor variable assessed (calculated as the sum of AICc weights divided by the number of models) for each of the key fish assemblage metrics (abundance, species richness, diversity (Shannon's H), and proportion of juveniles). Symbols represent the shape of the relationship and are included only if the variable was selected in the most parsimonious model(s) for a given assemblage metric: U (U-shaped), ∩ (peaked), ↗ (positive linear), ↘ (negative linear), and ~ (bimodal). Asterisk (*) next to distance from *Posidonia* meadow in the abundance column was to indicate that the peaked relationship (∩) observed was primarily driven by one point. Therefore, the ↗ is used to represent the positive linear relationship observed if we were to remove said point (see section 4.2.5.1).

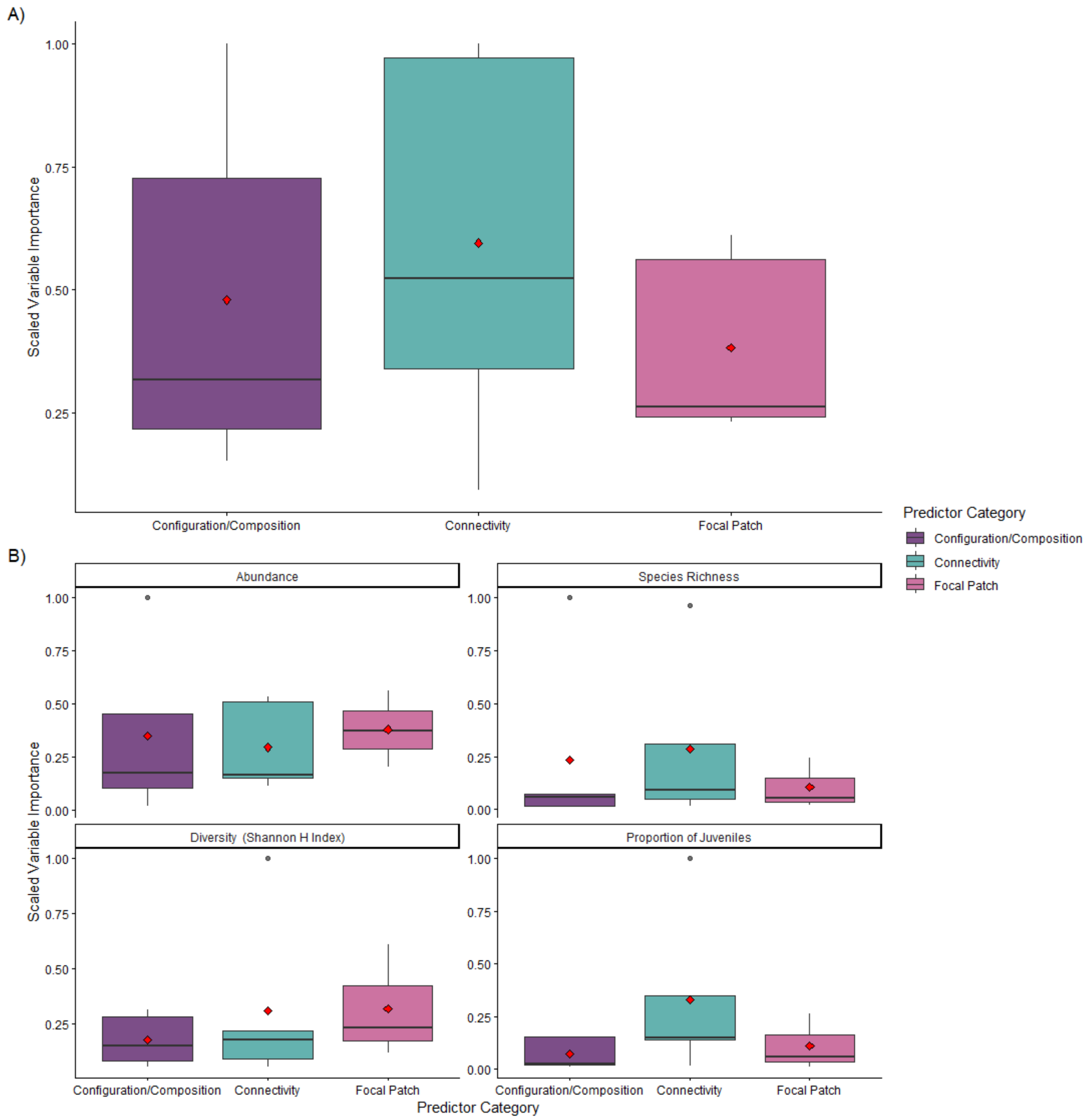


**Figure 4.3** - Relative variable importance of three categories of predictors (seascape configuration/composition, structural connectivity, focal patch characteristics). A) Scaled variable importance for each predictor category across all four assemblage models. B) Boxplot indicating the spread of relative variable importance within categories of predictors among the four different univariate fish assemblage metric models (abundance, species richness, Shannon H diversity, and proportion of juveniles). Red diamond indicates the mean. Solid points indicate outliers. Relative variable importance has been scaled within each univariable model to enable robust comparison across models (See section 4.3.1).

For total fish abundance, full subset model selection identified five models within delta AICc <2 with equivalent parsimony (1 predictor; Table S1). However, examination of parameter significance across these models revealed four variables with significant relationships to abundance (Table S2). Increasing distance from the estuary mouth had a negative linear association with fish abundance (Figure 4.4A). Distance from *Posdionia* meadows also had a unimodal relationship with total fish abundance (Figure 4.4B), though the decline at greater distances from *Posdionia* was influenced by a single data point, warranting cautious interpretation of this half of the pattern. Additionally, increasing the total area of *Posidonia* meadows within the seascape was associated with a linear decrease in fish abundance (Figure 4.4C). We observed that distance from rocky reefs unimodal relationship, peaking in abundance at 750m away, with both closer and more distant patches supporting lower fish abundance (Figure 4.4D).

Model selected identified a single top model for species richness that contained two predictors – distance from *Posidonia* meadows and the Total area of all habitats within the seascape (Table S1). Species richness was positively correlated with increasing distance from *Posdionia* meadows (Figure 4.4E). Total area of all habitats within the seascape showed a mostly negative asymptotic relationship with species richness, with richness declining steeply at lower habitat amounts before levelling off, with a slight increase at the highest amounts observed (Figure 4.4F)

A single top model was identified for fish diversity (measured as Shannon H Index) that contained two predictors – focal patch size and distance from marine protected area (Table S1). Diversity decreased linearly with increasing focal patch size (Figure 4.4G). Distance from marine protected areas (MPAs) was observed to have a slight, U-shaped relationship with diversity (Figure 4.4H). Diversity was relatively moderate within MPAs (0m), declined to is lowest value approximately 300m outside MPA boundaries, then increased to maximum values at greater distances from MPAs.

Model selection identified a single top model for the proportion of juveniles within the fish assemblage that contained one predictor – distance from mixed seagrass meadows (Table S1). Juvenile proportion exhibited a bimodal relationship with distance from mixed seagrass meadows, with peaks around 350m and 1700m (Figure 4.4I). However, the ecological interpretation of the second peak warrants caution given the limited number of observations at these greater distances.

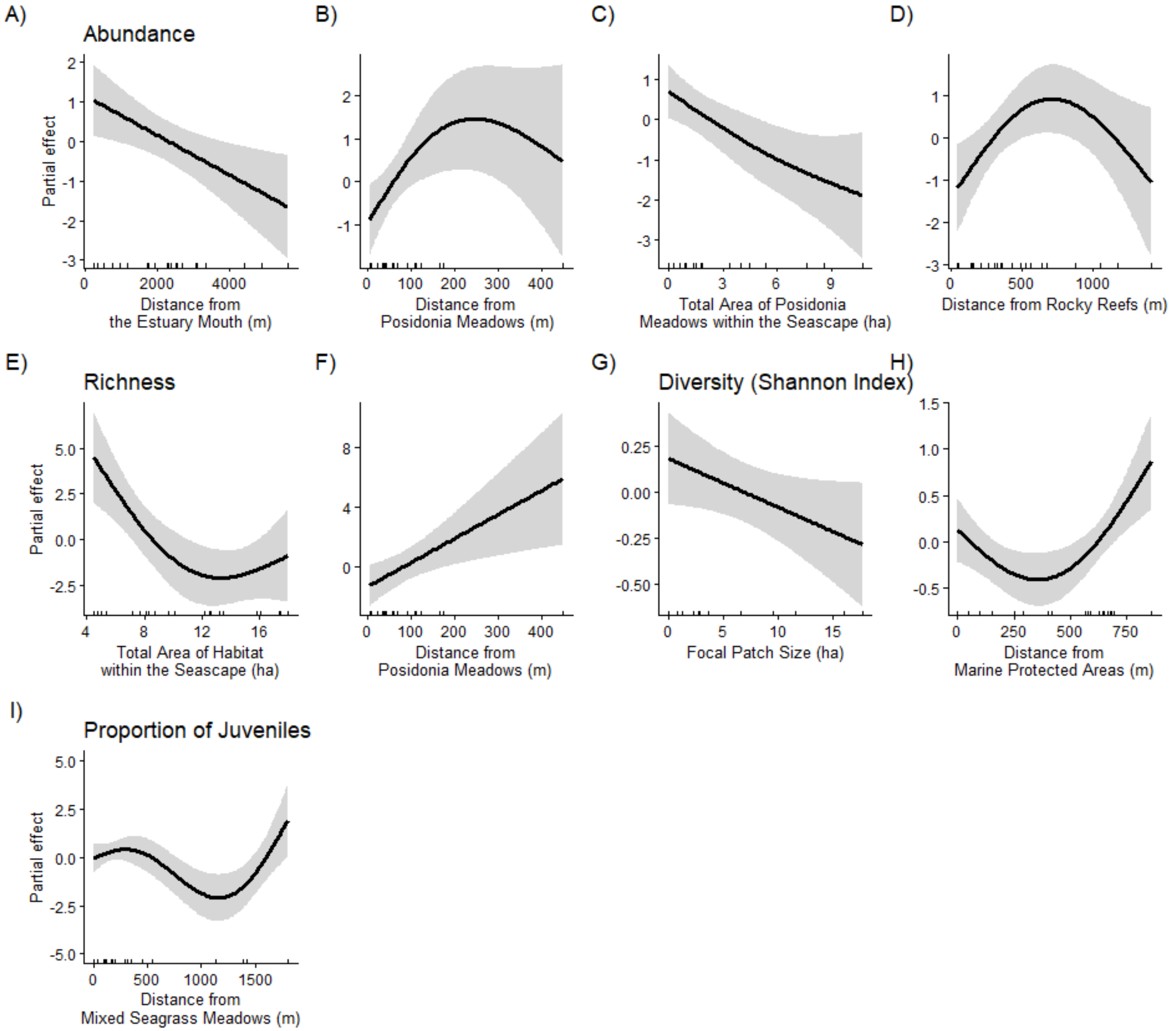


**Figure 4.4** - Partial effects of significant predictors on fish assemblage metrics in *Zostera capricorni* meadows. Relationships shown for: (A-D) abundance with distance from estuary mouth, distance from *Posidonia* meadows, total area of *Posidonia* meadows within the seascape, and distance from rocky reefs; (E-F) species richness with total area of habitat within the seascape and distance from *Posidonia* meadows; (G-H) diversity (Shannon Index) with focal patch size and distance from marine protected areas; (I) proportion of juveniles with distance from mixed seagrass meadows. Shaded areas show 95% confidence intervals; tick marks indicate observed data distribution.

### *4.3.2 Multivariate community composition*

The NMDS ordination of fish assemblages revealed distinct relationships between environmental variables and community structure (Figure 4.5, 2D-stress = 0.141). Distance from the estuary mouth emerged as the dominant drivers of community composition as indicated by its long vector pointed towards the lower left quadrant. Distance from mixed meadows influenced community structure in a similar direction as estuary mouth distance, though with relatively less strength. Landscape fragmentation index had the second longest vector, shifting communities towards the upper quadrant. Distance from *P. australis* meadows and focal patch size showed moderate influence on community composition, with vectors of similar direction and magnitude pointing toward the lower right side of the ordination. Several ray species, including the Bluespotted Maskray, Eastern Fiddler Ray, Estuary Stingaree, and Common Stingaree, clustered in this region of the ordination space, indicating their association with greater focal patch size and distance from *P. australis* meadows. Increasing distance from artificial structures was associated with a shift in community composition towards the right quadrant, with increasing distance associated with the cluster of ray species.

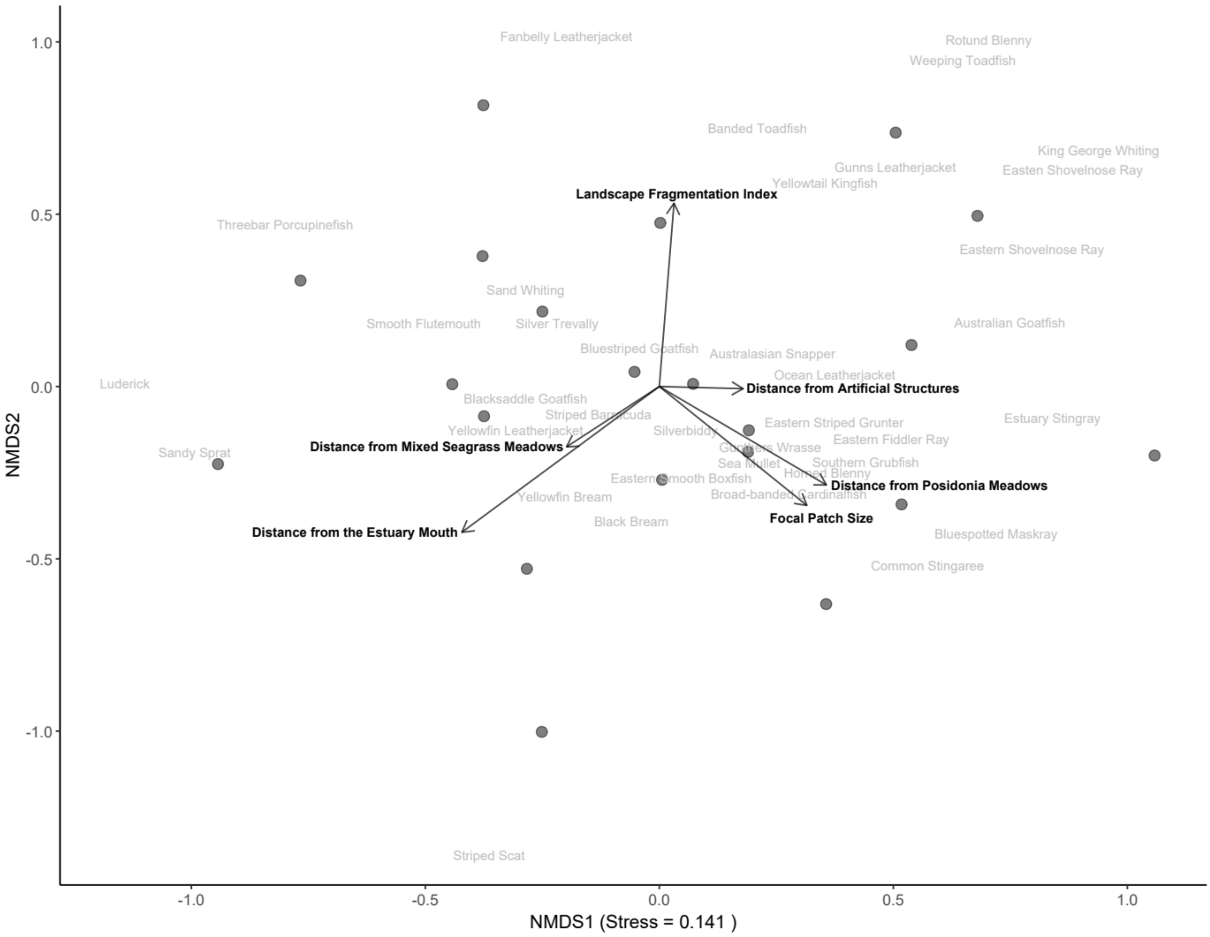


**Figure 4.5** - Non-metric multidimensional scaling (NMDS) ordination of fish assemblages in *Z. capricorni* meadows (2D-stress = 0.141). Environmental vectors indicate the direction and strength of influence for key seascape variables: distance from estuary mouth (m), distance from mixed meadows (m), focal patch size (ha), landscape fragmentation index, total habitat area within the seascape (ha), distance from *P. australis* meadows (m), distance from artificial structures (m), and mean seagrass cover (%). Black points represent individual sites. Species names are also displayed in ordination space. Longer vectors indicate stronger influence on community structure. Species close to each other in ordination space have similar environmental responses, while those far apart have different habitat associations

# 4.4 | Discussion

Understanding the relationships between seascape characteristics, focal patch characteristics, and key fish assemblage metrics (abundance, richness, diversity, juvenile density, and juvenile proportion) is crucial for advancing seagrass seascape ecology in estuarine environments and informing evidence-based management. This study demonstrates that key fish assemblage metrics are often more associated with characteristics describing the seascape than the focal patch itself (Figure 4.2 & 4.3), with metrics describing structural connectivity to surrounding estuarine habitats and seascape configuration generally emerging as among the most important predictors of key fish assemblage metrics (Figure 4.3A) and the multivariate community composition (Figure 4.5). Focal patch characteristics, while influential for some metrics, had more limited relationships than expected based on previous literature examining patch scale ecology of seagrass meadows specifically (Smith et al. 2008; 2010; Macreadie et al. 2010; Smith et al. 2011; 2012). Despite this, while structural connectivity was still among the most important category of predictors for three of the four assemblage metrics (species richness, diversity, juvenile proportion; Figure 4.3B), the relative importance of these categories of measures varied among the fish assemblage response metrics (Figure 4.3B), suggesting the presence of differential ecological mechanisms underlying different aspects of the fish assemblage.

Our analysis also revealed a prevalence of non-linear relationships, with 40% (4/10) of all significant relationships exhibiting non-linear patterns (Figure 4.3) – not counting distance from *Posidonia* meadows due to its non-linearity being driven by one value towards the maximum of the observed distances. The prevalence of non-linear relationships suggests that ecological thresholds and trade-offs between competing ecological mechanisms may interact to shape the structure of fish assemblages in *Z. capricorni* meadows. Such relationships are not uncommon in seascape ecology (Liu et al. 2007; Peters et al. 2007; Boström et al. 2011; Soranno et al. 2014; Weijerman et al. 2015; Boström et al. 2017), but this study is among the first to characterise some of them in temperate *Zostera*-associated fish assemblages in estuarine systems. This challenges common restoration approaches that assume linear improvements in outcomes based on increasing habitat quality or area (Bradshaw 1984; Cortina et al. 2006; Suding and Hobbs 2009) and instead highlights the importance of considering the broader seascape in conservation and restoration design.

We also observed high mean juvenile proportions throughout the seagrass patches sampled (mean juvenile proportion: 57 % +/- 5% SE across all sites), indicating the importance of *Z. capricorni* habitats as nurseries within temperate Australian estuaries. Furthermore, the results showed that juvenile and overall abundance responded similarly to seascape characteristics, though juvenile proportion showed some distinct patterns with distance from mixed seagrass meadows. This indicates that seascape characteristics that influence overall assemblages may simultaneously shape nursery habitat quality, with specific seascape configurations potentially enhancing the nursery function of *Z. capricorni* patches.

### *4.4.1 Community composition and seascape ecology*

The assessment of multivariate community composition provides greater context for understanding how seascape characteristics influence fish community structure in *Z. capricorni* meadows. The strong influence of the estuarine gradient on community structure (Figure 4.5) aligns with previous studies in similar systems showing similar influences (Jelbart et al. 2007; Teichert et al. 2018; Henderson et al. 2021; Goodridge Gaines et al. 2022; Perry et al. 2023) and supports the fundamental role of estuarine position as a mediating factor in estuarine seascape ecology. The differing direction of influence that focal patch size and landscape fragmentation had on community composition suggests these variables represent opposing ends of a similar ecological process within the seascape (Figure 4.3A & G; Figure 4.5). This relationship suggests that different species respond to varying aspects of habitat configuration - with some preferentially using larger contiguous patches, while others prefer more fragmented landscapes that provide diverse edge habitats and connectivity to complementary resources. For example, both the Common Stingaree (*Trygonoptera testacea*) and the Bluespotted Maskray (*Neotrygon australiae*) were strongly associated with larger focal patch sizes, while species like the Smooth Flutemouth (*Fistularia commersonii*), Threebar Porcupinefish (*Dicotylichthys punctulatus*), Sand Whiting (*Sillago ciliata*), and Silver Trevally (*Pseudocaranx georgianus*) associated with smaller focal patch sizes (Figure 4.5). Most notably, total habitat area showed minimal influence on community structure despite significantly influencing species richness. This suggests that while total habitat quantity within the seascape affects the number of species present, it may not fundamentally restructure which species occur. Instead, the spatial arrangement of habitat (connectivity to other habitats and fragmentation) appears more influential in determining community composition than absolute habitat amount. These findings challenge habitat conservation approaches focused solely on area preservation without consideration of spatial arrangement and demonstrates the need for multi-scale seascape approaches for effective conservation and restoration.

## *4.4.2 The influence of seascape configuration and structural connectivity on Zostera associated fish communities*

The configuration and structural connectivity of habitats within the broader seascape (as defined by our seascape sampling unit – 300m circular radius around the sampling point) significantly influenced key fish assemblage metrics in *Z. capricorni* meadows, with both the total area of different habitat types (seascape configuration) and their spatial proximity (structural connectivity) playing important roles (Figure 4.2). Notably, while the results of our variable importance analysis suggest both these aspects of the seascape are important, in this study, structural connectivity seemed be more influential overall than seascape composition (Figure 4.3A), highlighting the importance of considering multiple aspects of the seascape and their relative importance. In the following sections we outline the potential ecological mechanisms behind each relationship observed in the most parsimonious model(s) for each fish assemblage metric.

### 4.4.2.1 *Posidonia australis* meadows

Both the total area of *Posidonia* within the seascape and distance from focal patches to *P. australis* meadows significantly influenced fish abundance, with both relationships pointing toward similar ecological interpretations. Total area of *Posidonia* meadows was associated with a linear decrease in abundance, while distance to *Posidonia* showed a positive relationship (Figure 4.3B & C), meaning that *Zostera* patches with less nearby *Posidonia* and those located further away supported higher fish abundance. One may suggest that the result of this convergent pattern is a result of collinearity between distance from *Posidonia* and the total amount of *Posidonia* within the seascape, however examination of Pearson correlation coefficients between the two indicate only low levels of collinearity (-0.31). This makes sense given the pattern of occurrence of *Posdionia* and *Zostera* meadows throughout the estuary, where frequently *Zostera* occurs on the shoreward edge directly parallel to *Posidonia* meadows (thus close proximity), but the size of the *Posidonia* meadows varies considerably (Figure 4.1). This convergent pattern suggest that assemblages associated with *Posidonia* meadows may exert competitive pressure on *Zostera* meadows or serve as sources of predation risk. *Posidonia* meadows typically support greater densities of predatory species and generally larger bodied fish compared to *Zostera* meadows (Middleton et al. 1984). The negative relationship with total area indicates that seascapes with extensive *P. australis* (which may support a greater absolute number of individuals), may support greater number of predators that spillover into nearby *Z. capricorni* patches. This could reduce fish abundance in focal *Zostera* patches through direct predation, increased competition for resources, and/or behavioural avoidance (Orth et al. 1984; Hovel and Lipcius 2001; Macreadie et al. 2010). This idea is further supported by the observed increase in abundance as distance from *Posidonia* increases, in line with what we would expect to observe if *Posidonia* meadows were a source of additional competition and/or predation, suggesting that this influence is a function of structural connectivity, that increases accessibility of *Zostera* patches by *Posidonia* associated species.

Alternatively, these patterns could reflect competitive interactions rather than predation pressure, where *Posidonia* meadows may support fish communities that compete with *Z. capricorni* associated species for shared resources during foraging movements across the seascape. Such foraging movements have been observed in these systems (Taylor et al. 2018; Swadling et al. 2024). The consistency between both metrics – composition (total area) and structural connectivity (distance) – provides evidence that the influence of *P. australis* on *Zostera* fish abundance operates at multiple spatial scales and is not simply an artifact of proximity.

### 4.4.2.3 Rocky reefs

Distance to rocky reefs showed peaked relationships for total fish abundance (Figure 4.4D). This non-linear pattern suggests multiple ecological mechanisms may be operating across the spatial gradient. Rocky reefs often are involved in natural ontogenetic habitat shifts of estuarine-dependent species, where they often serve as subsequent habitats used following the juvenile stage (Gillanders et al. 2003; Sheaves et al. 2015). As such, since fish in rocky reefs have been known to forage in adjacent and connected seagrass meadows (Taylor et al. 2018; Swadling et al. 2024), these larger bodied, more mature fish may naturally outcompete smaller more juvenile fish in the focal *Z. capricorni* patch, leading to decreased fish abundance. Furthermore, the foraging of rocky reef associated fish in adjacent habitats can creates elevated competition for resources and enhanced predation pressure (if the forging species is a fish predator) potentially leading to reduced abundance in the focal seagrass patch. However, the peaked relationship (rather than a simple positive correlation with distance) suggests a landscape supplementation effect operating simultaneously with these predation/competitive effects. Close to rocky reefs, the positive effects of landscape supplementation may be suppressed due to greater levels of competition/predation. However, as distance from the rocky reef increases, the competition and predation rates may decrease, no longer supressing the positive influence of landscape supplementation on abundance, thus leading to the peak in abundance at intermediate distances. The decline after intermediate distances may represent the point at which the focal seagrass patch is no longer connected enough to rocky reefs to benefit from landscape supplementation.

### 4.4.2.4 Distance from marine sanctuary zones

Distance from marine sanctuary zones (MPAs) exhibited a U-shaped relationship with species diversity (Figure 4.3G). The elevated diversity within sanctuary zones likely reflects the well-documented effects of administrative protection on fish and the habitats on fish communities, where reduced fishing pressure and habitat protection can enhance species diversity (Villamor and Becerro 2012; Pettersen et al. 2022). The minimum diversity observed approximately 300m outside the MPA boundaries and the subsequent increase in diversity further as we move beyond this distance is more challenging to interpret but may reflect spatial patterns in fishing pressure around MPA boundaries. Sanctuary zones in Port Stephens are directly adjacent to administrative zones that allow recreational fishing (including Habitat Protection zones that allow fishing but protect seagrass, and General Use zones; (Transport NSW 2024). “Fishing the line” is a common tactic where fishers target areas immediately adjacent to no-take boundaries (Kellner et al. 2007), which has been documented in multiple regions around the world and leads to increases in fishing intensity near MPA borders (Yamasaki and Kuwahara 1989; Johnson et al. 1999; Murawski et al. 2004). This can alter fish densities and community structure outside (and sometimes within) MPAs, with impacts depending on species mobility, with less mobile species showing greater reductions in density compared to highly mobile species (Kellner et al. 2007).

While we didn’t observe any significant relationship between distance from sanctuary zones and fish abundance, the potential localised increase in fishing pressure near MPA boundaries, combined with gear- and species-specific selectivity (Kuparinen et al. 2009) may disproportionately target certain species, particularly those popular for recreational fishing. This selective removal could reduce species evenness in the assemblage and thus decrease diversity near the boundary while having a minimal impact on total abundance if non-targeted species compensate numerically. Spatial analysis of fishing activity intensity in relation to a MPA in Portugal demonstrated that traditional line fishing increased within a few hundred metres of MPA boundaries before declining at greater distances (Horta e Costa et al. 2013) a pattern that could explain the decrease in diversity and subsequent increase observed here – though it is possible that these relationships with fishing behaviour vary among regions. However, as we lack any specific data on fishing activity and behaviour in Port Stephens, these remain possible explanations that warrant further investigation.

### 4.4.2.5 Total amount of habitat within the seascape

Total amount of habitat within the seascape exhibited a negative asymptotic relationship with species richness that showed a slight increase at the greatest habitat amounts observed (Figure 4.3E), independent of fragmentation patterns and focal patch size. Seagrass meadows with little other habitat nearby might represent specialised habitats where the heterogeneity of the seascape is greater and thus species richness is increased (Lamont and Pausas 2024). As the total habitat amount increases, the homogeneity of the seascape increases and/or edge effects become less prominent, leading to a decrease in species richness (Lamont and Pausas 2024). The slight uptick at the end may suggest a threshold where large continuous habitat areas support additional species that require larger amounts of habitats or more extensive resources to maintain viable populations (Lamont and Pausas 2024). However, due to our seascape sampling unit (300m buffer around the point), we may have only captured a portion of the theoretical curve that may explain this relationship, where continuing to increase the total habitat amount beyond this point could lead to a further increase in richness. As such, it is important to interpret this with caution.

### 4.4.2.6 Seascape configuration versus structural connectivity

These findings collectively highlight that both seascape composition and structural connectivity shape fish assemblages in *Z. capricorni* meadows, but their relative importance varies among habitat types and response metrics. This complexity highlights the need for management approaches that consider how much of each habitat type exists within a seascape and how these habitats are spatially arranged relative to one another. Conservation and restoration strategies should aim to create and conserve seascapes with appropriate compositions of complementary habitat types in alignment with their desired goals. The spatial positioning of restored or protected patches should also be considered to optimise connectivity benefits and minimise potential negative interactions such as elevated predation risk or competitive pressures.

### *4.4.3 Patch-scale relationships with fish communities*

Focal patch size exhibited a significant negative relationship with fish assemblage diversity (Figure 4.4G), likely through mechanisms related to edge effects and species-specific habitat preferences, as evidenced by the effect of focal patch size on multivariate composition (Figure 4.5). At smaller focal patch sizes, edge habitats comprise a greater proportion of the total area of the patch, and in seagrass meadows these zones often feature distinct microhabitats and resource availability that support unique assemblages (Macreadie et al. 2009; 2010; Smith et al. 2008). The negative relationship we observed reflects how edge effects in small focal patches create conditions where both edge-adapted species and core habitat specialists can co-occur leading to an increase in diversity. Similar patterns have been observed in seagrass meadows across multiple regions, with small to intermediate patches often supporting greater richness than larger, more homogenous patches (Jelbart et al. 2007; Boström et al. 2011). The negative relationship may also reflect reduced competitive exclusion in smaller patches, where limited space and resources prevent dominant species from monopolising the habitat, and as a result maintain richness through competitive co-existence (Chesson 2000). While our multivariate analysis revealed compositional shifts with focal patch size (Figure 4.5), we cannot definitively classify the observed species as either core habitat specialists or edge adapted species, as there is limited research on the ecological niches at this scale for most species within our assemblage. Moreover, the ecological niche of a singular species shifts throughout its ontogeny (Werner and Gilliam 1984; Mittelbach et al. 1988; Nakazawa 2015), with juveniles potentially favouring more sheltered areas due to increased vulnerability to predation (Eklöv and Persson 1996; Laegdsgaard and Johnson 2001; Holbrook and Schmitt 2002; Scharf et al. 2006), further complicating classification.

It is important to note that while focal patch size influenced diversity, it showed no significant relationship with overall fish abundance or species richness in our analysis. This suggests that patch size primarily influences community evenness and species composition rather than fish density or the absolute number of species present. Additionally, while patch size was not included within the final most parsimonious model for the proportion of juveniles (and as such we cannot comment on the shape or direction of the association), it was among the more important predictors as indicated by the variable importance analysis (Figure 4.2). This suggests that the shape of the patch and thus edge-to-centre ratios may be more important for early life stages than the absolute focal patch size, warranting further investigation into this pattern.

### 4.4.4 Juvenile assemblage responses: implications for nursery function

Our results highlight that these *Z. capricorni* habitats are dominated by juvenile fish (mean juvenile proportion: 57 % +/- 5% SE across all sites). This is intriguing as the importance of *Zostera* as a nursery habitat is often undervalued in conservation policy and public awareness (Boström et al. 2014). A study by Middleton et al. (1984) comparing *Zostera* to *Posidonia* in Gamay Bay (Botany Bay) observed smaller fish sizes and a greater number of juvenile recruits in *Zostera* meadows, suggesting that *Zostera* meadows may provide a habitat for initial settlement and recruitment before individuals move to *Posidonia* at a later ontogenetic stages. While we did not compare our sites to *Posidonia*, the prevalence of juveniles throughout the assemblages observed here provide evidence that the importance of *Zostera* for juvenile fish extends beyond the system studied by Middleton et al. (1984), providing further evidence of *Zostera* as a critical foundation for fisheries production in these estuarine systems.

As juvenile abundance is mathematically determined by the product of total fish abundance and juvenile proportion, and juvenile proportion only showed significant relationships with mixed meadow distance (Figure 4.3), spatial patterns in juvenile abundance predominantly reflect variations in total fish abundance. Given the prevalence of juveniles throughout the assemblage, it is perhaps unsurprising that juvenile abundance responded similarly to our various predictors as overall fish abundance. This similarity in relationships contrasts with our initial hypotheses' and predictions that there might be distinct habitat requirements between juvenile assemblages and the overall assemblage. However, given that juveniles dominate these *Z. capricorni* assemblages, the overall community patterns may be driven by juvenile habitat associations, potentially explaining the consistency between juvenile abundance and overall abundance. Nevertheless, juvenile proportion – the relative abundance of juvenile fish compared to other life stages – did show a distinct response pattern with one measure, exhibiting a bimodal relationship with distance from mixed seagrass meadows (Figure 4.4I).

This study reveals that specific seascape configurations may optimise nursery function by promoting elevated juvenile abundance – a key characteristic distinguishing better nursery habitat (Beck et al. 2001). While prior literature has established seagrass meadows as a habitat which supports a greater density of juvenile fish (Jackson et al. 2001; Heck et al. 2003; McDevitt-Irwin et al. 2016; Whitfield 2017) our analysis shows that not all seagrass habitats provide equivalent nursery value. The greatest juvenile fish abundances were found in areas characterised by specific seascape configurations: low total area of P. *australis* meadows within the seascape, further away from *P.*

*australis* meadows, in close proximity to mixed seagrass meadows, moderate distances away from rocky reefs, and closer to the estuary mouth. These findings also raise concerns when contextualised within historically degraded systems or areas that face continued habitat loss due to anthropogenic impacts. Many estuarine systems experience altered seascape configuration, including changes in the abundance of various seagrass species, loss of complementary and critical estuarine habitats, and shifts in the spatial arrangements of the remaining habitat patches as a result of anthropogenic impacts (Waycott et al. 2009; Duarte et al. 2020; Dunic et al. 2021). If optimal nursery function is associated with specific seascape configurations and connectivity patterns, degraded systems may support reduced juvenile production even when focal seagrass patches seem ostensibly sound.

These results support one of the emerging hypotheses in marine nursery ecology – the seascape nursery concept (Nagelkerken et al. 2015) - and show that nursery value varies substantially within a habitat type based on focal patch characteristics, seascape configuration, and structural connectivity. Future research should investigate how these spatial dependencies and focal patch characteristics influence larval settlement, juvenile survival rates, and successful recruitment to adult populations, providing a more complete assessment of nursery function across heterogeneous seascapes.

### *4.4.5 Management implications*

The complex relationships between seascape configuration, structural connectivity, and fish assemblages offer valuable insights for seagrass conservation and restoration in estuarine systems. While our study was conducted in a single estuary with a smaller sample size - constraining our ability to test interactions between these variables - these findings contribute to the growing body of evidence supporting multi-scale approaches to habitat management (Pittman et al. 2021).

A key finding from our analysis is the importance of both seascape configuration and structural connectivity in predicting key fish assemblage metrics when compared to focal patch characteristics alone (Figure 4.3) and provides evidence that location and the seascape surrounding the patch is more important than the specific condition of the focal patch. This highlights the importance of considering the seascape within restoration and management design. Rather than focusing primarily on the size, shape, or quality of individual patches, managers should consider how restored or protected patches fit within the broader mosaic of estuarine habitats and suggest that aligning seascape configurations with specific ecological objectives could enhance the outcomes of management actions. Furthermore, our findings suggest that strategic positioning of protected areas or restoration projects relative to existing habitats may also influence their effectiveness by influencing the connectivity of the restored patches to pre-existing areas. Moreover, the prevalent non-linear relationships we observed suggest that improvements in habitat conditions may yield complex ecological responses rather than straightforward linear improvements. By incorporating these considerations into seagrass management frameworks, conservation practitioners may better support diverse and abundant fish communities while optimising limited conservation resources.

While this study highlights the importance of seascape characteristics, we do not want to imply that focal patch characteristics should be disregarded entirely. There is likely a minimum patch size threshold bellow which seagrass habitats cannot support viable fish populations - which the patches sampled here are above. Additionally, where seagrass studies examine focal patches in isolation, patch size and shape have been consistently associated with fish assemblage metrics (Smith et al. 2008, 2010; Smith, Jenkins & Hutchinson 2012). The limited influence of focal patch metrics in our study may partially reflect the structure of our study estuary, which predominantly included larger patches (on the scales of 1-20 hectares rather than 10-100s of metres). Studies in different systems with broader ranges of patch sizes and larger sample sizes may be better at elucidating the relative importance of focal patch versus seascape characteristics and identify potential threshold below which patch-scale attributes become more critical determinates of fish assemblage structure.

### *4.4.6 Limitations and future directions*

While our study provides valuable insights into the complex relationships between seascape characteristics and fish assemblages in *Z. capricorni* meadows, several limitations warrant consideration when interpreting our findings. Our sampling occurred at a single timepoint during summer, lacking the temporal replication that would capture seasonal dynamics in fish assemblage structure and habitat associations (Schneider 2017; Lefcheck et al. 2019). Additionally, poor water visibility limited our spatial coverage to the lower portion of the estuary, potentially biasing our understanding of the full estuarine gradient's influence on fish assemblages. This spatial constraint particularly affects our ability to fully characterize relationships in upper estuarine environments where different ecological processes may dominate. Furthermore, our sample size limited out ability test interactions between continuous predictors, particularly interactions with distance from the estuary mouth that may reveal how estuarine gradients modulate relationships between seascape characteristics and fish assemblages. While our analysis identified important relationships with seascape composition and structural connectivity, this potential interactive influence of estuarine position remains unexplored. Studies with larger sample sizes with sufficient power to test these complex interactions would enable better assessment of how environmental context and connectivity shapes seascape-fish relationships.

Additionally, our correlative approach, while revealing complex associations, limits causal inferences regarding the mechanisms driving observed patterns. Future studies should conduct manipulative experiments to establish causation and understand the relationships highlighted within this study. For example, manipulating specific habitat characteristics using artificial seagrass patches may provide stronger evidence for the mechanisms underlying observed patterns, although such studies are difficult to do at scale. Such experiments could be complemented by investigations into species interactions using approaches such as behavioural studies and giving-up density (GUD) experiments to quantify predation risk and foraging trade-offs across different habitat configurations. The integration of isotopic analyses, animal tracking studies, and dietary analysis alongside survey style sampling studies could further establish connectivity patterns and trophic dynamics within seagrass seascapes.

Given these limitations -particularly regarding constraints with sample size and testing of interactions - we recommend the direct relationships described here be considered as potentially illustrative of this specific system rather than prescriptive guidelines for management and restoration. Nonetheless, our results reinforce the value of considering seascape configuration and connectivity alongside traditional patch-scale metrics when prioritising conservation or design restoration projects in estuarine systems.

## *4.5* | Conclusion

This study advances our understanding of fish seascape ecology by revealing the complex non-linear relationships between seascape characteristics and fish assemblages across multiple spatial scales. Our findings demonstrate that fish communities in seagrass meadows are primarily shaped by seascape metrics that characterise configuration/composition and structural connectivity rather than focal patch characteristics (e.g., patch shape, size, and seagrass cover), with structural connectivity generally being more important than seascape configuration. Importantly, we found that juveniles comprise a large proportion of the fish assemblage in *Z. capricorni* meadows (57 % +/- 5% SE). Given that juveniles comprised a large part of these assemblages, juvenile abundance patterns largely mirrored overall abundance patterns, indicating that seascape characteristics shaping overall fish abundance simultaneously influence nursery habitat quality in these juvenile-dominated systems. The predominance of non-linear relationships – driven by landscape supplementation /complementation, edge effects, and competitive dynamics – suggests that traditional linear approaches to habitat management may fail to capture critical ecological thresholds. This complexity reinforces the need for seascape management that maintains diverse habitat configurations throughout estuarine systems rather than focusing solely on individual patches. Future research with greater temporal and regional replication will be essential for validating these ecological patterns across various scales.

# Chapter 5 - Strategic restoration planning in marine systems: A generalisable decision-support framework integrating site suitability, seascape understanding, and spatial prioritisation

# Abstract

## *Context*

Anthropogenic impacts have caused unprecedented degradation of habitats such as seagrass meadows, kelp forests, coral reefs, and oyster reefs worldwide, disrupting ecosystems and diminishing critical ecosystem services. This has led to an increase in the importance and prevalence of habitat restoration – the process of assisting the recovery of an ecosystem that has been historically degraded, damaged, or destroyed. Given restoration's high cost and effort, improving efficiency by maximising the ecological impact of restoration is paramount in our rapidly changing environment. However, much of restoration design and site selection focuses on the habitat forming species itself, with limited consideration of outcomes for associated biotic assemblages. There is increasing recognition that broader ecological processes driven by the seascape surrounding the patch itself are among the key drivers that shape the associated biotic communities within these patches. Despite repeated calls for integrating seascape ecology into restoration design, there are limited guidelines and workflows for incorporating this into restoration site selection.

## *Objective*

Here I present a framework that bridges ecological theory and practical application through: (1) habitat suitability modelling to identify appropriate restoration sites; (2) integration of landscape patterns and patch characteristics to predict associated assemblage outcomes; and (3) identification of optimal placement and habitat patch configuration for specific restoration objectives using spatial prioritisation. I demonstrate this framework using seagrass meadows and fish communities, comparing different prioritisation scenarios that reflect varying ecological objectives (e.g., seagrass habitat suitability, fish diversity, and fish abundance) against each other to understand how considering both the habitat former itself and their associated assemblage in site selection changes the predicted ecological outcomes. In addition to this, I compared different prioritisation scenarios against a baseline scenario informed by a seagrass researcher with extensive local knowledge of the study system to assess the potential improvements this framework may have over traditional approaches and to understand the limitations of a purely data-driven modelling approach.

## *Results*

Based on the results of varying restoration sites selected under different scenarios using the framework, I observed that the prioritisation of individual ecological metrics maximised predicted

restoration outcomes for that specific metric (as expected) - but created significant trade-offs in other ecological outcomes (e.g., optimising for based on suitability for the habitat forming species as opposed to fish abundance). We also observed that multi-priority approaches still exhibited trade-offs between metrics, although with reduced severity.

Compared to the baseline scenario, sites selected using the framework were predicted to increase fish community outcomes by 7-65% depending on the prioritisation scenario and metric evaluated, while simultaneously selecting restoration sites with greater mean seagrass habitat suitability scores and reduced variability. However, comparison with expert-selected sites revealed complementary strengths, where they identified site-specific constraints invisible to quantitative models (as they were not or are unable to be quantified), while the framework systematically balanced multiple ecological metrics that expert judgement lacks the knowledge to simultaneously optimise quantitatively.

## *Conclusions*

These results demonstrate that this framework functions most effectively as a decision-support tool that enhances rather than a replacement to expert knowledge. This study demonstrates that the systematic integration of previously separate approaches (habitat suitability modelling, predicted ecological outcomes for associated assemblages, spatial prioritisation) can improve the effectiveness and efficiency of restoration site selection, but optimal real-world outcomes require practitioners to interpret the results within the context of local knowledge, site-specific constraints and adaptive management principles.

## 5.1 | Introduction

There is a growing sentiment within the field of restoration ecology that successful ecosystem restoration extends beyond simply the establishment and restoration of the habitat former itself but also depends on the recovery and support of associated biological communities (Brudvig 2011; Suding 2011; Cross et al. 2020). However, a key challenge in achieving this is that habitat formers and their associated assemblages often respond to different ecological processes and environmental conditions at varying spatial scales. Habitat forming species – such as seagrasses, oyster reefs, kelp forests, and coral reefs – are sessile organisms whose establishment depends on complex local environmental conditions including temperature, hydrodynamics, depth, sediment characteristics/availability of substrate (depending on the species), with these conditions often being influenced by ecological feedback loops from the habitats themselves (Boström et al. 2017; Pausas and Bond 2022; Unsworth et al. 2024). In contrast, the distribution of biotic assemblages inhabiting these habitats - particularly those that are highly mobile - are often significantly influenced by landscape processes and characteristics such as connectivity, landscape configuration, and positioning within the broader landscape mosaic (Turner 1989; Pittman 2017b; Fletcher and Fortin 2018; Olds et al. 2017; Bradley et al. 2019; 2020; **Chapter 3 & 4**). This difference in the scale of relevant processes suggests that when selecting restoration sites that maximise habitat suitability for the habitat forming species, these same sites may not necessarily maximise outcomes for associated assemblages. For example, while an area may be environmentally suitable for a seagrass meadow to be restored due to high water clarity and favourable hydrodynamics, it may be isolated and disconnected from the wider seascape, making that particular area less favourable for associated assemblages, potentially creating an ecological trap – an area which organisms settle to but which is poor quality, resulting in reduced survival (Robertson and Hutto 2006; Hale and Swearer 2016). Consequently, selection of restoration sites focused solely on establishment of the habitat former may not be able to deliver benefits for the broader ecological community that restoration often seeks to support (Cross et al. 2020). This disconnect between the conditions ideal for the habitat forming species itself and its associated assemblages highlights the need to explicitly consider how the broader landscape influences outcomes for biotic assemblages when selecting restoration sites.

While habitat suitability models (HSMs) have become a popular quantitative site selection method to identify areas suitable for restoration of the habitat in recent years (Bertelli et al. 2022), they are typically designed to understand what areas are more likely for the habitat forming species to establish and survive (Elith et al. 2011; Bertelli et al. 2022). HSMs predict the likelihood of species occurrence based on spatially explicit environmental data with multiple different modelling approaches (Hirzel and Le Lay 2008; Elith and Leathwick 2009; Elith et al. 2011), each with their own benefits and limitations (Elith and Leathwick 2009; Bertelli et al. 2022). They provide a quantitative methodology to identify candidate areas for restoration that are similar in environmental conditions to existing and/or historical habitat patches (Elith and Leathwick 2009), and have been used successfully to identify suitable restoration sites for various threatened habitat forming species (Elsäßer et al. 2013; Hu et al. 2021; Zheng et al. 2021). Although, in marine systems, HSMs tend to be underutilised compared to terrestrial systems (Robinson et al. 2011). In seagrass restoration, the usage of HSMs has increased since 2016 (Bertelli et al. 2022), with advanced methods now emerging that assess suitability under both present day conditions and future scenarios involving climate change and disturbances (Dalby et al. 2025), with these approaches aiming to increase the resilience of restored sites to future conditions.

By identifying sites with appropriate environmental conditions, HSMs effectively address the critical first-order question of where the habitat forming species can grow and survive. Though, as HSMs model the environmental niche of the habitat former per se, they do not incorporate the landscape/seascape characteristics that drive the structure of associated assemblages in the identification of restoration sites. This is not a flaw in the HSM methodology itself, but rather a mismatch between what these models are designed to predict (occurrence of the habitat former based on local environmental conditions) and what restoration often aims to achieve more broadly (recovery of ecosystem function and associated biodiversity). Thus, while HSMs are mostly employed to identify candidate restoration sites where the habitat former can survive, additional approaches are needed to be used in tandem to evaluate how spatial context and landscape characteristics influence broader assemblage outcomes in restoration, particularly for mobile fauna whose distributions are shaped more by connectivity and seascape configuration than by local patch conditions (**Chapter 3 & 4;** Pittman 2017b).

Addressing this mismatch between what HSMs are designed to do versus what restoration often aims to achieve more broadly requires integrating the core principles of spatial ecology with an understanding of the underlying landscape ecology into restoration design (Pittman et al. 2021; Wedding et al. 2025). This has long been recognised in the field of conservation, where the selection and design of reserves (e.g., marine protected areas or national parks) often leverages concepts from landscape ecology and integrates them into the selection process with the aim of improving conservation outcomes (Kool et al. 2013; Kujala et al. 2018; Moilanen et al. 2022). This has historically been done more often in terrestrial systems than in marine systems, where it is now increasingly appreciated (Kool et al. 2013; Kujala et al. 2018; Moilanen et al. 2022). Despite landscape ecology's importance and adoption throughout conservation planning, there is limited consideration of the spatial context of the surrounding landscape when it comes to selecting sites for habitat restoration (Gilby, Olds, Connolly, Henderson, et al. 2018; Pittman et al. 2021; Wedding et al. 2025). This has prompted continued calls for more strategic placement and design of restoration sites among landscapes (Gilby, Olds, Connolly, Henderson, et al. 2018; Gilby et al. 2020; Pittman et al. 2021; Gilby et al. 2023; Wedding et al. 2025), emphasising that where we restore may be as important as how much we restore, particularly when targeting outcomes for mobile assemblages. Indeed, the results of **Chapter 4** support this idea directly, showing that seascape structural connectivity was - on average - the most important category of predictors across four key fish assemblage metrics (abundance, species richness, diversity, proportion of juveniles), followed by measures of seascape configuration, then focal patch characteristics (**Chapter 4** – Figure 4.3).

Given the high costs and limited resources (budget, time, personnel) for restoration projects (Bayraktarov et al. 2016; Abelson et al. 2020), strategic approaches that optimise ecological outcomes (inclusive of both survival & establishment of the target habitat and support/recovery of associated assemblages) while minimising costs are needed for achieving restoration goals, particularly when projects involve multiple competing stakeholders and objectives. Spatial prioritisation approaches such as *Marxan*'s simulated annealing approach (Watts et al. 2017) or *Zonation*'s hierarchical ranking algorithms (Lehtomäki and Moilanen 2013) provide an effective solution for this issue. These algorithms are designed with the principle of complementarity, a fundamental concept in conservation, restoration, and spatial prioritisation, whereby sites targeted for conservation or restoration should complement, instead of repeating, each other's ecological outcomes and biodiversity values (Kukkala and Moilanen 2013; Watts et al. 2017). In terrestrial and marine systems, these tools have been used extensively to integrate landscape ecology concepts and biodiversity features into strategic conservation planning for existing habitats (e.g., design of legislated protected areas), identifying cost-effective balanced priority areas (Kukkala and Moilanen 2013; McIntosh et al. 2017; Oleson et al. 2017; Young et al. 2017; Pittman et al. 2022). However, despite widespread use throughout systematic conservation planning, the application of spatial prioritisation approaches to quantitative restoration site selection and planning is uncommon (McBride et al. 2010; Wiens and Hobbs 2015; Gilby, Olds, Connolly, Henderson, et al. 2018). This is especially the case in marine systems (Gilby, Olds, Connolly, Henderson, et al. 2018; Virtanen et al. 2018; Lester et al. 2020) where the potential utility of systematic planning approaches to restoration is increasingly noted (Lester et al. 2020; Fraschetti et al. 2021). Even in terrestrial restoration contexts, only a handful of studies have employed these approaches, including forest restoration for birds (Grand et al. 2024), boreal forest restoration (Robinne et al. 2020), wetland restoration (Lin et al. 2022), and habitat offsetting for mining impacts (Kujala et al. 2015). To my knowledge there are no documented applications of such spatial prioritisation software for habitat restoration in marine systems, despite repeated called for such approaches and growing recognition of their potential utility. These techniques represent an opportunity in restoration design to enhance efficiency by systematically identifying sites that have the potential to simultaneously maximise the odds of survival of the restored habitat itself and outcomes for the associated assemblages within resource constraints.

In this study I present a framework that integrates habitat suitability modelling, seascape ecology, and spatial prioritisation into a unified decision-support system for restoration site selection, specifically designed to consider both the habitat forming species and the outcomes of their associated assemblages. Previous studies have applied individual components of this approach separately, including predictive modelling of restoration outcomes (Gilby et al. 2020), habitat suitability modelling for restoration site selection (Bertelli et al. 2022; Dalby et al. 2025), and integration of restoration outcome modelling with spatial prioritisation in terrestrial systems (Grand et al. 2024; Jalkanen et al. 2025). However, to my knowledge this is the first study to comprehensively integrate all these components into a unified framework, particularly for marine restoration applications. My approach explicitly considers both the environmental suitability for the habitat former and the predicted outcomes for associated assemblages, recognising that these may be driven by different factors. While this framework is broadly applicable across restoration contexts, here I demonstrate its implementation using seagrass restoration site selection, comparing restoration sites selected under different prioritisation scenarios that reflect varying management objectives (e.g., seagrass establishment, maximising outcomes for fish communities, or both) and evaluate these against a baseline scenario where potential restoration sites were selected by an experienced seagrass researcher in a traditional more qualitative approach. Additionally, I considered a few hypothesises on the expected outcomes of the various prioritisation scenarios. I hypothesised that restoration sites selected solely using seagrass habitat suitability modelling and using a more traditional ad-hoc approach (baseline scenario), will be predicted to have lower outcomes for the key fish assemblage metrics than the scenarios incorporating these measures directly, while selecting sites of similar suitability for seagrass. Furthermore, based on the varying patterns of relationships observed between seascape characteristics and the fish assemblage metrics in **Chapter 3 & 4**, I hypothesise that these differences will impact the restoration sites selected in different prioritisation scenarios, with different sites and seascape configurations selected among the scenarios.

# 5.2 | Methods

## *5.2.1 Workflow overview*

This restoration site selection framework integrates ecological theory with practical application through three interconnected components designed to optimise the outcomes of habitat restoration for both the habitat former and their associated assemblages within resource constraints (Figure 5.1). The workflow consists of three main steps: 1) data collection and field surveys, 2) predictive modelling including habitat suitability modelling for the target habitat forming species and assemblage modelling (in this case fish assemblages but can be applied more broadly to any associated assemblage), and 3) spatial prioritisation to identify optimal restoration sites and configurations (details on each section is described below). This approach addresses key restoration challenges by combining ecological assessment, predictive modelling, and systematic prioritisation to identify optimal restoration sites and configurations for both the habitat former and associated assemblages.

It is important to note that this framework focuses on the technical aspects of site selection and design. It exists within the larger restoration workflow/framework after the establishment of restoration objectives, priorities, and desired outcomes, a process which should involve extensive stakeholder and community engagement (Mace et al. 2007; Wilson et al. 2009; Lehtomäki and Moilanen 2013). As such, this framework serves as a decision-support tool not a decision-making tool. Decision-making and priority setting - the process of going from objective/outcome formulation to negotiating and implementing the final plan - is not discussed here as it usually involves stakeholder engagement and is highly specific to each individual case. However, this topic is covered extensively throughout the literature (Mace et al. 2007; Pressey and Bottrill 2009; Wilson et al. 2009; Runge 2011; Kukkala and Moilanen 2013; Lehtomäki and Moilanen 2013).

Here I demonstrate this process using a case study of seagrass restoration with the focus on ecological considerations to illustrate the integration of suitability modelling and spatial ecological understanding into restoration planning. Despite the examination of only one habitat type (seagrass) in this example, in practice, restoration planning should most likely integrate multiple habitat types simultaneously to maximise ecosystem-wide benefits, leverage complementary ecological functions, and promote facilitative processes (Bruno et al. 2003; McAfee et al. 2022; Vozzo et al. 2023; 2024).

The scenarios presented here (prioritising seagrass habitat suitability and various fish assemblage outcomes including total abundance, species richness, diversity, and proportion of juveniles) represent example prioritisation approaches that might align with different management objectives. For instance, prioritising seagrass habitat suitability may align with goals focused on ecosystem recovery, while fish-focused scenarios might serve recreational fisheries interests. These are illustrative examples rather than prescriptive recommendations, and actual implementation should involve stakeholder consultation to determine appropriate weightings and priorities based on local management priorities and values.

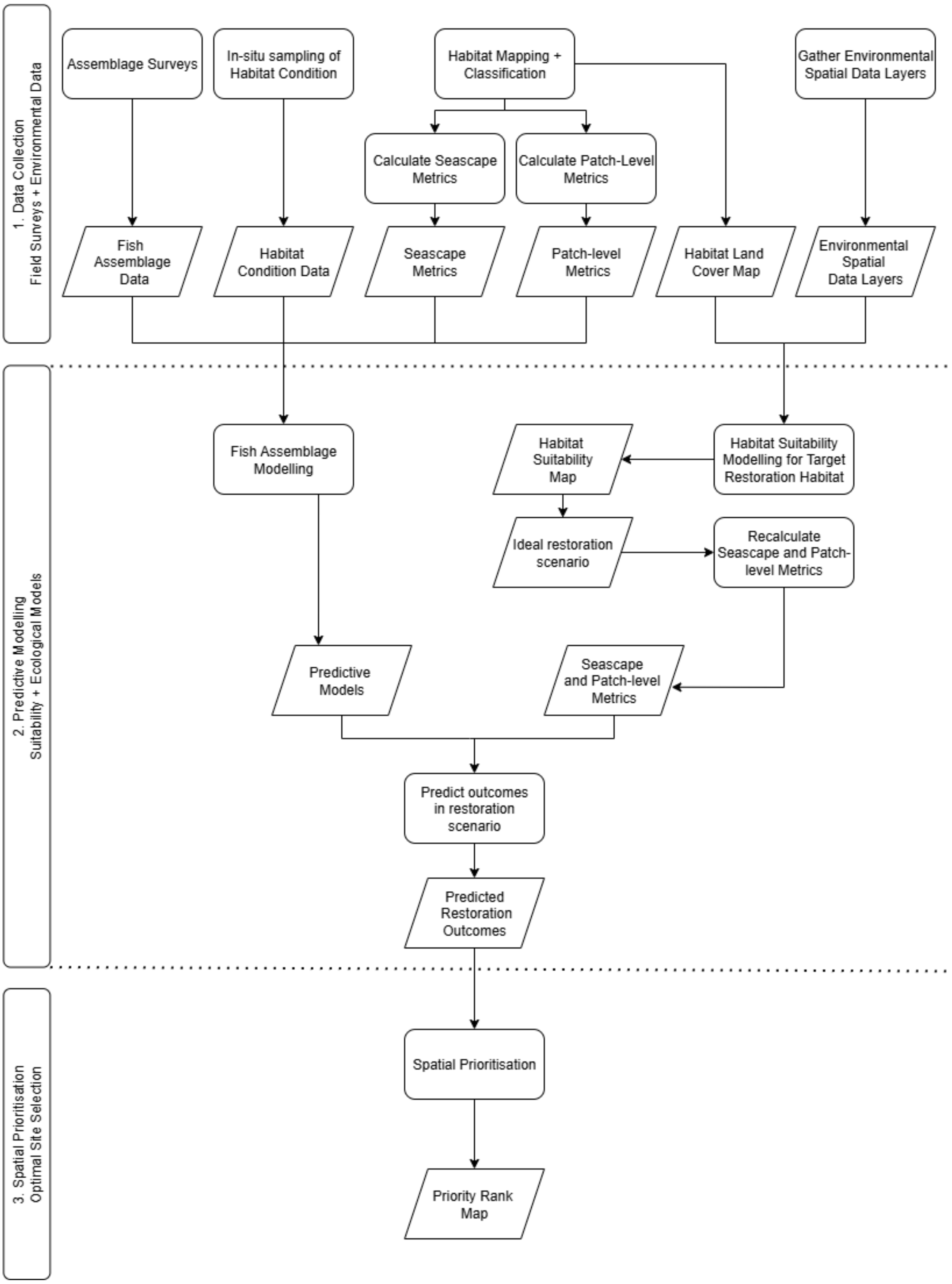


**Figure 5.1** – Overview of the analysis workflow comprising of three major components: 1) Data collection stage involving field surveys of assemblages and habitats alongside the collation of spatial environmental data. 2) Predictive modelling stage, where predictive models of the associated assemblage metrics are constructed and habitat suitability modelling for the target habitat is undertaken. 3) Spatial Prioritisation/Optimisation stage, where a prioritisation algorithm is used to identify priority restoration areas. Round boxes indicate methodological steps and rhombuses represent products from methodological steps. Each step of the workflow is explained in further detail bellow.

### 5.2.2 Study area

Port Stephens, a temperate tide-dominated drowned-valley estuary in New South Wales, Eastern Australia located within the *Port Stephens – Great Lakes Marine Park*, served as my study site to undertake this workflow (Figure 5.2). This study site was selected due to the availability of fish spatial survey data (See **Chapter 4**), extensive and robust estuarine habitat maps (NSW Department of Primary Industries 2021; West et al. 2025), in addition to a variety of in-situ water sampling points across a temporal and spatial distribution from which I could develop spatial data layers.

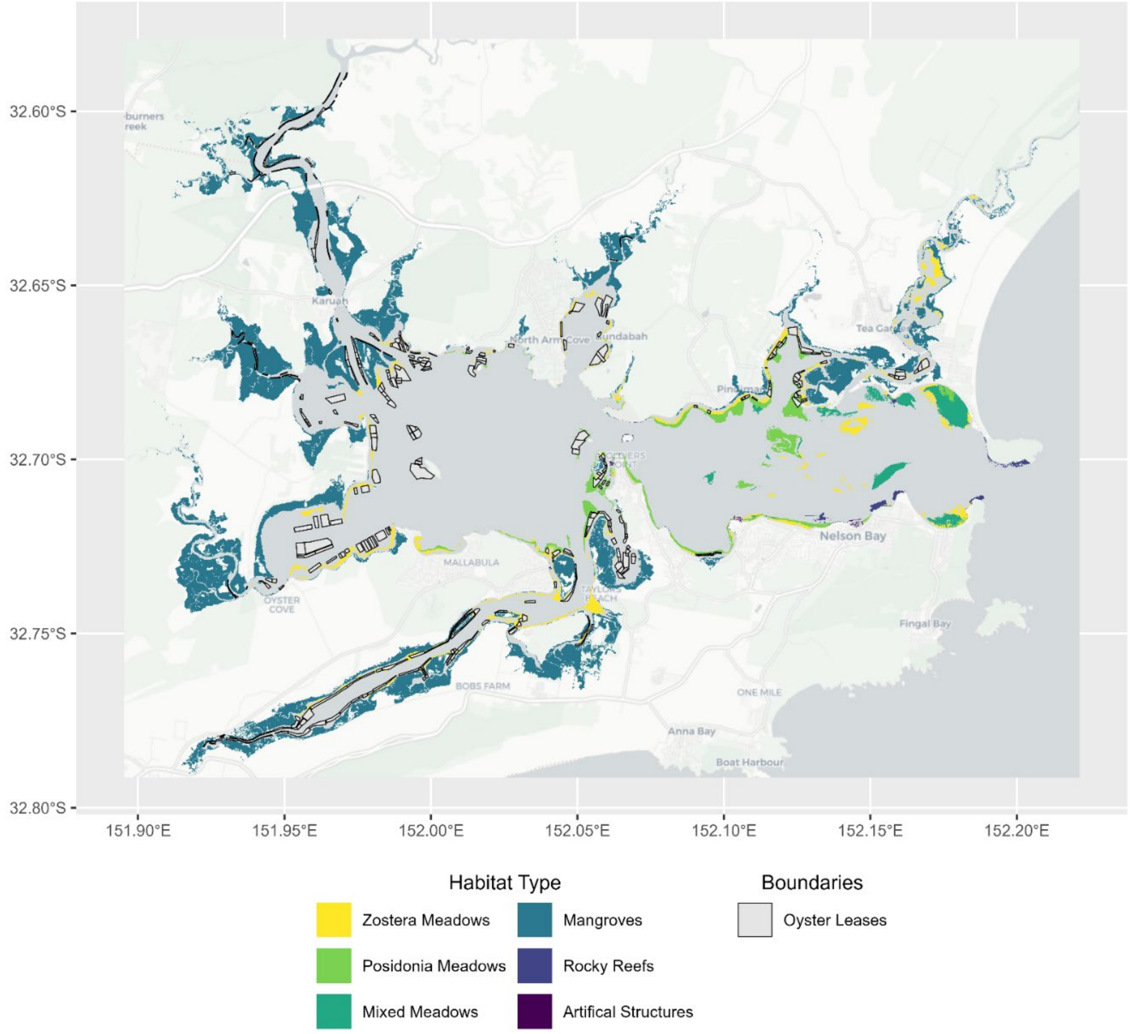


**Figure 5.2** - Map of Port Stephens Estuary (New South Wales, Eastern Australia; 32°41'44.0"S 152°04'18.2"E) with key estuarine habitats. Habitat Types mapped include: *Zostera capricorni* Meadows, Mixed Meadows, Rocky Reefs, *Posidonia australis* Meadows, Mangroves, Artificial Structures, and Oyster Leases.

## *5.2.3 Data collection/layers*

### 5.2.3.1 Biological data

#### *5.2.3.1.1 Fish surveys*

Fish assemblage data (abundance, species richness, diversity, and the proportion of juveniles within the assemblage) was collected using unbaited stereo-remote underwater stereo video across *Zostera capricorni* (Z. *capricorni*) meadows throughout Port Stephens (detailed methodology is provided in **Chapter 4** – Section 4.2.4). Critical to this stage is ensuring adequate spatial coverage and measuring key environmental and seascape characteristics that may influence associated assemblages. The quality and comprehensiveness of data collected in this component is important as it directly influences the reliability of subsequent modelling and prioritisation steps.

#### *5.2.3.1.2 Habitat mapping*

I obtained spatial data on the presence and distribution of *Z. capricorni* and other estuarine habitats (mangroves, mixed seagrass meadows, *Posidonia* meadows, estuarine rocky reefs, and artificial structures), artificial structures, and oyster leases throughout Port Stephens from NSW Department of Primary Industries spatial data portal (NSW Department of Primary Industries 2021; West et al. 2025).

### 5.2.3.2 Environmental covariates

I developed layers describing the environmental parameters, seascape, and focal patch characteristics of the study area derived from a variety of publicly and privately available datasets using a variety of different methods in line with best practices outlined throughout the literature (Table 5.1).

**Table 5.1** – Environmental Covariates developed for the habitat suitability modelling and predictive assemblage modelling.

| Predictor Variable | Unit | Explanation | Methods | Models Used In |
|---|---|---|---|---|
| Depth | m | Bathymetry Model | Sourced from (NSW Department of Climate Change, Energy, the Environment and Water 2025; NSW Office of Environment and Heritage (OEH) 2025) | Seagrass Habitat Suitability |
| Temperature | ºC | Median Temperature across 2.5 years prior and after habitat sampling period | GAM Prediction + In-situ bias correction as per Ahmed et al. (2025) | |
| Salinity | PSU | Median salinity across 2.5 years prior and after habitat sampling period | Spatio-temporal Kriging using the *spacetime* R package (Pebesma 2012) | |
| Turbidity | NDTI | Median turbidity across 2.5 years prior and after habitat sampling period | Landsat Remote Sensing Data | |
| Weighted Wind Fetch | Index | Cumulative effect of wind exposure across a water body, accounting for both fetch distance and the relative frequency of winds from different directions | As per (Rohweder et al. 2008) | |
| Intertidal Exposure | % | The percentage of time that any pixel within the raster is exposed to tidal inundation | Sourced from (Bishop-Taylor et al. 2025) | |
| Key Boating Channels | Categorical (0/1) | If the area is located within a key boating channel | Sourced from Transport NSW (2025) | |
| Boating Speed Limit Zones | Categorical | The maximum speed limit of an area within the estuary (4 Knots/8 Knots/ No Speed Limit) | | |
| Marine Protected Areas | Categorical | If the area is located within a marine protected area (No Protection/Habitat Protection Zone/Sanctuary Zone) | | |
| Distance to Mangroves | m | Closest distance to a Mangrove Habitat | Cost Distance Analysis | Seagrass Habitat Suitability + Fish Assemblage Prediction |
| Distance to Artificial Structures | m | Closest distance to any artificial structure | | |
| Distance to Mixed Seagrass Meadows | m | Closest distance to a Mixed Seagrass Meadow | | |
| Distance to Posidonia Meadows | m | Closest distance to a Posidonia Meadow | | |

| | | | | |
|---|---|---|---|---|
| Distance to Rocky Reefs | m | Closest distance to a Rocky Reef Habitat | | |
| Distance from the Estuary Mouth | m | Closest distance to the Mouth of the Estuary | | |
| Focal Patch Size | hectares | The size of the focal patch the camera is within for fish sampling | *Landscapemetrics* R package (Hesselbarth et al. 2019) | Fish Assemblage Prediction |
| Total Amount of Mangroves within the Seascape | Hectares | The area of Mangrove habitats found within a 300m buffer of the sampling point | | |
| Total Amount of *Z. capricorni* within the Seascape | Hectares | The area of *Z. capricorni* meadows found within a 300m buffer of the sampling point | | |
| Total Amount of Mixed Seagrass Meadows within the Seascape | Hectares | The total area of Mixed Seagrass meadows found within a 300m buffer of the sampling point | | |
| Total Amount of *Posidonia australis* within the Seascape | Hectares | The area of *Posidonia australis* meadows found within a 300m buffer of the sampling point | | |
| Total Amount of Rocky Reefs within the Seascape | Hectares | The area of rocky reef found within a 300m buffer of the sampling point | | |
| Landscape Fragmentation Index | Index | The level of seascape fragmentation found within a 300m buffer of the sampling point | | |

### *5.2.4 Predictive models for fish assemblage metrics*

Using the fish survey data (obtained in **Chapter 4**), I constructed predictive spatial models for four key fish assemblage metrics: abundance, species richness, diversity (measured as Shannon's H), and the proportion of juvenile fish within the population. I took a modelling approach that was more suited to prediction than the statistical inference that was used with this same data in **Chapter 4**. I used Random Forest models, a machine learning ensemble method well-suited for constructing predictive models with complex non-linear relationships among multiple variables while handling variable interactions and avoiding overfitting (Prasad et al. 2006; Cutler et al. 2007). Each of the four key fish assemblage metrics were modelled separately, with each as a response variable, with the seascape characteristics, focal patch characteristics, and environmental variables outlined in Table 5.1 as predictors. Prior to analysis, we removed highly colinear variables using a conservative Pearson correlation coefficient threshold of 0.65 as per Dorman et al. (2012). For correlated variable pairs, we retained the variable that captured the greatest variation and demonstrated the strongest ecological relevance based on domain knowledge and established literature (as per best practice outlined in Dorman et al. 2012). The number of trees (500) was selected based on stabilisation of out-of-bag error rates, ensuring model convergence and avoiding overfitting. I assessed model performance using 5-fold cross validation, evaluating predictions with spearman correlation coefficient between the observed and predicted values, root mean squared error (RMSE), and mean absolute error (MAE).

### *5.2.5 Seagrass habitat suitability modelling*

Various habitat suitability modelling approaches exist, each with distinct strengths and weaknesses depending on the scenario (Elith et al. 2006; Valavi et al. 2022). In this chapter, I selected a Maximum Entropy Modelling (MaxENT) approach, using the R package *dismo* (Hijmans et al. 2017), as it is particularly robust against model overfitting, handles complex variable interactions, and generally performs better than other types of SDMs (Araújo and New 2007; Elith et al. 2011). Environmental data layers used for suitability modelling were selected based on their importance to seagrass survival as expressed in the literature (Table 5.1; Aoki et al. 2020; Bertelli et al. 2022). Additionally, I included distance to various different habitats as a data layer (e.g., mangroves, mixed seagrass meadows, *Posidonia* meadows, rocky reefs; Table 5.1), as recent literature has suggested the importance of cross-habitat facilitative processes in determining suitability of a site for restoration (McAfee et al. 2022; Vozzo et al. 2023; 2024).

I assessed predictor variables for collinearity using Pearson correlation coefficients. Variables with Pearson correlation coefficients >0.7 were removed to reduce model overfitting and improve parameter estimation (Elith et al. 2006; Dormann et al. 2013; Valavi et al. 2022). I randomly partitioned the presence dataset into training (75%) and testing (25%) subsets before running the model. As the habitat mapping approach used by NSW DPI to generate the *Z. capricorni* habitat maps had comprehensive coverage across the entire estuary (NSW Department of Primary Industries 2021; West et al. 2025), I did not include a sampling bias layer in the habitat suitability modelling.

Model performance was evaluated using 5-fold cross-validation, with model fit assessed using the area under the receiver operating curve (AUC). AUC values above 0.9 indicate a model with excellent predictive power, 0.9-0.7 indicate good, and below 0.7 are considered models with poor predictive power (Jiménez-Valverde and Lobo 2007). I generated habitat suitability predictions for present day conditions across Port Stephens using the trained MaxENT model and environmental predictor layers (Table 5.1) with the *predict()* function (R Core Team, 2023).

### 5.2.6 Idealised restoration scenario development

I restricted the resulting seagrass habitat suitability map to the areas where the MaxENT model achieved optimal balance between sensitivity (true positive rate) and specificity (true negative rate) using the ‘spec sens’ sensitivity threshold in the *dismo* package (Hijmans et al. 2017). I then constructed an idealised post-restoration seascape assuming complete restoration of all suitable *Z. capricorni* habitat areas (as recommended in Moilanen et al. 2022). For this restoration scenario, I recalculated all spatial covariates (Table 5.1) and applied the random forest models to predict the fish assemblage metrics across the expanded *Z. capricorni* meadows.

### 5.2.7 Spatial prioritisation

To identify priority areas for *Z. capricorni* restoration based off seagrass habitat suitability and/or predicted fish outcomes I used *Zonation 5* (hereafter referred to as *Zonation*) spatial prioritisation software (Moilanen et al. 2022). *Zonation* uses spatial data on feature distributions (e.g., species distributions, abundance, habitats, ecosystem services etc.) to identify areas that should be prioritised for balanced outcomes, optimising outcomes across all input features (Moilanen et al. 2022). I chose *Zonation* over alternative approaches such as *Marxan*’s spatial annealing methodology (Watts et al. 2017) because of its robustness to small variations in the data and its flexibility - as it requires no pre-set targets or budgets - allowing decision makers more flexibility to explore different target/budget options without re-running analyses (Moilanen et al. 2022).

I used the Core Area Zonation marginal loss rule (CAZ2) for all prioritisation solutions. This rule ensures high average coverage of input features, at the cost of slightly reduced coverage for the worst-off features (Moilanen et al. 2022). In *Zonation*, I set retention values to 1 for areas with pre-existing *Z. capricorni* patches (representing full retention of feature layers without intervention e.g., pre-existing seagrass areas will continue to persist without intervention) and to 0 for all other areas (representing no retention without restoration e.g., no seagrass will be there without active restoration). As I did not have any data relating to the potential monetary cost of restoration throughout the study site, I assumed each cell had an equal monetary cost. The output of a *Zonation* spatial prioritisation analysis is a priority rank map, which ranks areas within the landscape from those that are the most important to restore (highest priority) to those which are the least important to restore (lowest priority; Moilanen et al. 2022).

### 5.2.7.1 Scenario development and prioritisation

I developed several restoration scenarios based on different hypothetical management priorities focused only on ecological considerations for the habitat former and their associated assemblage (Table 5.2). These scenarios were designed to illustrate how the prioritisation process can accommodate different management strategies and focuses, rather than to suggest optimal restoration strategies. First, I performed single metric prioritisation, where restoration sites were selected solely off individual metrics (habitat suitability, abundance, richness, diversity, or juvenile proportion). Second, I performed a balanced prioritisation scenario where all the metrics were included and weighted equally (‘*All Assemblage Metrics’;* Table 5.2). Third, I evaluated scenarios where all fish metrics and seagrass habitat suitability were included, but with varying relative weightings of the former against the latter (50-50, 40-60, 30-70, 20-80, 10-90). These approaches prioritise suitability for the habitat former while attempting to maintain some ecological benefits for the associated assemblage, balancing potential trade-offs. These weighting scenarios serve as examples of how different management contexts might approach prioritisation. For instance, restoration programs with limited budgets may emphasise seagrass habitat suitability to maximise the chance of establishment, while programs with a greater focus on fisheries goals may emphasise fish assemblage metrics. The flexibility to adjust these weightings within *Zonation* allows the framework to be adapted into diverse management contexts and stakeholder priorities. Only the 30-70 scenario is presented in the main body as it represents the median of this range of potential weightings, maps for all other weighted scenarios can be found in **Appendix D** (Figure D1 & D2). Using the priority rank maps developed in each of the scenarios, I selected the top 5th percentile priority areas to represent the final restoration sites selected for visualisations.

This spatial prioritisation analysis focused exclusively on habitat suitability and fish assemblage metrics as a demonstration of the framework's core functionality. I did not include other potential ecosystem services (e.g., erosion mitigation, carbon sequestration, larval supply/recruitment, sediment stabilisation, nutrient cycling) due to data limitations and the scope constraints of this study, though additional metrics could be accommodated when the data becomes available. Quantitative layers characterising cultural and social importance of locations were also not included for similar reasoning but could similarly be accommodated into the process if available. It is important to reiterate that priorities for restoration should be set in collaboration and discussion with key stakeholders and traditional land owners prior to beginning this process (Mace et al. 2007; Wilson et al. 2009; Pressey and Bottrill 2009; Runge 2011; Kukkala and Moilanen 2013; Lehtomäki and Moilanen 2013), and that different weightings for different components/layers within the analysis are ultimately arbitrary and should be set based off the values of the stakeholders and practitioners.

**Table 5.2** – Prioritisation Scenarios detailing the metrics prioritised within the scenario and their weights.

| **Prioritisation Scenarios** | **Relative Weighting** |
|---|---|
| Abundance Only | 100% |
| Richness Only | 100% |
| Diversity Only | 100% |
| Juvenile Proportion Only | 100% |
| Habitat Suitability Only | 100% |
| All Assemblage Metrics (Abundance, Richness, Diversity, Juvenile Proportion) | Equal (25% each) |
| All Assemblage Metrics (Abundance, Richness, Diversity, Juvenile Proportion) + Suitability | Equal (20% each) |
| All Assemblage Metrics + Habitat Suitability Weighted - 30/70 | Habitat suitability weighted 70%, all assemblage metrics weighted 30% (7.5% each) |

### *5.2.8 Comparison to restoration sites selected by a manager and between prioritisation scenarios*

To evaluate the various restoration scenarios generated from this framework against current restoration site selection practices, I established a baseline restoration scenario using expert judgement as a baseline for comparison. An independent fisheries scientist familiar with Port Stephens and seagrass ecology and restoration was asked to select potential restoration sites across the study site using traditional site selection approaches. The expert was provided with the same baseline spatial data layers used in my analysis to derive the *Zostera* habitat suitability map (Table 5.1) alongside maps outlining the distribution of estuarine habitats within the study site (Figure 5.2; (NSW Department of Primary Industries 2021), but was not given access to habitat suitability maps, predicted fish assemblage outcomes, or any prioritisation results to ensure a representative and unbiased site selection based on their expertise. They were instructed to select ~42 hectares of potential restoration sites (equivalent to the area encompassed by the top 5th percentile priority rank restoration solutions) using their professional judgement, experience, understanding of the target species, and local knowledge (Figure 5.5B). Once the sites had been selected for the by the seagrass researcher, I then applied the predictive assemblage models (Section 5.2.4) to estimate fish assemblage outcomes across the sites selected, creating a baseline scenario that are comparable to the framework outputs.

Statistical comparisons between different restoration scenarios were conducted using a one-way analysis of variance (ANOVA), with restoration scenario as a factor (e.g., traditional approach, single metric, balanced prioritisation, and weighted prioritisation). Individual cell-level predictions of fish assemblage metrics and seagrass habitat suitability served as response variables, with all cells from the selected sites within each prioritisation scenario included as replicates in the analysis. Additionally, for each scenario, I assessed both the fish outcomes predicted and seagrass habitat suitability for the areas selected in each scenario and the percentage difference of these values from the baseline scenario.

To visualise the differences between the various prioritisation scenarios I calculated the mean values of the predicted fish assemblage outcomes and seagrass habitat suitability values across all final selected sites (sites that ranked in the top 5th percentile of priority in the priority rank map). This mean was derived from cell-level predictions after recalculating seascape characteristics and focal patch metrics based on each scenarios' final seascape and were normalised by metric (to mean = 1) to enable comparison of relative performance across metrics that occur on different scales.

# 5.3 | Results

## *5.3.1 Zostera capricorni habitat suitability modelling*

The final *Z. capricorni* habitat suitability model included 9 predictors and had excellent predictive power with an AUC of 0.91 (**Appendix D –** Figure D3). Predicted suitability was generally higher in shallower regions of the estuary, particularly along the northern side and in the protected bay areas (Figure 5.3A). The high confidence distribution of *Z. capricorni* (as determined by the *spec sens* threshold) was more restricted, with areas of high suitability primarily focused around the northern bay and along the edges of the estuary (Figure 5.3B). The top five variables that were the most important (represented by percentage variable importance – out of 100%) in predicting habitat suitability of an area for *Z. capricorni* meadows were: depth (91.22%), distance from *Posidonia* meadows (1.99%), turbidity (1.78%), distance from mangroves (1.45%), and salinity (1.22%).

Habitat suitability decreased rapidly with depth down to 10m, with a rapid drop in suitability around ~4m of depth (Figure 5.4A) and was greatest within close proximity (0-100m) of *Posidonia*, changing little at greater distances (Figure 5.4B). In contrast, areas within about 10m of mangrove habitat were predicted to have decreased suitability (Figure 5.4C). *Z. capricorni* habitat suitability peaked at moderate levels of turbidity (around NDTI of 0) before dropping off at higher turbidity (Figure 5.4D). Lower turbidity levels were associated with decreased suitability from the peak, but greater suitability than highly turbid areas.

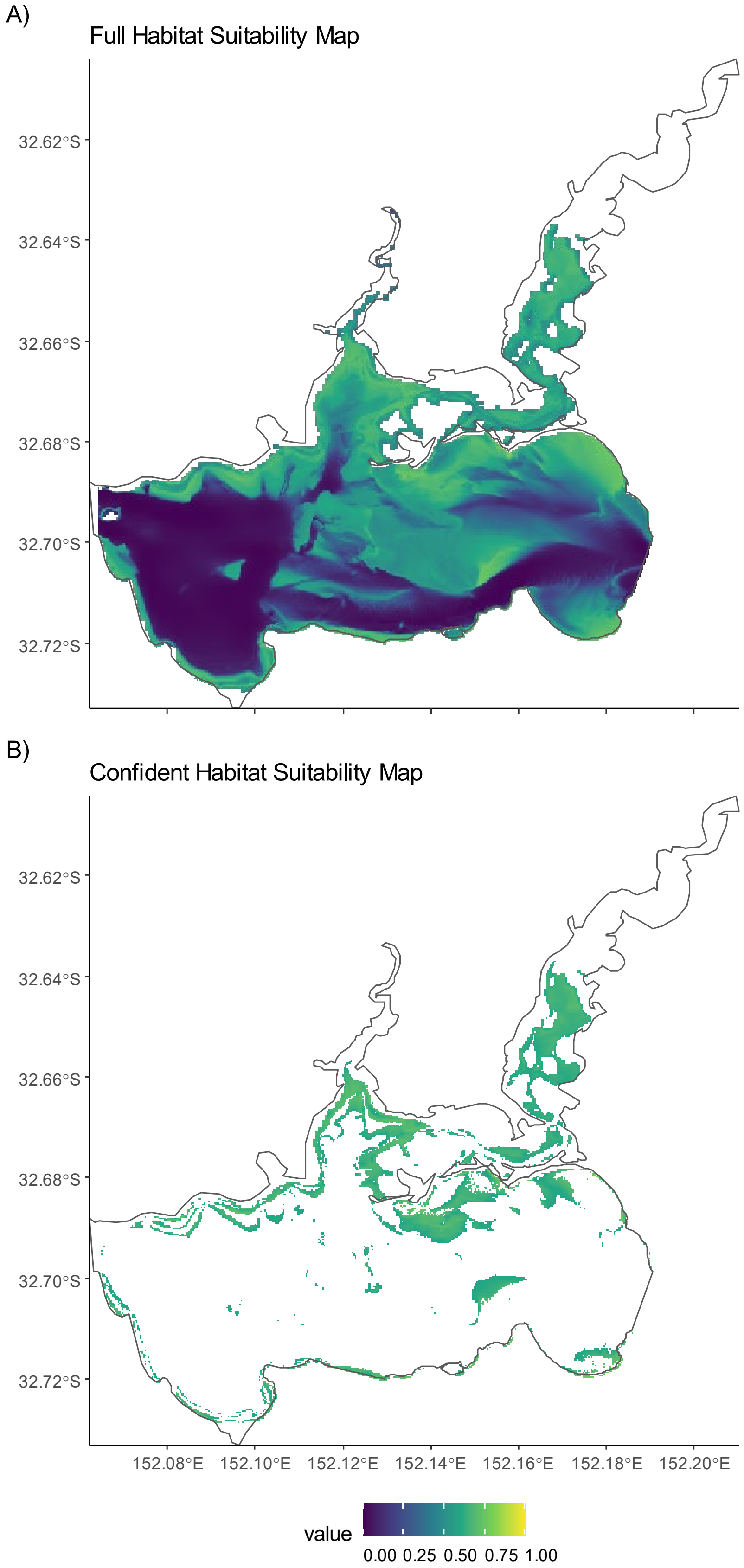


**Figure 5.3** – A) full *Zostera capricorni* habitat suitability map; B) areas with suitability values above the *"spec sens"* threshold (areas suitable for restoration).

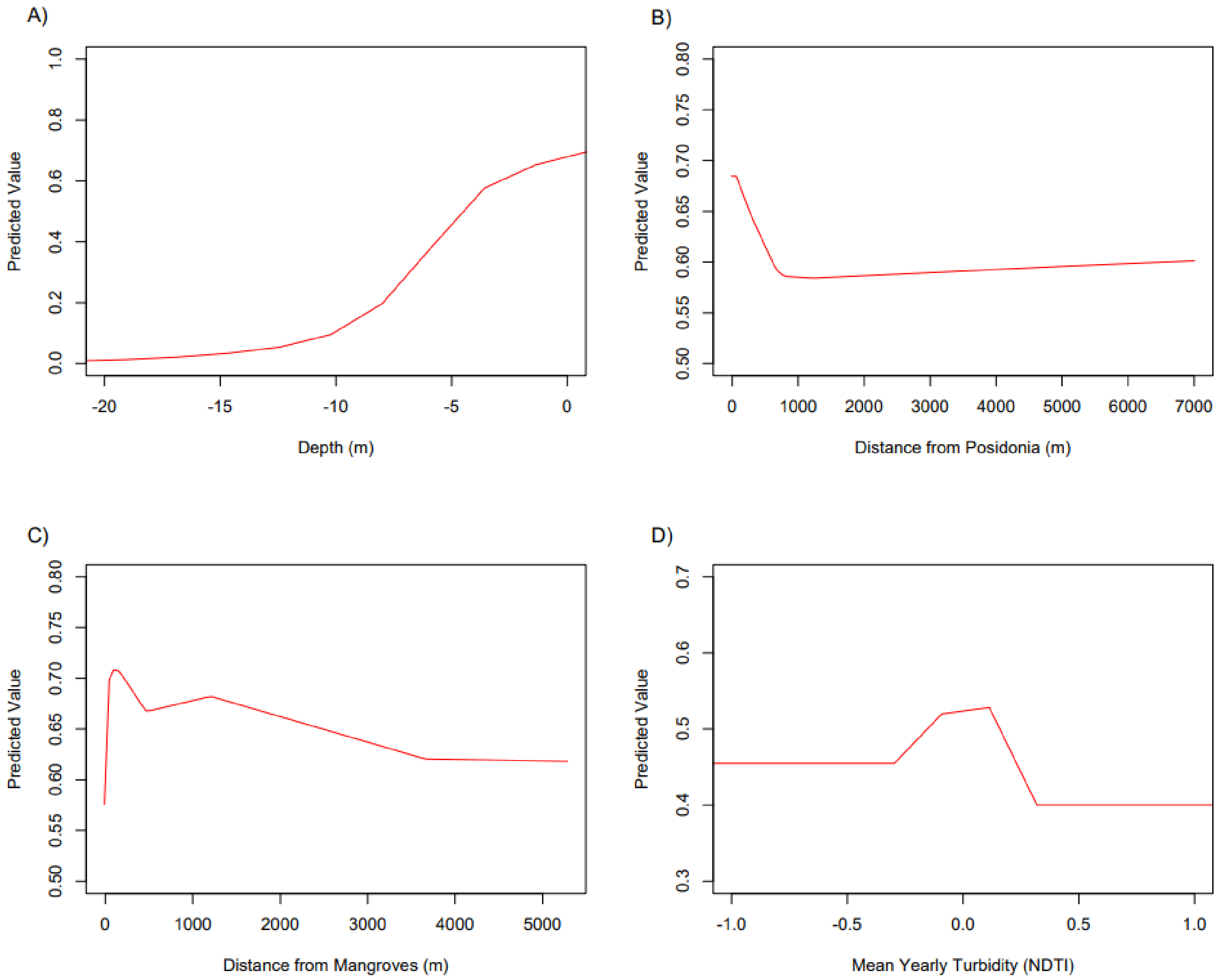


**Figure 5.4** - Response curves for selected environmental variables showing predicted *Z. capricorni* habitat suitability relationships with A) depth (m), B) distance from *Posidonia* meadows (m), C) distance from mangroves (m), and D) mean yearly turbidity (NDTI). Y-axes for each plot are scaled independently for ease of visualising patterns.

### *5.3.2 Predicted fish assemblage outcomes*

Under the full restoration scenario (Figure 5.5A), areas predicting the greatest abundance, richness, and diversity exhibited varying spatial patterns throughout the estuary (Figure 5.6A-C). The greatest abundance was predicted near the estuary mouth and within smaller patches in the central areas, with moderate abundance along the northern edge (Figure 5.6A). Species richness was highest in central patches and near the estuary mouth, with moderately high richness on the southern edge (Figure 5.6B). Diversity was greatest in patches near the estuary mouth and throughout the southern and middle sections of the estuary (Figure 5.6C). The distribution of the predicted juvenile proportion diverged from this pattern, being greatest in the Pindimar Bay region and along the northern side of the estuary (Figure 5.6D)

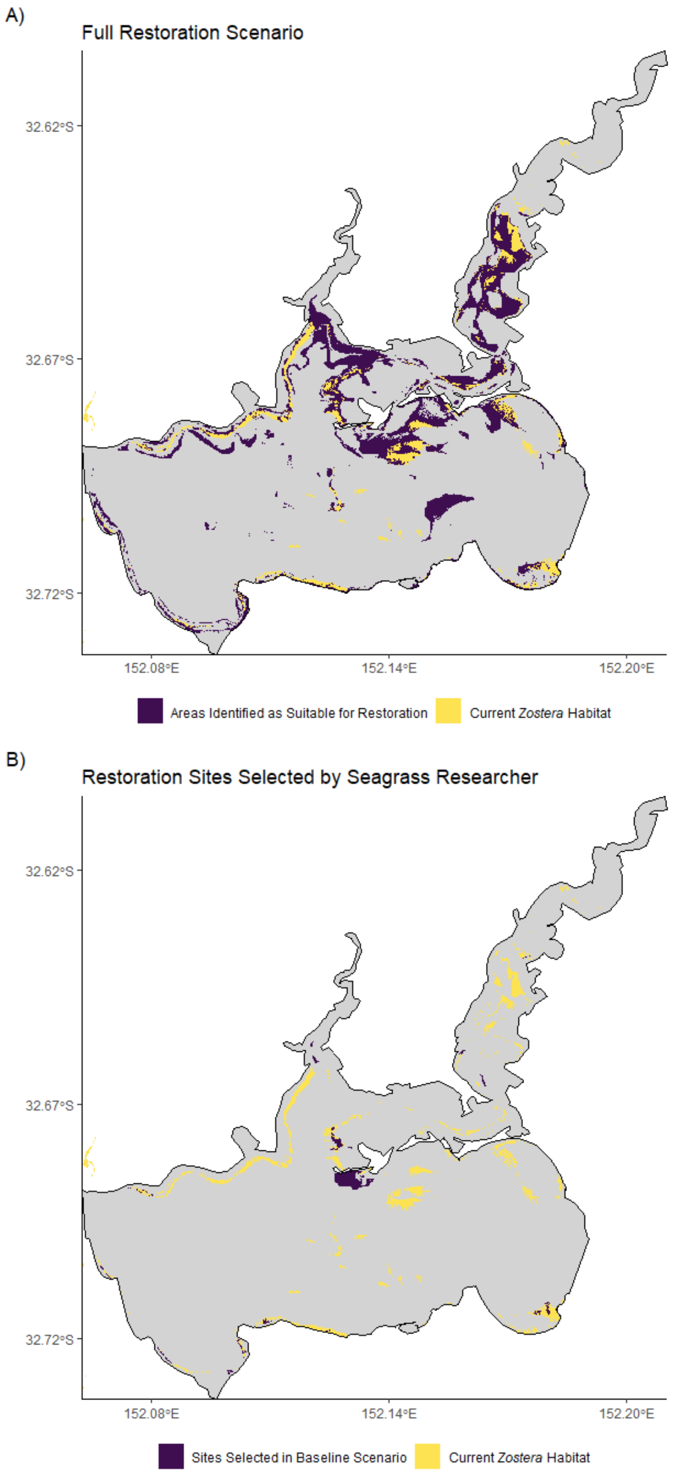


**Figure 5.5** – A) Map showing the full restoration scenario that was used for prediction and prioritisation. It combines areas with pre-existing *Z. capricorni* meadows (light colour) and the areas from the confident habitat suitability map (Figure 5.5; areas suitable for restoration; dark colour). This represents the idealised post-restoration seascape assuming complete restoration of all suitable *Z. capricorni* habitat areas (as recommended in Moilanen et al. 2022). B) Map showing the areas selected by the seagrass researcher familiar with the study site (baseline scenario; dark colour) used for comparison with the sites selected via the framework, alongside the current extent of *Zostera* meadows in the lower estuary (light colour).

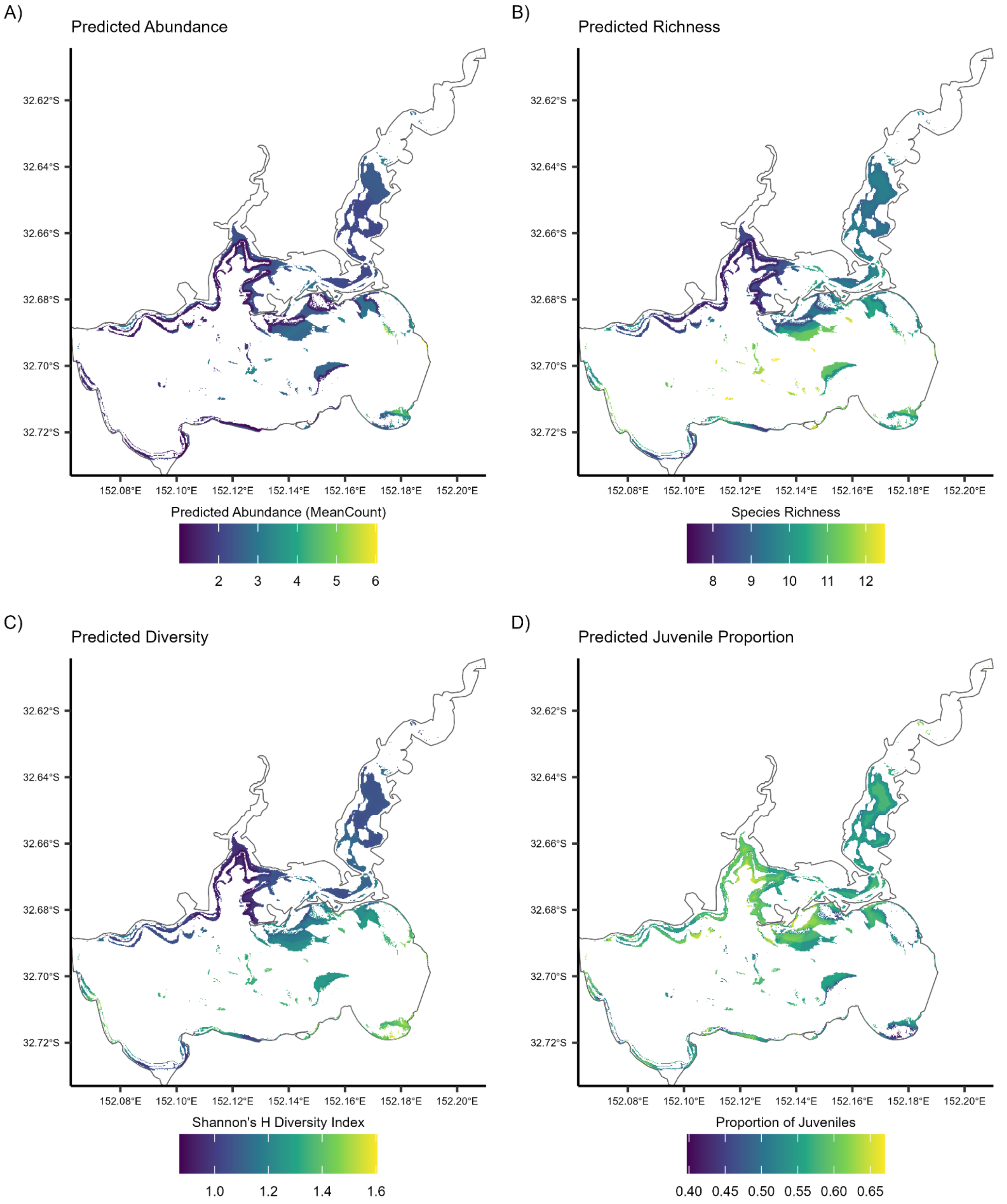


**Figure 5.6** – Maps showing the predicted values based off the full restoration scenario for four key fish assemblage metrics. A) Predicted Abundance. B) Predicted Richness. C) Predicted Diversity. D) Predicted Proportion of Juvenile Fish within the assemblage.

### 5.3.3 Priority rank maps

As predicted, prioritisation scenarios based upon single metrics generally reflected the spatial pattern of those metrics under the full restoration scenario (Figure 5.6 & 5.7). Priority areas for abundance, richness, and diversity only scenarios were concentrated in the lower-middle section of the estuary and southeastern areas (Figure 5.7B-C). The '*Juvenile Proportion Only*' scenario identified priority areas primarily in Pindimar Bay and along the northern estuary edge (Figure 5.7E). The suitability-only scenario followed habitat suitability patterns (Figure 5.3A), with highest priority areas around Pindimar Bay and estuary edges (Figure 5.7A). When considering the top 5% priority sites (>= 0.95 threshold), different prioritisation scenarios select distinct spatial arrangement of restoration sites (Figure 5.8).

The '*All-Assemblage Metrics'* scenario (Figure 5.8F) tended to converge towards the abundance, richness, and diversity only priority-rank maps (Figure 5.8B-D), as the maximum values for these metrics occurred in similar regions (Figure 5.6). The highest ranked areas tended to be in those regions due to the gains in those metrics being greater than the loss in juvenile proportion from not selecting those areas. When *Z. capricorni* habitat suitability was added ('*All Assemblage Metrics + Seagrass Habitat Suitability*' scenario), the high priority areas for restoration tended to be like that of the '*All-Assemblage Metrics'* scenario, but with more areas in the northern side of the bay, which had a higher level of habitat suitability (Figure 5.7G). When suitability was weighted more (70-30; Figure 5.7H), the priority-rank map tended to converge upon the map generated for the *'Seagrass Habitat Suitability Only'* scenario (Figure 5.7A). Although the final selected sites (top 5th percentile) varied in location (Figure 5.8A & H).

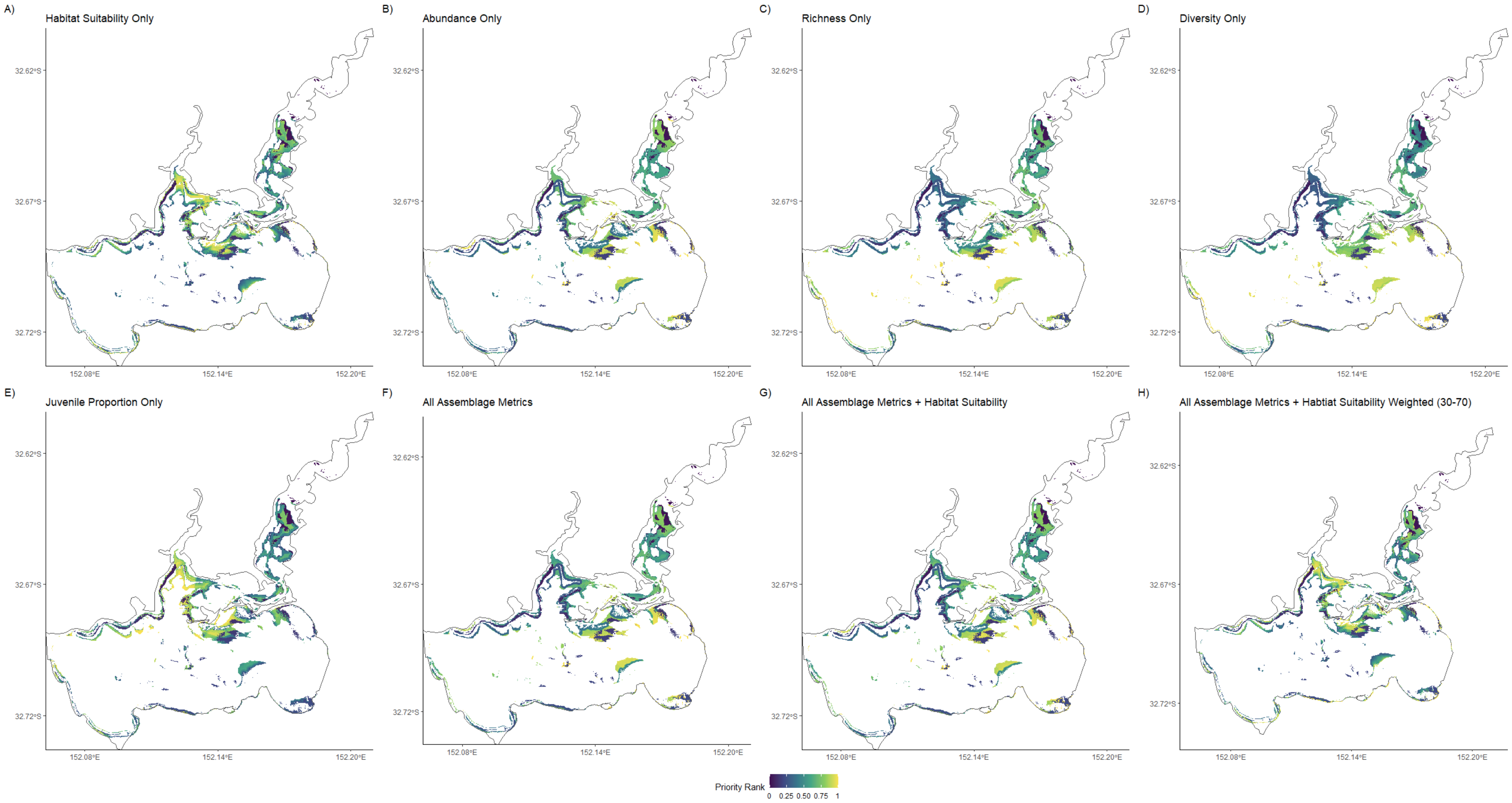


**Figure 5.7** - Priority rank maps for all the various single metric prioritisation scenarios. The rank of a cell (0-1) indicates the priority/order in which the cell should be restored.

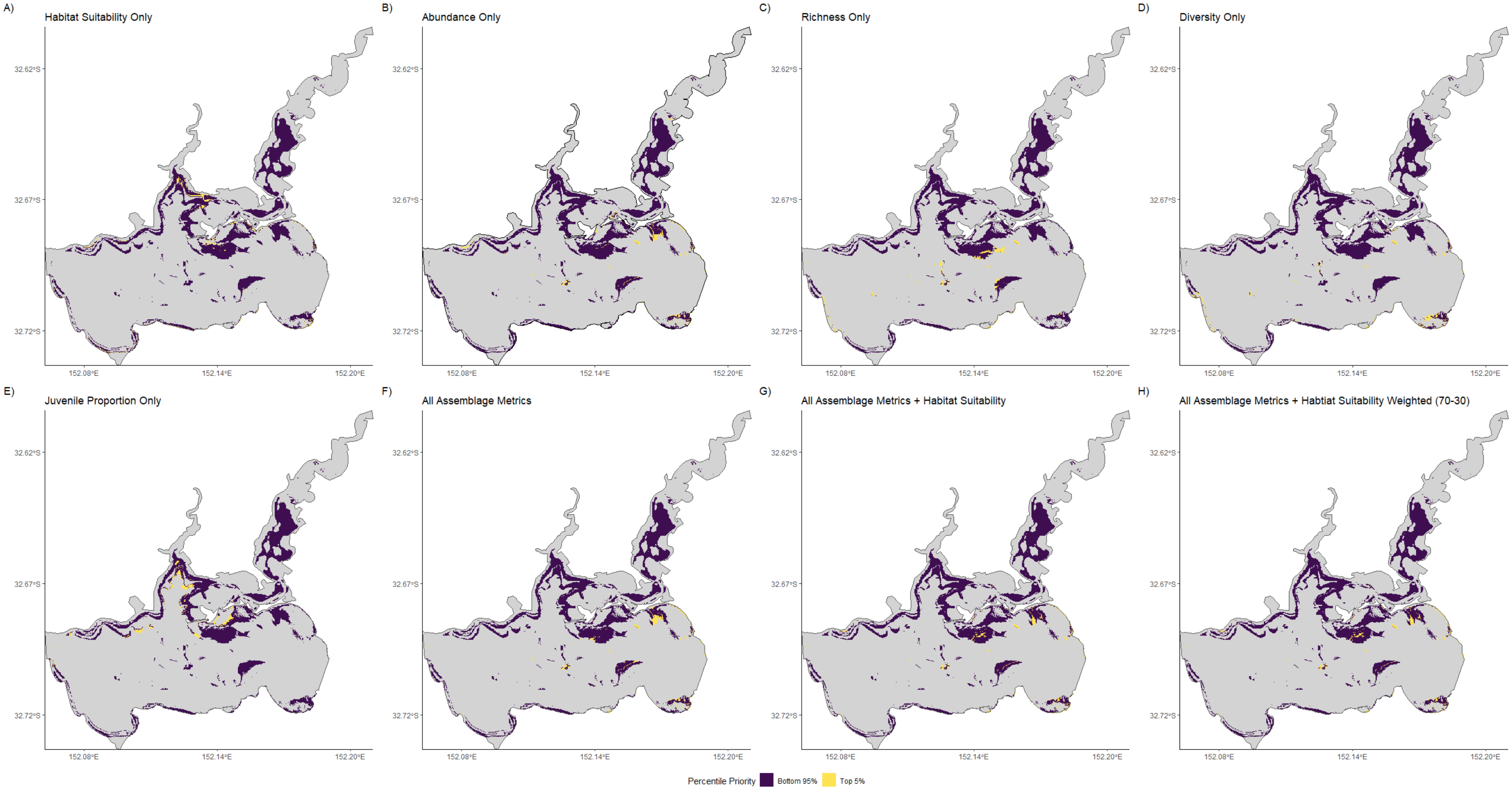


**Figure 5.8** – Final restoration sites selected as determined by the top 5$^{th}$ percentile priority ranks from Figure 5.7. Yellow areas represent areas selected (areas that were within the top 5$^{th}$ percentile of priority; Figure 5.7). Purple areas represent areas not selected.

### *5.3.4 Comparison among restoration prioritisation scenarios and to the baseline scenario*

The scenario that had the greatest average performance was the '*All Assemblage Metrics + Habitat Suitability*' scenario (Figure 5.9). However, targeted prioritisation of individual metrics (e.g., '*Abundance Only*' etc.) maximised predicted outcomes for those specific metrics (Figure 5.9). As all metrics got incorporated into the prioritisation process, the overall average performance and the balance of all outcomes increased at the expense of some individual metrics' performance (Figure 5.9). Furthermore, in both the unweighted scenarios considering all fish assemblage metrics (e.g., '*All Assemblage Metrics'* and *'All Assemblage Metrics + Habitat Suitability'*), juvenile proportion had the lowest predicted outcome of all assemblage metrics. As habitat suitability was weighted more, the predicted outcomes converged towards the *'Seagrass Habitat Suitability Only'* prioritisation scenario.

The restoration sites selected within different prioritisation scenarios differed greatly from the sites selected by a researcher with local knowledge of the system, with low percentage overlap between them (1.09 - 4.44%; Table 5.3). Furthermore, generally (except for juvenile proportion metric) all scenarios developed from the framework predicted better outcomes than the traditional approach (baseline scenario) with higher average performance across normalised metrics (Figure 5.9) and large differences in performance between the various metrics (Figure 5.10). The magnitude of improvement depended on which metrics were prioritised. The largest differences between the baseline scenario and the prioritisation solutions were observed for fish abundance (range = 6%-67%; Figure 5.10A). Additionally, the traditional site selection approach selected sites with a wider range of seagrass habitat suitability values and the lowest median and mean suitability compared to all other scenarios (Figure 5.11). While most traditionally selected areas were above the *'spec sens'* confidence threshold (0.581), this approach included some less suitable areas alongside generally suitable ones (Figure 5.11).

**Table 5.3** – Percentage overlap between the baseline Scenario and the various restoration site selection solutions derived from the integrated workflow.

| Scenario | Percent Overlap |
|---|---|
| Baseline (Traditional Site Selection Approach) | _ |
| Diversity Only | 4.44 |
| Abundance Only | 3.71 |
| All Assemblage Metrics + Habitat Suitability | 3.42 |
| Habitat Suitability Only | 3.22 |
| All Assemblage Metrics + Habitat Suitability Weighted (30-70) | 3.01 |
| All Assemblage Metrics | 2.93 |
| Juvenile Proportion Only | 2.74 |
| Richness Only | 1.09 |

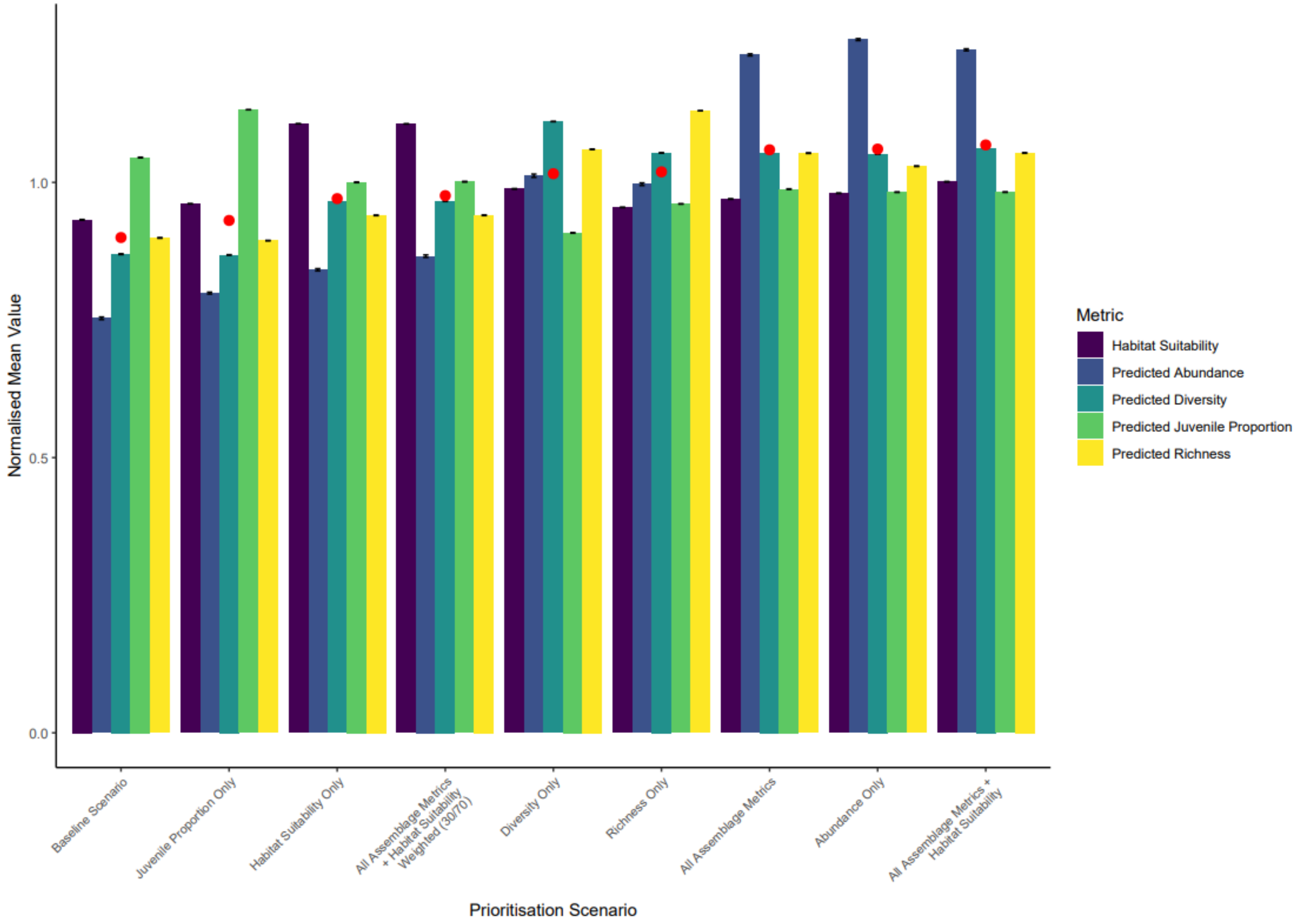


**Figure 5.9** – Normalised performance of restoration sites selected from different restoration prioritisation scenarios across multiple outcomes, where 1.0 = average performance across scenarios for each metric. Red dots show the overall average performance across all metrics for each scenario. Error bars represent the standard error. Scenarios are arranged by overall average performance from highest to lowest. Alternative visualisations that facet the values by metric are available in **Appendix D**.

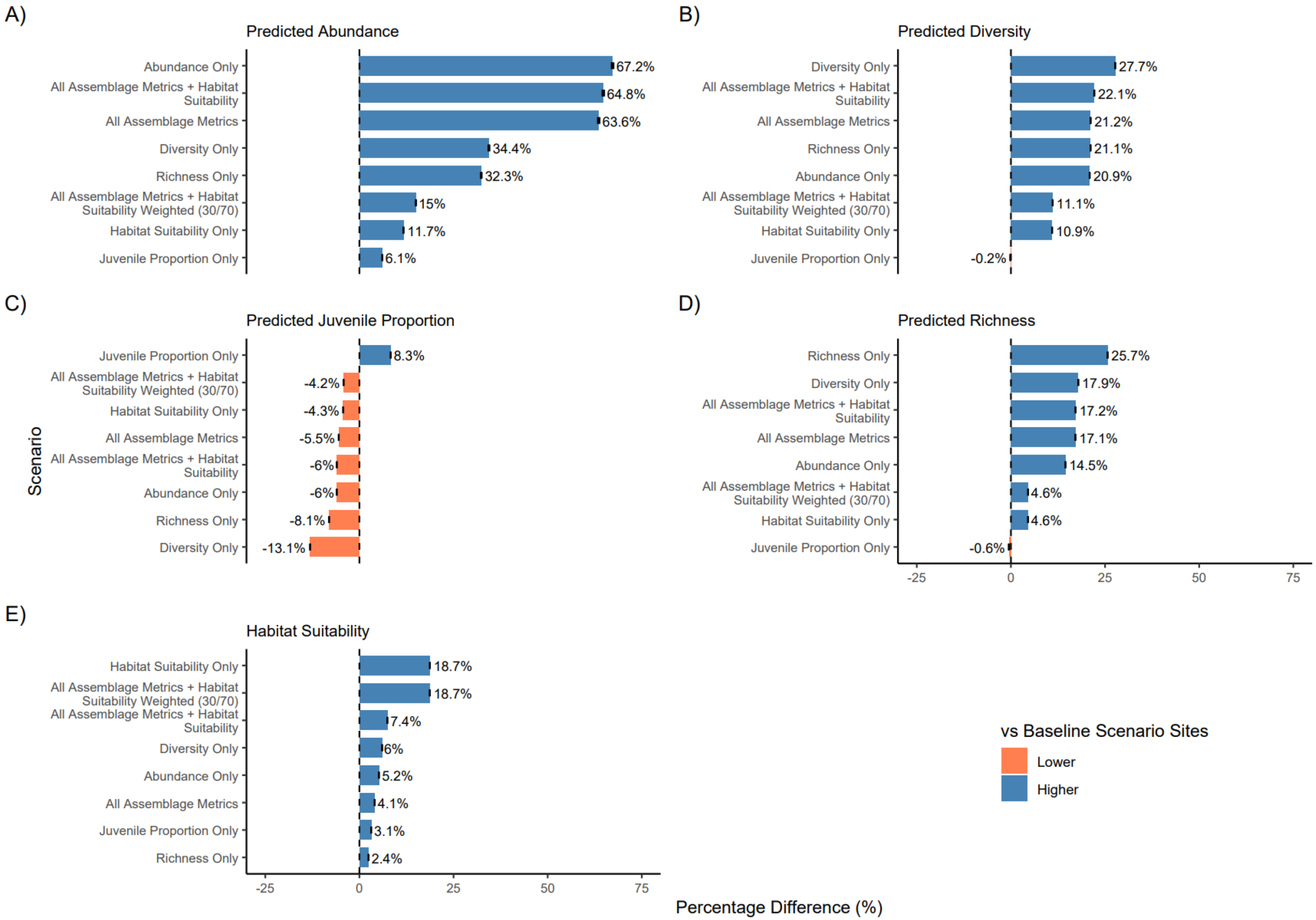

A)
Predicted Abundance
Abundance Only
All Assemblage Metrics + Habitat Suitability
All Assemblage Metrics
Diversity Only
Richness Only
All Assemblage Metrics + Habitat Suitability Weighted (30/70)
Habitat Suitability Only
Juvenile Proportion Only
67.2%
64.8%
63.6%
34.4%
32.3%
15%
11.7%
6.1%
B)
Predicted Diversity
Diversity Only
All Assemblage Metrics + Habitat Suitability
All Assemblage Metrics
Richness Only
Abundance Only
All Assemblage Metrics + Habitat Suitability Weighted (30/70)
Habitat Suitability Only
Juvenile Proportion Only
27.7%
22.1%
21.2%
21.1%
20.9%
11.1%
10.9%
-0.2%
C)
Predicted Juvenile Proportion
Juvenile Proportion Only
All Assemblage Metrics + Habitat Suitability Weighted (30/70)
Habitat Suitability Only
All Assemblage Metrics
All Assemblage Metrics + Habitat Suitability
Abundance Only
Richness Only
Diversity Only
8.3%
-4.2%
-4.3%
-5.5%
-6%
-6%
-8.1%
-13.1%
Scenario
D)
Predicted Richness
Richness Only
Diversity Only
All Assemblage Metrics + Habitat Suitability
All Assemblage Metrics
Abundance Only
All Assemblage Metrics + Habitat Suitability Weighted (30/70)
Habitat Suitability Only
Juvenile Proportion Only
25.7%
17.9%
17.2%
17.1%
14.5%
4.6%
4.6%
-0.6%
-25
0
25
50
75
E)
Habitat Suitability
Habitat Suitability Only
All Assemblage Metrics + Habitat Suitability Weighted (30/70)
All Assemblage Metrics + Habitat Suitability
Diversity Only
Abundance Only
All Assemblage Metrics
Juvenile Proportion Only
Richness Only
18.7%
18.7%
7.4%
6%
5.2%
4.1%
3.1%
2.4%
-25
0
25
50
75
Percentage Difference (%)
vs Baseline Scenario Sites
Lower
Higher

**Figure 5.10** – Percentage difference in the predicted outcome in assemblage metrics and habitat suitability for the selected restoration sites (based off the top 5th percentile priority ranks) across various restoration prioritisation scenarios compared to the baseline (seagrass researcher selected in a traditional qualitative manner) scenario for: A) Predicted abundance, B) Predicted diversity, C) Predicted juvenile proportion, D) Predicted species richness, and E) Habitat suitability. Blue bars indicate scenarios predicted to perform better than baseline scenario sites, orange bars indicate scenarios predicted to perform worse. Scenarios are ordered by magnitude of difference within each panel. The dashed vertical line at 0% represents performance equivalent to the baseline scenario sites.

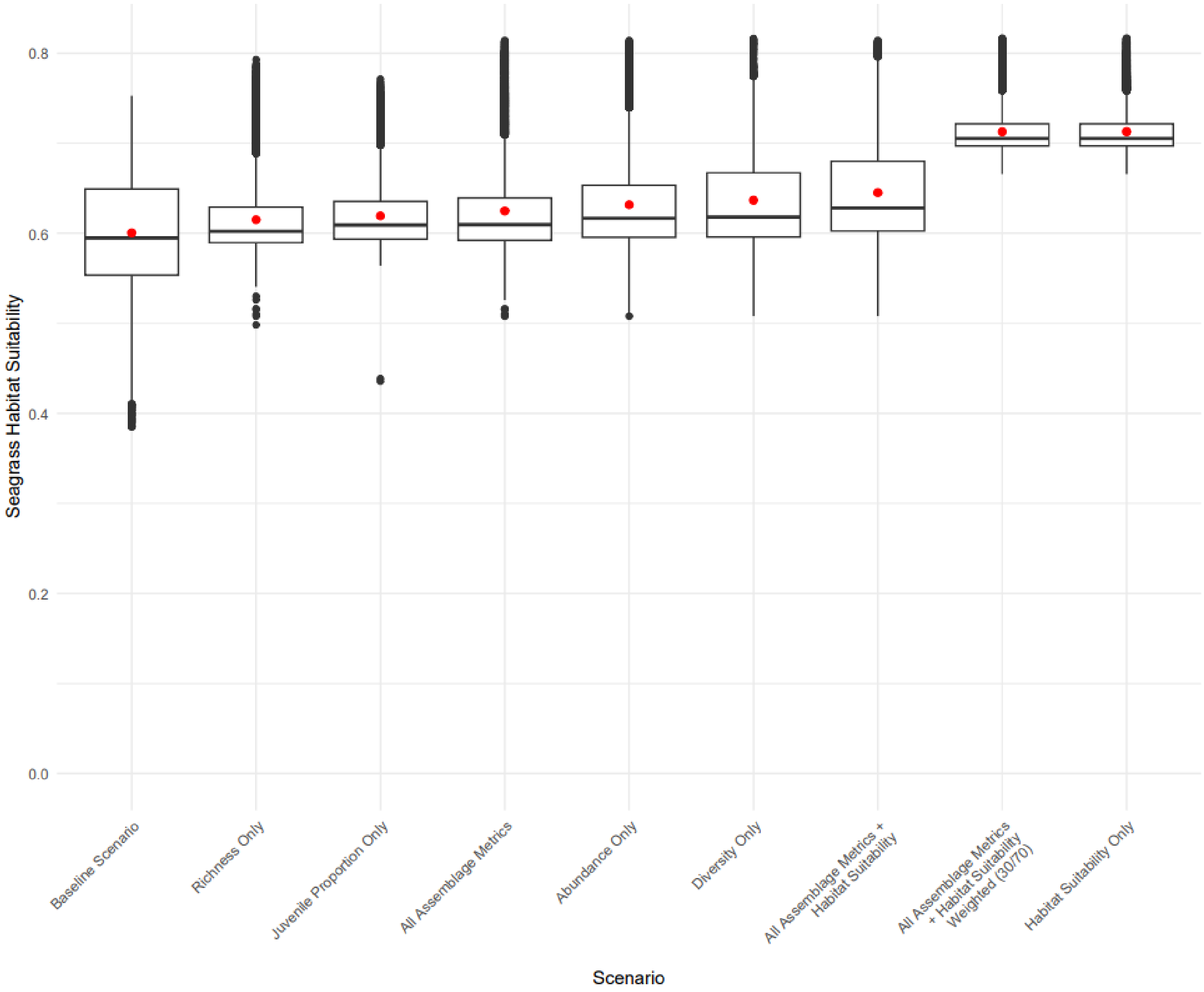


**Figure 5.11** – Distribution of *Zostera* habitat suitability values of restoration sites selected for the various prioritisation scenarios arranged by increasing median habitat suitability. Centre-line represents the median value. Red dots indicate the mean value. Lines extending from the boxes indicate distance from the interquartile range (IQR) to the minimum and maximum values observed. Black dots represent statistical outliers as defined by the formula: Quartile 1/3 +. 1.5*IQR.

## 5.4 | Discussion

This study demonstrates a novel systematic planning approach for marine restoration by developing an integrated framework that incorporates suitability for the habitat forming species with predicted assemblage outcomes alongside spatial prioritisation that supports decision making for restoration site selection (Figure 5.1). Using seagrass restoration as a case study, I've illustrated how a quantitative evidence-based framework can be applied to identify restoration sites that balance habitat suitability and ecological outcomes - fish assemblages in this case - according to different management priorities.

The results demonstrate that considering fish assemblages alongside habitat former suitability leads to significantly different restoration outcomes compared to approaches focused solely on the habitat forming species. This highlights the importance of incorporating seascape ecology and considering both the associated assemblage and the habitat former itself into restoration planning, as the broader seascape and its characteristics influence restoration outcomes. The case study showed that different restoration objectives - whether prioritising fish abundance, diversity, juvenile proportion, habitat suitability, or all metric together - result in different spatial configurations of selected sites, with significant trade-offs between predicted ecological outcomes.

Building on this seascape-informed approach, the integrated framework consistently outperformed traditional site selection approaches for all desired restoration outcomes except juvenile proportion. It achieved higher predicted values for fish assemblage metrics (Figure 5.10), while selecting areas with greater habitat suitability for seagrass (Figure 5.11). This demonstrates that the comprehensive integration of these previously separate approaches (habitat suitability modelling, assemblage prediction, and spatial prioritisation) has the potential to significantly increase restoration effectiveness and efficiency, delivering greater ecological returns when restoring a similar amount of habitat.

While this systematic approach represents a pathway to incorporate seascape ecology into restoration planning in a way that considers both the habitat former and their associated assemblages, optimal implementation requires integration with local/traditional knowledge, ground-truthing, and adaptive management to achieve optimal real-world outcomes (Stori et al. 2019; Lester et al. 2020). As such, it is important to emphasise that this framework and its products functions as a decision support tool which complements and enhances expert judgement throughout the decision-making process rather than being a decision-making tool. The priority rank maps, and restoration solutions should be used in conjunction with in-situ validation and ground-truthing of predicted suitable areas, collaboration with local practitioners and traditional knowledge holders familiar with site-specific nuances/conditions, and integration with existing planning processes and regulatory frameworks.

### *5.4.1 Outcome-specific spatial patterns in selected sites*

As demonstrated in the case study, different restoration objectives resulted in different spatial arrangement of restoration sites throughout the study area, with significant differences and trade-offs between predicted ecological outcomes (Figure 5.9 & 5.10). I hypothesised that based on the varying shapes and magnitudes of relationships between seascape characteristics and the fish assemblage metrics, in addition to the differing relative variable importance of the various seascape categories among fish assemblage metrics in **Chapter 4**, this may result in varying distribution and configuration of restoration sites selected by the framework. The results of the case study supported this hypothesis, as when scenarios prioritised different fish assemblage metrics or considered seagrass habitat suitability alongside fish assemblage metrics, the areas which were prioritised - and subsequently selected - for restoration varied significantly (Figure 5.7 & 5.8). This finding supports the growing notion within the literature that integrating seascape understanding into restoration design may increase outcomes, and suggest that restoration projects should be designed with these components in mind (Gilby, Olds, Connolly, Henderson, et al. 2018; Pittman et al. 2021; Wedding et al. 2025).

The juvenile proportion metric showed particularly distinct spatial patterns compared to other assemblage metrics (Figure 5.7 & 5.8), with the best areas predicted to be around Pindimar Bay (on the northern side of the study site), further illustrating how different ecological objectives can lead to different spatial solutions. This pattern may also explain why my framework underperformed relative to sites selected using the traditional qualitative approach (Figure 5.10), as that scenario had a large proportion of their proposed restoration sites within this region, thus leading to increased outcomes for the juvenile proportion metric. These results highlight the importance of clearly defining restoration objectives before applying a spatial prioritisation process, and illustrate that depending on an individual project’s goals, the location and configuration of restoration sites need to be tailored for that specific objective. As such, in the absence of generalisable solutions that optimise every metric at once, there is no “one-size fits all” solution when it comes to habitat restoration.

### 5.4.2 Trade-offs in ecological outcomes

The results of the case study supported my hypothesis that sites selected using seagrass habitat suitability modelling and a more traditional qualitative approach (the baseline scenario) would have lower outcomes for the key fish assemblage metrics than the scenarios incorporating these metrics directly (Figure 5.9). However, I also predicted that the scenarios incorporating fish assemblage metrics would also selects sites of similar seagrass habitat suitability to the '*Habitat Suitability Only*' scenario, which was rejected by the results (Figure 5.11).

Notably, the scenarios prioritising *Z. capricorni* habitat suitability (both weighted suitability scenario and the '*Habitat Suitability Only*' scenario) often showed significantly worse predicted fish assemblage outcomes than the other prioritisation scenarios (Figure 5.9). All scenarios except the *All Assemblage Metrics + Habitat Suitability Weighted (30-70)* scenario selected restoration sites with lower mean and median seagrass habitat suitability (Figure 5.9), indicating that focusing on assemblage metrics within the spatial prioritisation process may lead to trade-offs in site suitability for seagrass. Despite this, it is important to note that the areas that were candidates for selection (as specified in the idealised restoration scenario; Section 5.2.6) already occurred within regions of the estuary that the *Zostera* habitat suitability model was confident in. So, while there was still a gradient of suitability values within the candidate sites, from which the 'Habitat Suitability Only' scenario maximised, theoretically they are all still above the modelled threshold for *Zostera* suitability.

This highlights a potential management consideration where the trade-off between potential ecological benefits for associated assemblages must be weighed alongside the potential loss in site suitability for the habitat forming species. This issue was also present in the best performing scenario where all the fish assemblage metrics were equally weighted alongside suitability ('*All Assemblage Metrics + Seagrass Habitat Suitability*'). While this scenario was predicted to be the best solution for a project aiming to balance all outcomes, there may be a greater risk restoring those areas compared to the scenarios prioritising suitability more. These findings illustrate the importance of explicitly considering a project's risk tolerance and management priorities in restoration planning decisions, and that significant trade-offs occur when trying to optimise for singular or multiple criteria (for example, prioritising fish diversity led to the lowest predicted proportion of juveniles). Optimal approaches will depend on specific local contexts and constraints.

These trade-offs illustrate an important concern in restoration planning – the potential for creating ecological traps (Robertson and Hutto 2006; Hale and Swearer 2016). In this context, sites selected solely on the basis of physical suitability for seagrass/the habitat former may inadvertently create ecological traps for associated fauna if broader seascape characteristics are not considered. For example, a restored seagrass meadow in an otherwise suitable location might successfully establish and persist yet provide suboptimal habitat for fish assemblages due to unfavourable seascape configuration, lack connectivity to other habitats, or absence of key neighbouring habitat types. Indeed, this may explain the results observed in the case study, where the '*Habitat Suitability Only*' prioritisation scenario had significantly lower predicted fish assemblage outcomes than many of the other scenarios (Figure 5.9). By incorporating predicted assemblage outcomes alongside habitat suitability into the restoration planning process, this framework highlights the importance of considering multiple ecological dimensions to ensure that restored habitats deliver the intended ecological functions for both the habitat forming species and their associated assemblages.

### *5.4.3 Seascape influences as drivers of Zostera habitat suitability*

As expected, depth was a predictor that contributed the most to the suitability of an area for *Z. capricorni* alongside turbidity (the third most important predictor – though it explained little variance **Appendix D** - Table S1). This reflects seagrasses light requirements for photosynthesis that is critical for their establishment, growth, and persistence (Aoki et al. 2020; Bertelli et al. 2022). The influence of the structural connectivity measures (distance from *Posidonia* meadows and distance from mangroves; second and fourth most important predictors respectively) in predicting site suitability for *Zostera* suggests that suitability of an area for *Zostera* is influenced not only by local environmental conditions, but also the broader seascape. Distance from mangroves was the variable that contributed the fourth most to the seagrass habitat suitability model. I observed reduced suitability directly adjacent to mangroves (0-10m), with peak suitability occurring at intermediate distances around 100-200m away from the mangrove edge (Figure 5.4). Distance from *Posidonia* meadows contributed second most to the model, with peak suitability for *Z. capricorni* being in close proximity (0-100m) to *Posidonia* before declining and levelling out at greater distances (Figure 5.4). This finding further supports the recognition of the role that cross-habitat facilitative processes play in determining the suitability of an area for restoration (Bruno et al. 2003; McAfee et al. 2022; Vozzo et al. 2023; 2024), not only at a local-scale but at more broadly across the seascape (van de Koppel et al. 2015; Vozzo et al. 2023). The pattern observed for distance to *Posidonia* meadows likely reflects the wave attenuation capacity of *Posidonia* (and seagrasses more generally; (Fonseca and Cahalan 1992; Lowe et al. 2007; Donatelli et al. 2019), with the large three-dimensional structure of *Posidonia* being particularly effective at wave dissipation (Lowe et al. 2007; Infantes et al. 2012).

Since *Posidonia* typically occurs in slightly greater depths than *Z. capricorni* (Duarte 1991), it is often found on the seaward side of *Z. capricorni* meadows at the study site (Figure 5.2). As such, wave attenuation is likely one of the key facilitative processes that is increasing the suitability of the areas directly adjacent to *Posidonia.* Additionally, *Posidonia* is known to provide other facilitative processes such as sediment stabilisation (de Boer 2007; Contti Neto et al. 2022) and nutrient processing (Romero et al. 2006), likely further contributing to the suitability of the surrounding area. In contrast, areas near mangroves are often highly exposed during the low tide periods, are often highly turbid, have high levels of sediment accretion , and may be shaded more often by the mangrove canopy (Furukawa and Wolanski 1996; Lovelock et al. 2015). However, based off the results observed here, the influence of mangroves seems to be beneficial once outside the range of these deleterious effects, potentially increasing the suitability of the surrounding area for *Z. capricorni* through facilitative processes such as sediment dynamics (Furukawa and Wolanski 1996), nutrient processing (Mishra and Apte 2020), and animal/plant mediated facilitation (e.g., bioturbators oxygenating sediments; Bugnot et al. 2022).

These results indicate that restoration efforts may benefit from targeting sites that can leverage existing estuarine habitats with known beneficial facilitative processes (e.g., restoring *Zostera* on the shoreward side of *Posidonia* meadows) or by conducting simultaneous/sequential multi-habitat restoration to cultivate such processes as a part of restoration activities (e.g., restoring kelp next to oyster reefs as done by (McAfee et al. 2021). This supports the broader premise that restoration planning should move beyond single-habitat approaches towards seascape strategies that account for habitat connectivity and facilitative habitat interactions (Vozzo et al. 2023; 2024).

## *5.4.4 Limitations and considerations for implementation*

### 5.4.4.1 Model limitations and ecological constraints

While this framework demonstrates clear improvements over more qualitative practice (the baseline scenario), several important considerations emerge for real-world implementation. Despite the seagrass habitat suitability model showing an excellent level of predictive power (AUC = 0.91), the technique shares the same limitation as all habitat suitability modelling efforts in that it is important to consider why areas predicted to be suitable for the habitat may not have habitat there in reality. There are many possible explanations for this, but a few explanations for this mismatch may be previous habitat loss/degradation, model inaccuracy, and unknown variables influencing environmental suitability of a site.

Historical degradation and recovery lag may explain why some areas are suitable but currently unvegetated. Seagrass meadows may have been historically present but subsequently lost due to past disturbances that have since been remediated. However, natural re-establishment of these areas is often limited by biological constraints such as limitations in seed dispersal and slow recovery rates leave areas environmentally suitable but biologically inaccessible without active restoration intervention (Waycott et al. 2009; Unsworth et al. 2023). Ecological lag may mean that even when environmental conditions have returned to suitable levels, the time for natural colonisation may occur over an extended period of time - particularly in isolated areas or when source populations are distant (Barclay and Van Den Driessche 1975; Geist and Hawkins 2016). As such, active restoration is often necessary even in areas that appear environmentally suitable.

Another explanation may be that the habitat suitability model, while robust, lacks data layers representing extreme events or episodic/periodic disturbances that often influence site suitability (Smale and Wernberg 2013; Kendrick et al. 2019; Dunic et al. 2021). For example, the crescent-shaped area in the middle of the estuary was identified as being highly suitable for restoration but is regularly exposed to extreme sediment flux during storm events, burying existing meadows under sand (Daniel Swadling, pers. comm.). Such site-specific knowledge is difficult to capture in broad-scale environmental data layers without high resolution, high quality environmental monitoring programs, highlighting both the increasing need for comprehensive datasets to fill these critical gaps and successfully get the best out of these quantitative approaches.

#### 5.4.4.2 Limitations in comparing framework-selected sites vs. expert-selected sites

The comparison between framework-selected sites and traditionally selected sites (baseline scenario) is limited by sample size (n=1 expert), meaning that the "traditional" site selection approach is represented by a single individual's decision-making. While this researcher has experience in seagrass systems, site specific local knowledge, and the considerations regarding restoration design in the region, their site selection choices may not be representative of broader restoration practice and individual variation in expert judgement could substantially influence the comparison. Future work should expand this comparison by engaging multiple researchers and restoration practitioners to select sites independently, generating a more robust sample of expert-selected sites that better captures the variability in traditional site selection approaches. Despite this limitation, the comparison still provides valuable insights into how systematic frameworks can complement expert judgement (and vice versa) in restoration planning.

### 5.4.4.3 Integration of local knowledge and expertise

The comparison between researcher-selected sites and my model predictions reveals complementary strengths that highlight the value of local expertise in practical implementation of quantitative restoration workflows. The researcher familiar with the study site avoided certain areas identified as suitable by the model (for example, regions near Tea Gardens; Figure 5.3A) due to knowledge of site-specific factors not captured in environmental datasets – such as frequent dredging operations and persistent flood impacts. This local knowledge represents variables that are "unknown-unknowns" (factors that significantly influence restoration success but are not captured in environmental datasets), which are often invisible to purely quantitative modelling approaches. This demonstrates how local knowledge can assist in identifying factors not captured in available environmental datasets.

Conversely, the systematic approach identified opportunities that expert judgment alone might overlook, particularly in balancing multiple ecological outcomes simultaneously. The complementary strengths of both approaches suggest that optimal restoration planning requires integration of systematic analysis with local expertise. These limitations underscore the fundamental challenge that modelling frameworks have, where their effectiveness is constrained by the quality and quantity of available environmental and assemblage data, a critical bottleneck in the widespread adoption of quantitative restoration planning approaches. Together, both the comparison to the selected baseline scenario sites and the seagrass habitat suitability map demonstrate that while the framework provides potential powerful analytical decision-support capabilities, effective implementation requires practitioners with local expertise to interpret results and navigate site-specific considerations that cannot be captured in spatial models.

### 5.4.4.4 Data requirements as foundation for success

The importance of high resolution and high-quality spatial datasets in these workflows is not to be understated. Predictive processes, modelling approaches, and spatial prioritisation are extremely reliant upon the accuracy, reliability, and availability of input data to ensure robust modelling of outcomes and habitat suitability (Anderson et al. 2016). One of the biggest barriers to the widespread adoption of a framework like the one described here, is the limited availability of these datasets in marine systems, particularly in estuaries (Ganju et al. 2016), despite repeated calls throughout the literature for investment in this area (Cloern et al. 2016; Ganju et al. 2016). Estuarine systems are under extreme impact due to the compounding pressures of anthropogenic effects and anthropogenic climate change and exhibit high spatial and temporal variability (Gillanders et al. 2011; Cloern et al. 2016; Scanes et al. 2020), and as such these systems require comprehensive high-resolution data for effective modelling and restoration planning (Cloern et al. 2016; Ganju et al. 2016). Spatial resolution of these datasets should match the scale of restoration interventions, while the temporal resolution must capture both seasonal variation and interannual trends in key environmental parameters. Datasets that span multiple time periods to characterise environmental variability and capture extreme events are particularly limited (Cloern et al. 2016; Ganju et al. 2016; Rezek et al. 2019), yet are essential for predicting long-term habitat suitability underneath changing environmental conditions (Hirzel and Le Lay 2008; Bertelli et al. 2022; Dalby et al. 2025). Investment in comprehensive environmental monitoring programs throughout marine systems is therefore critical if practitioners and managers are to implement quantitative restoration planning approaches into practice. Despite these challenges, when adequate data is available, the implementation of a framework such as the one described in this chapter has many broader implications that extend beyond just improving restoration success and outcomes.

## *5.4.5 Broader implications*

### 5.4.5.1 Economic implications and cost-effectiveness

The framework’s ability to systematically identify sites with higher predicted outcomes for the habitat former alongside the associated assemblage has important economic implications for restoration programs operating under budget, time, and personnel constraints. By targeting areas that maximise ecological return on investment while balancing losses within other criteria, mangers can potentially achieve greater restoration outcomes per dollar spent compared to more qualitative opportunistic restoration site selection. However, implementing the framework would require upfront investments in spatial data acquisition, modelling expertise, and validation. While these initial costs may seem substantial, the potential for increased restoration success and enhanced ecological outcomes may result in favourable long-term cost-effectiveness.

#### 5.4.5.2 Adaptability and transferability

While I used seagrass as a case study, this framework is broadly applicable across marine and terrestrial restoration contexts. The core components (habitat suitability modelling, associated assemblage prediction incorporating seascape understanding, and spatial prioritisation) could be adapted to any system where adequate environmental data and species abundance/occurrence information is available. Additionally, the multi-criteria optimisation component of the spatial prioritisation process is particularly valuable for restoration projects attempting to target multiple outcomes simultaneously.

The spatial prioritisation processes' flexibility allows for system-specific and project-specific modifications while maintaining the core systematic approach (Moilanen et al. 2022). This adaptability allows managers to incorporate diverse objectives based on local priorities and available data. For example, different outcomes associated with ecosystem services the habitat provides could potentially be incorporated (e.g., carbon sequestration, water quality improvements, erosion mitigation), fish species distribution models, larval dispersal models, or cultural and social values (e.g., traditional ecological knowledge, recreational fishing importance, cultural heritage sites) into the prioritisation process, though such applications would require validation and adaptation to local contexts.

#### 5.4.5.3 Scalability

This frameworks scalability and implementation feasibility largely depends on data availability. In data-rich areas, with extensive environmental and assemblage monitoring programs, immediate implementation may be possible with existing datasets. However, in data-poor area, baseline environmental monitoring and surveys may be required before carrying out this process (Figure 5.1. Step 1). Regional adaptation would require consideration of local environmental drivers, species assemblages, and restoration practices. For example, tropical seagrass systems might require different environmental predictors (e.g., proximity to coral reefs, cyclone impacts) compared to temperate systems. The framework's modular design facilitates these adaptations while maintaining the core spatial prioritisation approach.

## *5.4.6 Future directions*

### 5.4.6.1 Integration with climate change projections

Incorporation of climate change projections into the habitat suitability models (as done by Dalby et al. 2025), will be critical going forward in order to ensure the long-term viability of potential restoration sites, and should be incorporated into restoration projects. As environmental conditions continue to change, restoration sites must be selected not only for their current suitability but also for suitability in current conditions. The spatial prioritisation component of the framework could also account for this (if a project wishes), where current and future suitability could be incorporated as prioritisation layers to identify areas suitable both now and in the future.

In estuarine environments, the complex interplay between sea level, depth, temperature, runoff from increased wave events make modelling environmental conditions under climate change scenarios difficult, as it requires more sophisticated approaches than simple additive changes to individual parameters (e.g., +2°C to temperature or +4m to depth). Despite this complexity, due to the importance of considering the suitability of areas for restoration under current and potential future scenarios, it is critical that extra funding and research be put into developing models of estuaries under climate change scenarios.

### 5.4.6.2 Limitations of current spatial prioritisation tools

Current spatial prioritisation processes like *Marxan* and *Zonation* (used here), while powerful for conservation planning, present limitations when applied to restoration contexts (as done in this framework) as they were not designed specifically with application intention in mind (Kukkala and Moilanen 2013; Watts et al. 2017; Moilanen et al. 2022). These tools require the establishment of an ideal “full restoration scenario” from which the restoration solution is derived in order to function effectively. But this process can’t dynamically update predictions based upon restoring a subset of the full restoration scenario or design optimal spatial arrangements when managers specify a target restoration amount (e.g, “restore 10 hectares”). This represents a significant gap between restoration planning needs and available computational tools. Future research could explore more advanced computational approaches that can directly optimise restoration site and patch design given area constraints. Machine-learning based approaches like graph neural networks combined with an iterative learning algorithms offer promising potential for addressing this challenge but require significantly greater computational power and volume of data (Zhou et al. 2020). Such developments could enable managers to input their available restoration budget or area targets and receive optimised spatial designs that maximise ecological outcomes within those constraints with a greater degree of accuracy than my outlined approach. Developing these next-generation tools would represent a significant advance beyond current practice, moving from having to set a pre-defined restoration scenario and predicting from there, to dynamically generating optimal restoration designs.

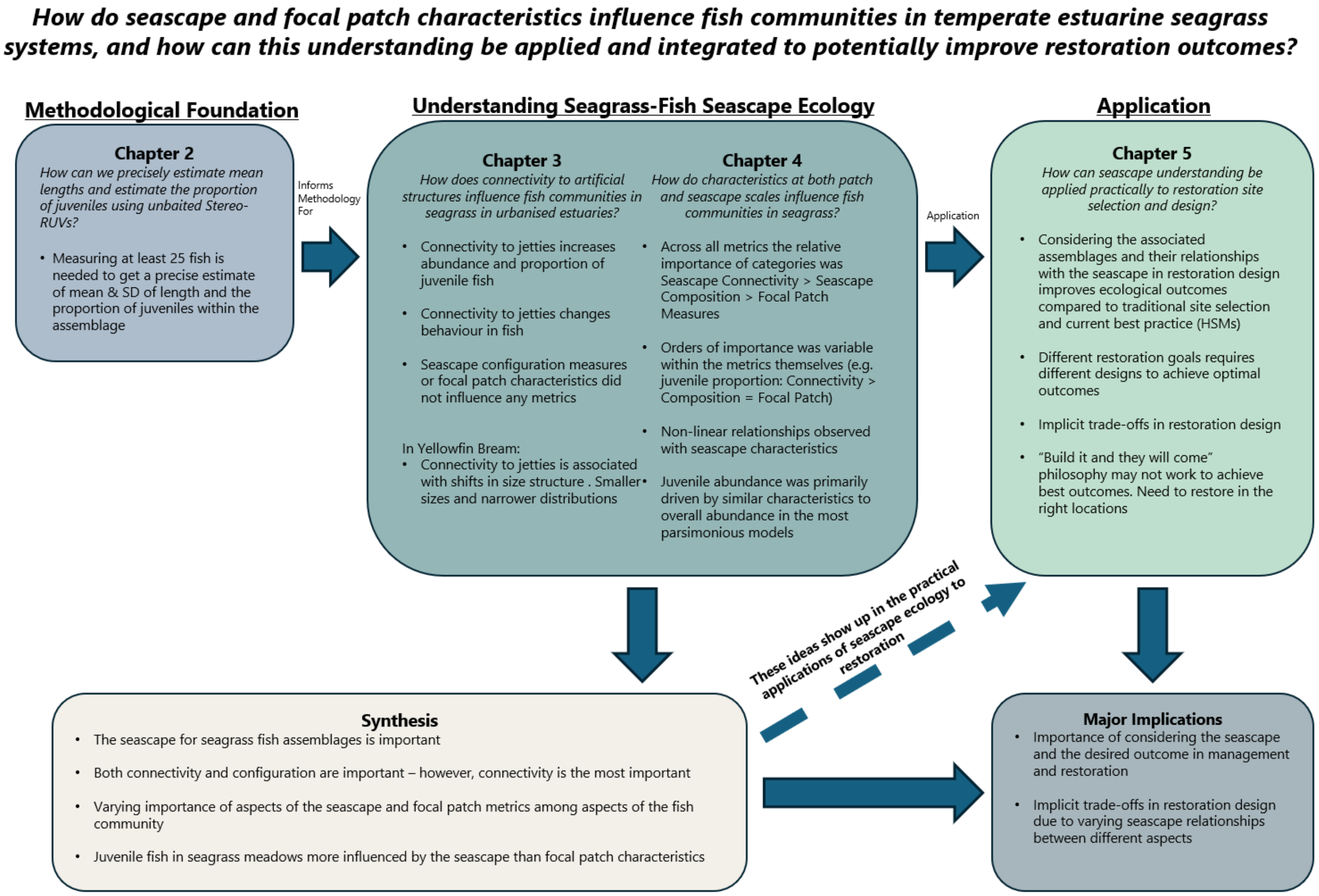
## 5.5 | Conclusion

This study outlines a decision-support framework for restoration site selection that integrates habitat suitability modelling for the target habitat forming species, predicted outcomes for associated assemblages that incorporates seascape understanding, and spatial prioritisation to quantitatively identify sites based on a set of user-defined priorities. The results of the case study indicate that it is important to consider the seascape in restoration site selection, as different locations were associated with increases or decrease different key assemblage metrics. Additionally, different prioritisation scenarios showed trade-offs between competing restoration goals, particularly between areas optimising specifically for habitat suitability versus those optimising for assemblage outcomes, highlighting the need for practitioners and managers to clearly define restoration objectives and consider trade-offs in consultation with stakeholders before site selection.

Incorporating both seagrass habitat suitability and fish assemblage metrics informed by seascape understanding into restoration planning showed increased overall average performance compared to the baseline approach and current best practice (selecting restoration sites based on habitat suitability modelling alone), emphasising the need for restoration to shift to more landscape/seascape aware strategies that recognise the complex, multi-scale nature of these systems. In the comparison with sites selected by a seagrass researcher familiar with the local study site a traditional more qualitative approach (the baseline scenario), the framework-selected sites achieved 7-65% better predicted fish assemblage outcomes while simultaneously selecting areas with higher habitat suitability. However, further comparison highlighted the value of local expertise in identifying site-specific constraints invisible or unquantifiable to quantitative modelling approaches. As such, the framework’s strength lies not in replacing expert judgement and local knowledge, but in systematically balancing multiple objectives that are difficult to optimise simultaneously through qualitative approaches alone.

While my approach offers a pathway to integrate seascape ecology into restoration planning in a way that considers both the habitat former and their associated assemblages, optimal implementation requires integration with local knowledge, ground-truthing, and adaptive management cycles. Moreover, the transferable nature of this approach suggests broad applicability across marine and terrestrial systems where adequate environmental and species data is available. As the demand for habitat restoration grows amid accelerating environmental change, systematic frameworks like the one proposed here offer a pathway to maximise ecological returns (both in the establishment of the targeted habitat former and associated biotic assemblages) on restoration investments and potentially aid in the conservation of these habitats into the future.

# Chapter 6 - General Discussion



***How do seascape and focal patch characteristics influence fish communities in temperate estuarine seagrass systems, and how can this understanding be applied and integrated to potentially improve restoration outcomes?***

**Methodological Foundation**

**Chapter 2**

*How can we precisely estimate mean lengths and estimate the proportion of juveniles using unbaited Stereo-RUVs?*

- Measuring at least 25 fish is needed to get a precise estimate of mean & SD of length and the proportion of juveniles within the assemblage

**Understanding Seagrass-Fish Seascape Ecology**

**Chapter 3**

*How does connectivity to artificial structures influence fish communities in seagrass in urbanised estuaries?*

- Connectivity to jetties increases abundance and proportion of juvenile fish
- Connectivity to jetties changes behaviour in fish
- Seascape configuration measures or focal patch characteristics did not influence any metrics

In Yellowfin Bream:
- Connectivity to jetties is associated with shifts in size structure . Smaller sizes and narrower distributions

**Chapter 4**

*How do characteristics at both patch and seascape scales influence fish communities in seagrass?*

- Across all metrics the relative importance of categories was Seascape Connectivity > Seascape Composition > Focal Patch Measures
- Orders of importance was variable within the metrics themselves (e.g. juvenile proportion: Connectivity > Composition = Focal Patch)
- Non-linear relationships observed with seascape characteristics
- Juvenile abundance was primarily driven by similar characteristics to overall abundance in the most parsimonious models

**Application**

**Chapter 5**

*How can seascape understanding be applied practically to restoration site selection and design?*

- Considering the associated assemblages and their relationships with the seascape in restoration design improves ecological outcomes compared to traditional site selection and current best practice (HSMs)
- Different restoration goals requires different designs to achieve optimal outcomes
- Implicit trade-offs in restoration design
- "Build it and they will come" philosophy may not work to achieve best outcomes. Need to restore in the right locations

**Synthesis**

- The seascape for seagrass fish assemblages is important
- Both connectivity and configuration are important – however, connectivity is the most important
- Varying importance of aspects of the seascape and focal patch metrics among aspects of the fish community
- Juvenile fish in seagrass meadows more influenced by the seascape than focal patch characteristics

**Major Implications**

- Importance of considering the seascape and the desired outcome in management and restoration
- Implicit trade-offs in restoration design due to varying seascape relationships between different aspects

**Figure 6.1** – Thesis overview showing key findings and their integration. Methodological development (Chapter 2) enabled investigations demonstrating that seascape characteristics including connectivity and configuration primarily drives fish community structure in seagrass (Chapter 3-4), which then helped inform the design of the restoration framework that aimed to apply seascape ecology into restoration practice (Chapter 5). Contains synthesis of the various chapters and their associated major implications.

## 6.1 | Overview and summary of key findings

Previous historical degradation of natural ecosystems has placed critical habitats and communities under threat (Duarte et al. 2020), and as such it has never been more important to improve methodologies, develop ecological understanding, and attempt to improve the ways we conduct restoration (Abelson et al. 2020; Pittman et al. 2021; Wedding et al. 2025). This urgency is compounded by climate change impacts and ongoing anthropogenic pressures that continue to degrade these vulnerable systems (Duarte et al. 2020). However, in order to design, apply, and implement conservation, management, and restoration strategies effectively, it is critical to understand the underlying ecology of these systems and their associated habitats and biota, as haphazard strategies are insufficient in an age of uncertainty and accelerating environmental change (Bayraktarov et al. 2016; Abelson et al. 2020; Duarte et al. 2020; Wedding et al. 2025). Understanding these complex ecological relationships requires moving beyond single-habitat approaches to consider the broader seascape context that shapes ecosystem function and resilience (Pittman 2017b; Pittman et al. 2021).

The discipline of seascape ecology (Pittman 2017b) aims to understand these systems by merging the principles and ecological theories of landscape ecology (Turner 1989; Fletcher and Fortin 2018) with quantitative marine ecology and geosciences, and has emerged as one of the highest priority research areas in modern marine ecology - especially for often highly mobile fish communities, where the influence of the seascape is often greatest (Pittman 2017a; Pittman et al. 2021). As per (Pittman 2017a), the seascape is defined as "*spatially heterogeneous and dynamic marine space that can be delineated at a wide range of scales in time and space, where human influence is integral to a system but not necessarily central*", and comprises of four key aspects defined as the "4Cs": **C**ontext, **C**onfiguration (inclusive of seascape composition), **C**onnectivity, and **C**onsideration of scale (Pittman 2017b; Pittman et al. 2021; discussed in depth in **Chapter 1** – Section 1.4.2.2).

Seascape ecology has significant potential to be applied to marine restoration practice to improve outcomes, efficiency, and cost effectiveness of restoration and management (Pittman et al. 2021; Wedding et al. 2025). However, despite growing research over the past decade, there is still a lack of understanding regarding various aspects of the seascape (the 4Cs) and research in marine systems (Pittman et al. 2021). This knowledge gap stems from several interconnected challenges: the high costs and logistical complexity of conducting seascape-level surveys and statistical analysis (Barry et al. 2017; Canonico et al. 2019; Ramírez et al. 2022), the lack of standardised methodological approaches for quantifying multi-scale habitat relationships (Lecours 2017; Pittman et al. 2021), and limited frameworks for translating ecological understanding into practical restoration guidance (Abelson et al. 2016; 2020). Consequently, restoration practitioners often lack the tools and knowledge needed to incorporate seascape understanding into site selection and design decisions (Lester et al. 2020). This knowledge gap has practical implications, with less than 13% of restoration projects taking seascape context into account when selecting restoration sites and designing said sites (Gilby, Olds, Connolly, Henderson, et al. 2018). With the UN's "Decade of Ecosystem Restoration" (2021-2030; United Nations 2019) now at its midpoint, alongside globally expanding restoration efforts (Kennedy et al. 2011; Gilby, Brook, Duncan, Ortodossi, et al. 2018; Liversage and Chapman 2018; Boström-Einarsson et al. 2020; Layton et al. 2020; Vergés et al. 2020), addressing gaps in methodological sampling that enable precise and cost effective seascape surveys for research and monitoring, seascape understanding, and frameworks to apply this understanding to restoration practice is critical for increasing the likelihood of successful and ecologically relevant restoration in the Anthropocene (Abelson et al. 2020; Pittman et al. 2021; Wedding et al. 2025).

This thesis aimed to address these knowledge gaps and critical interconnected challenges by addressing the overarching question: "how do seascape and focal patch characteristics influence fish communities in temperate estuarine seagrass systems, and how can this understanding be applied and integrated to potentially improve restoration outcomes?" (Figure 6.1). Following a logical progression from methodological foundations to ecological understanding to practical application, I addressed four key research questions: 1) What sampling effort is required for reliable assessment of key fish population parameters (mean and standard deviation of length, the proportion of juveniles) using unbaited stereo-RUV systems to enable precise cost and time efficient seascape level surveys? (**Chapter 2**); 2) How does connectivity to artificial structures and the broader seascape in addition to focal patch characteristics influence fish communities in seagrass in highly urbanised estuaries? (**Chapter 3**); 3) How do characteristics at patch and seascape scales influence fish community responses? (**Chapter 4**); and 4) How can this multi-scale ecological understanding be operationalised for strategic restoration planning that considers outcomes for associated organisms (fish in this case), as well as the target habitat itself? (**Chapter 5**)?

Each chapter contributed novel insights that have addressed critical knowledge gaps in marine seascape ecology and restoration practice. In **Chapter 2**, I established that approximately 25 fish measurement from distinct timepoints provides precise estimates of the mean and standard deviation of fish lengths and the proportion of juveniles within an assemblage. This provided the first assessment of the sample size required to generate precise estimates of these critical fish population parameters, a critical knowledge gap identified in a study by Williams et al. (2022). Moreover, this methodological foundation enabled reliable stereo-RUV throughout subsequent chapters, ensuring that I could be confident in the precision of my surveys, while increasing cost and time effectiveness.

In **Chapter 3**, I demonstrated that seagrass meadows with high connectivity to jetties (i.e., those in the near jetties treatment) had significantly greater total fish abundance and a higher proportion of juvenile fish. Examination of the size structure of a commercially and recreationally relevant species – *Acanthopagrus australis* (Yellowfin Bream) – showed that the population in seagrass near jetties had a significantly lower mean size with a narrower length distribution than those in seagrass far from jetties. Notably, neither focal patch nor measures of seascape composition influenced these responses, highlighting the specific importance of connectivity to artificial structures for fish communities in urbanised seascapes.

**Chapter 4** expanded the scope from examining the relationship of connectivity to a singular habitat type (jetties) alongside focal patch and seascape configuration measures, to look at the influence of all habitats within the seascape on seagrass associated fish assemblages. Seascape connectivity and configuration (inclusive of composition) were found to be more important than focal patch characteristics for predicting the response of key fish assemblage metrics (abundance, species richness, diversity, and juvenile proportion), with connectivity measures being the most important overall. Moreover, the relative importance of these predictor categories varied among the fish assemblage metrics. For example, for the proportion of juveniles, the order of importance of these predictor categories was connectivity, followed by seascape configuration, which was equal in relative importance to focal patch characteristics; while for total abundance seascape configuration was equally important to focal patch characteristics, which were both more important than measures of connectivity (**Chapter 4** - Figure 4.3). Furthermore, 40% of the relationships in the most parsimonious models were non-linear, highlighting the complexity of spatial ecological relationships and suggesting potential trade-offs and thresholds in how fish communities respond to seascape characteristics.

The ecological understanding developed in **Chapters 3 & 4** and over the course of this thesis was applied in **Chapter 5** where, I developed a decision-support framework for restoration site selection that integrates habitat suitability modelling, seascape patterns, and spatial prioritisation to help practitioners identify optimal restoration configurations that maximise desired ecological outcomes. Importantly, this framework (to my knowledge) is the first to integrate previously separate modelling components (habitat suitability modelling, prediction of restoration outcomes, and spatial prioritisation) and considers outcomes for both the habitat former and the associated ecological assemblages, fish in this case. I observed that sites selected using the framework varied depending on the assemblage metric(s) prioritised and that there are inherent trade-offs in restoration outcomes that occur when trying to optimise across multiple criteria, indicating that there is no "one-size fits all" solution when it comes to restoration – confirming hypothesises surrounding the practical application of seascape findings posited in **Chapters 3 & 4**. Additionally, comparison between sites selected using a more traditional approach by an expert seagrass researcher and sites selected using the framework also highlighted that quantitative modelling approaches are best used in conjunction with individuals with local knowledge of the study site, rather than acting as a replacement for this specialised understanding.

Through this research progression - from establishing robust protocols to advancing fundamental understanding of fish-seascape relationships and developing practical restoration tools - this thesis provides both scientific insights that further our ecological understanding and actionable frameworks for marine restoration in an era of accelerating environmental change. Collectively, these findings represent a shift from traditional single-scale restoration approaches towards integrated seascape-informed practice, providing a pathway to start moving towards designing context-appropriate interventions that account for habitat connectivity and multi-scale environmental relationships. Moving forward, the integration of seascape ecology into restoration practice is an important step towards achieving the ecosystem and habitat restoration at the scale needed to support marine biodiversity and ecosystem services/function under global change. In the following sections I synthesise some of the overarching themes that these findings have provided, discuss their broader implications for marine management and restoration, address practical considerations regarding the restoration framework, and conclude by addressing limitations of the studies conducted here and potential future directions of research.

## 6.2 | Methodological advances in fish video analysis enable precise and practical application

Understanding fish size structure is fundamental to marine ecology and fisheries management (Maunder and Punt 2013; Ono et al. 2015), as different life stages occupy distinct habitats and perform different ecological roles within seascape mosaics (Werner and Gilliam 1984; Dahlgren and Eggleston 2000). For example, juveniles often rely on shallow, structurally complex nursery habitats for protection and feeding, while adults may utilise deeper waters or different habitat types for foraging and reproduction (Beck et al. 2001; Nagelkerken et al. 2015). These ontogenic partitions means that seascape-scale conservation and restoration must account for size structure patterns to effectively support the full life history of their associated fish communities and maintain population connectivity across habitats.

Current approaches to measuring fish size structure from stereo-RUV data rely primarily on two methods: length at MaxN (the point in the video where the maximum number of an individual fish species is observed (Langlois et al. 2020) and length across all observations taken during systematic video sampling (like with MeanCount; Schobernd et al. 2013; Williams et al. 2022). However, these approaches have often been adopted without clear guidance on sample size, with researchers typically measuring a small number of individuals (1-10 fish per deployment) based on convenience rather than statistical requirements (Langlois et al. 2020; Williams et al. 2022). This limited sampling creates uncertainty about the precision of population parameter estimates and may introduce bias, particularly for metrics like juvenile proportions, which is critical for understanding recruitment success and nursery function of the sampled habitat.

The methodological advances presented in **Chapter 2** addresses these limitations by establishing evidence-based sampling targets for unbaited stereo-RUV analysis. Through systematic evaluation, this research demonstrated that approximately 25 individual fish measurements (ideally from distinct time points within the video) provide precise estimates of key fish population parameters, including mean length and juvenile proportions when surveying using unbaited stereo-RUVs. This finding represents a critical advancement over current more ad-hoc approaches by providing researchers with clear targets for data collection that balance precision with practical constraints such as cost and time effectiveness. Such practical constraints are important to address particularly when sampling at the scale required for seascape studies, which often require many samples to adequately sample the seascape and specify complex statistical models with lots of parameters (Pittman 2017a). As such, these sampling protocols proved essential for enabling the seascape-scale studies conducted in **Chapters 3 & 4** - and other studies like them - where reliable fish population data is required across a broad spatial scale.

This methodological foundation was equally critical for Stage 1 of the restoration framework described in **Chapter 5** (Data Collection; Figure 5.1), where site selection decisions depend on reliable predictions of fish assemblage outcomes. Not only is this important for the reliability of predictions, but it is also important for the cost effectiveness of these approaches. One of the key considerations regarding the practical implementation of quantitative spatial modelling frameworks in marine systems (like the one in Chapter 5) is the cost associated with generating the data required to undertake these processes (elaborated on bellow in Section 6.4). Therefore, the work in **Chapter 2** - by increasing the efficiency of underwater video analysis while ensuring precision - may increase the viability of these modelling approaches by reducing the cost and time required to gather said data.

## 6.3 | Location, Location, Location - the role of seascape connectivity, configuration, and context

The idea of location and its surrounding context being the most important contributing factor to the value of a specific area has been recognised for almost a century in real estate with the adage "location, location, location" (Thrall 2002). This concept of "location, location, location" represents one of the central findings of this thesis which summarises not only the main themes of **Chapters 3 & 4**, which aimed to understand the influence of the seascape, but also the ramifications of these results when applied to restoration site selection (**Chapter 5**), with characteristics describing the seascape configuration and seascape connectivity often being associated with key fish assemblage metrics across **Chapters 3 & 4**.

**Chapter 3** provided initial evidence by showing that connectivity to jetties (where seagrass was either directly adjacent to or far from jetties) alone was associated with significant changes in total fish abundance and juvenile proportion (Chapter 3 – Figure 3.2) and behaviour (Chapter 3 – Figure 3.3), alongside the size structure (Chapter 3 – Figure 3.5) and behaviour of a commercially and recreationally important fish *Acanthopagrus australis* (Yellowfin Bream). These findings align with studies looking at natural reefs in relation to artificial structures, where it has been shown that artificial structures can modify fish assemblages in connected natural habitats through indirect connectivity-mediated influences rather than direct structural impacts (Clynick et al. 2008; Layman and Allgeier 2020), demonstrating that even simple measures of binary connectivity (adjacent vs. distance) can significantly influence ecological patterns in seagrass systems. However, the results diverge from the expectations derived from landscape ecology (Turner 1989), as focal patch characteristics and seascape configuration metrics showed no significant influence on fish abundance, diversity, or community composition – influencing only certain behavioural responses. This suggests that in heavily urbanised and modified systems like Lake Macquarie, local connectivity to artificial structures may be more important than other traditional patch or seascape characteristics.

**Chapter 4** illustrated this concept of "location, location, location" explicitly through the results of the variable importance analysis, which showed that seascape metrics characterising structural connectivity to other habitats and seascape configuration/composition were the strongest predictors of total fish abundance, species richness, diversity, and the proportion of juveniles (Chapter 4 - Figure 4.3B), with connectivity being the most influential seascape characteristic (Chapter 4 - Figure 4.3A). Similar findings noting the importance of connectivity to predicting fish assemblage characteristics have emerged from connectivity studies in other marine habitats and systems (Olds et al. 2012, Martin et al. 2018), and align with the growing evidence from both terrestrial and marine systems that the broader landscape or seascape surrounding a habitat patch often is more important for predicting the characteristics of the associated assemblage than the characteristics of the patch itself (Bradley et al. 2019; 2020).

While all four components of the 4C's seascape framework (configuration, context, connectivity, and consideration of scale) are acknowledged as being important , it is not necessarily defined which aspects may be more important than others in various marine systems (Pittman 2017b; Pittman et al. 2021). **Chapters 3 & 4** provide novel insights into the general relative influence of some of these components. The dominance of connectivity and configuration/composition metrics overall in **Chapter 4** (Chapter 4 – Figure 4.3A) and the importance of connectivity in **Chapter 3** suggests that while all these 4Cs of the seascape are important, some may be more important than others – at least when it comes to predicting the responses of fish assemblages in these systems. Interestingly, this pattern contrasts with a recent finding from tropical coral-dominated systems, where Moustaka et al. (2025) found that local habitat composition and structural complexity were more important than the seascape characteristics measured for fish communities. This divergence likely reflects fundamental differences in system characteristics between tropical coral systems and estuarine temperate systems. Coral reefs are systems where fish community structure is closely associated with local three-dimensional complexity and benthic composition (Graham & Nath 2013), whereas temperate estuarine-dependent species occur in systems often with limited availability of hard substrate habitat, potentially shifting the relative importance towards connectivity and broader seascape configuration. Furthermore, fish in post-settlement stages in tropical coral reef systems tend to exhibit greater site fidelity to their focal patch (Chapman and Kramer 2000; Nash et al. 2015) compared to fish in temperate systems (Curley et al. 2013; Harasti et al. 2015; Lee et al. 2015; Swadling et al. 2024), which may result in greater relative importance of focal patch characteristics in these systems as observed in Moustaka et al. (2025). This indicates that the relative importance of the 4C's may vary among habitat types and biogeographic systems, adding additional nuance to the 4Cs framework. Furthermore, we observed differences between the relative importance of each category of variable (connectivity, composition, focal patch characteristics) and different summary measures of the fish assemblage (abundance, richness, diversity, proportion of juveniles; **Chapter 4**), adding further complexity to this framework.

The importance of seascape connectivity was particularly pronounced for juvenile fish throughout **Chapters 3 & 4**, providing evidence for how the broader seascape is associated with an individual patches' nursery function. In **Chapter 3**, high connectivity to jetties was associated with increased juvenile proportions and shifts in Yellowfin Bream size structure towards smaller individuals (Chapter 3 – Figure 3.2 & 3.5), suggesting that proximity to these artificial structures may enhance the nursery value of the focal seagrass habitat or facilitate spill over/migration of juveniles to the seagrass. This finding is most likely being driven by associated shifts in larval supply as a result of altered hydrodynamic conditions surrounding jetties (Saengsupavanich et al. 2022), with jetties providing three-dimensional structure ideal for juvenile recruitment (Fowler and Booth 2013; Layman and Allgeier 2020), or increase in resource availability/diversity as a result of increased access to jetty habitat (Bohnsack 1989; Bulleri and Chapman 2010; Munsch et al. 2014; Layman and Allgeier 2020). **Chapter 4** reinforced this pattern, revealing that juvenile proportion was predominantly associated with connectivity measures (Chapter 4 - Figure 4.3B), followed by measures of seascape configuration and focal patch characteristics which exhibited equal importance, highlighting that the nursery function of a particular patch in this system is not necessarily associated with the condition of the patch itself. These findings provide empirical evidence for the emerging seascape nursery concept and it's occurrence within estuarine seagrass systems, which posits that nursery value is determined not solely by patch-level attributes but by the surrounding seascape (Nagelkerken et al. 2015) – a pattern also observed in a recent study on macroalgal habitats in a tropical system (although in different orders; Moustaka, Robbins, et al. 2024) and a study by Bradley et al. (2019) which found that the surrounding seascape was more important than habitat type in determining use by juvenile fish.

Importantly, these relationships between fish assemblages and seascape characteristics were frequently non-linear. In **Chapter 4**, 40% of the observed relationships exhibited non-linear patterns, while fish behaviour showed similar complexity in **Chapter 3**. Such complex multi-dimensional non-linear relationships are not uncommon in landscape/seascape ecology (Tischendorf 2001; Maxwell et al. 2017; Pittman 2017b), owing to multiple competing ecological processes and the varying influences these processes have at multiple scales (Levin 1992; 2000; Schneider 2017). These non-linear relationships highlight that there are inherent ecological trade-offs and threshold effects that occur throughout the seascape. In an applied setting, these results imply that we cannot "have our cake and eat it too", that there is no one "optimal" area to conserve or restore that will lead to the best outcomes for every aspect of the associated fish community. Instead, these results suggest that a diversity of different areas, containing diverse seascapes, covering a broad range characteristics, is needed to holistically protect all aspects of the fish community.

Collectively, these findings regarding the importance of the seascape overall and also specifically for juvenile fish challenge the restoration paradigm of "build it and they will come" from the Field of Dreams hypothesis[1] (Palmer et al. 1997; Hilderbrand et al. 2005), demonstrating that restored habitats must be strategically placed within the seascape to maximise ecological outcomes for the associated assemblages. **Chapter 5** demonstrated exactly the above principles in practice when demonstrating the use of the framework to select potential restoration sites in a case study. In this chapter, when scenarios prioritised different assemblage metrics or considered seagrass habitat suitability with fish assemblage metrics, entirely different restoration sites and spatial configurations were selected (Chapter 5 – Figures 5.7 & 5.8), aligning with the varying relationships exhibited among assemblage metrics observed throughout **Chapters 3 & 4**. This spatial shifting of optimal sites depending on restoration priorities demonstrates that strategic placement within the seascape can be as important, if not more important, than optimising the size or quality of individual restored patches, reaffirming the proposed implications of the above seascape relationships in practical applications.

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[1] Yes, this scientific hypothesis is based on Kevin Costner's hit 1989 movie *Field of Dreams* - where he hears a ghostly voice say "Build it, he will come" in reference to building a Baseball field. Oh scientists…

## 6.4 | Implementing seascape-informed restoration in practice

Restoration success should be evaluated not only by the establishment of the habitat-forming species, but also by how well restored habitats fulfill their functional roles, such as - in the case of **Chapter 5** - providing quality habitat for fish assemblages. To assess and optimise these functional outcomes practitioners must adopt seascape informed approaches that account for the broader spatial context and that influence assemblage patterns. However, such frameworks have several barriers that prevent widespread adoption of such approaches.

A critical barrier to implementing seascape-informed restoration frameworks like the one developed in **Chapter 5** is the substantial data requirement both for habitat suitability modelling and for the prediction of assemblage outcomes. While the framework demonstrates clear ecological benefits and has potential for economic benefits via improved ecological return on investment, its practical uptake depends on whether practitioners can feasibly acquire the necessary data or leverage existing information/data required to undertake the various modelling steps. One potential solution is to adapt the framework to utilise existing citizen science initiatives and publicly available datasets rather than requiring new in-situ field surveys. For example, data from platforms like *iNaturalist*, can be used to gather presence-only data and could be combined with environmental layers to create species distribution models within target regions (Mesaglio and Callaghan 2021; Mason et al. 2025). Instead of predicting overall assemblage metrics like total abundance or diversity (as implemented in **Chapter 5**), the prioritisation step could be modified to identify restoration sites based on overlapping distributions of priority species (Lehtomäki and Moilanen 2013; Moilanen et al. 2022) – this approach has been successfully demonstrated by numerous studies who use spatial prioritisation via *Marxan* to identify MPAs that cover the distributional ranges of target species (review of *Marxan* - Watts et al. 2017). This adaptation would allow practitioners to incorporate considerations for both the target habitat former and the associated assemblages without collecting extensive in-situ data. However, this potential citizen science approach has some drawbacks that compromise its utility for seascape-scale restoration planning. While citizen science platforms like *iNaturalist* and *Atlas of Living Australia* can provide presence records (which cannot be used to derive measures of abundance) and programs like *Reef Life Survey* that collect quantitative abundance and size-structure data (which often isn't collected at a broad enough spatial scales in estuarine systems), neither can provide adequate data to predict which restoration sites may support the greatest fish densities or nursery value – information that requires dedicated seascape surveys of fish assemblages across potential restoration areas.

Beyond biological data constraints, the availability of environmental data presents a significant challenge to implementing habitat suitability models (one of the key components of the workflow described in **Chapter 5**) in many regions. Fine-resolution environmental data layers (e.g., temperature, salinity, pH, dissolved oxygen) are often unavailable or exist at scales too coarse for restoration planning – particularly in estuarine environments (Dafforn et al. 2016). Furthermore, extensive habitat maps like those produced by NSW Department of Primary Industries (NSW Department of Primary Industries 2025a; West et al. 2025) - which were critical to making the spatial analyses in **Chapters 3-5** feasible - may not be available in some regions (particularly estuaries in more regional areas, smaller estuaries, and/or estuaries of lesser economic significance to the region). Practitioners in regions lacking such datasets looking to implement quantitative restoration approaches would first have to generate them via in-situ sampling, remote sensing, manual delineation, or ground-truthing, substantially increasing time and cost of restoration planning before even beginning to model assemblage responses. This highlights the need for improved availability, reliability, and comprehensiveness of such datasets alongside improved data sharing infrastructure to facilitate uptake of quantitative spatial modelling frameworks.

The spatial variability of seascape relationships compounds these challenges and raises questions about the generalisability of predictive models of fish assemblage outcomes across systems. There is strong evidence and theoretical foundation to suggest that seascape-assemblage relationships vary across regions, estuaries, latitudinal gradients, habitat types, and taxonomic groups (Pittman 2017b; Bradley et al. 2020). Comparing the results between **Chapters 3 and 4** (which had very different study systems) also showed that this is indeed the case, with different seascape relationships observed between the two chapters. If seascape relationships are largely context-dependent, then implementing the **Chapter 5** framework would require developing both habitat suitability models for the habitat former and assemblage prediction models unique to each region or estuary – a prospect that may significantly increase cost and the practicality of implementation, particularly for restoration programs spanning multiple areas. Further studies and/or meta-analysis of currently available literature comprehensively testing if there are any generalisable associations that could reduce this site-specific calibration burden are of critical importance going forward. Alternatively, simulation-based approaches grounded in ecological theory and mathematical relationships (e.g., species-areas relationships; Fahrig 2013), diversity-disturbance relationships; Miller et al. 2011) may offer a pathway to generating a generalisable predictive framework that could be applied across systems without extensive local data collection.

These practical constraints – high data costs, limited environmental data availability, and the need for site-specific model calibration – likely explain why habitat suitability models and quantitative frameworks (like described in **Chapter 5**) remain underutilised in restoration practice despite being widely acknowledged as best practice (Abelson et al. 2020; Lester et al. 2020; Bertelli et al. 2022). Many restoration programs operate on tight budgets, owing to the significant cost that marine restoration has (Bayraktarov et al. 2016; Abelson et al. 2020), and often are constrained to where they are allowed to restore in the first place by legislation, local government, and key stakeholders (Hering et al. 2023; Bell-James et al. 2025). The framework developed in **Chapter 5** asks practitioners to not only conduct suitability modelling - already a significant analytical, cost, and time undertaking - but also to model assemblage responses based on seascape characteristics alongside performing spatial prioritisation, adding layers of complexity that may further limit practical adoption. Reducing barriers to entry through standardised workflows, open-source analytical tools, improved data sharing infrastructure, open transparent science, and reduced data collection costs will be essential to applying seascape ecology into practical applications going forward.

## 6.5 | Implications for restoration and management

Beyond the insights discussed above, this research has broader implications for the practice and economics of marine restoration. Marine restoration faces significant economic barriers, with high implementation costs and low financial feasibility limiting the appeal of restoration projects to government and industry investors (Bayraktarov et al. 2016; Abelson et al. 2020). These challenges have sparked growing conversations around “de-risking” restoration to improve its economic viability (Webster et al. 2017; Stovall et al. 2022). The research outlined in this thesis addressed these economic constraints by providing multiple pathways for improving cost-effectiveness and efficiency in marine research and restoration. Implementing the optimised stereo-RUV protocols (**Chapter 2**) may reduce the costs of monitoring and surveys while maintaining precision, enabling more comprehensive sampling programs within limited budgets. The restoration framework’s (**Chapter 5**) capacity to identify sites with 7-65% greater predicted fish ecological outcomes compared to traditional ad-hoc approaches may translate into improved return on investment for restoration programs globally. More broadly, a seascape approach may enable practitioners and managers to maximise restoration outcomes per dollar spent by targeting interventions where they will have the greatest seascape-level impact. However, realising these economic benefits requires consideration of the ecological complexity revealed throughout this thesis and a number of practical considerations for implementation (see above - Section 6.4). **Chapters 3 and 4** demonstrated that different assemblage metrics respond in varying ways to seascape characteristics, and **Chapter 5** confirmed that these differential responses have practical consequences. These findings indicate that it is a necessity for explicit discussions of ecological trade-offs during project planning, and as such, practitioners should look to develop stakeholder engagement processes that can communicate complex ecological trade-offs to diverse audiences and navigate competing objectives.

## 6.6 | Limitations and future directions

### *6.6.1 Temporal and spatial scaling of experiments and surveys*

#### 6.1.1 Consideration of spatial scale

Throughout this thesis, I used a seascape sampling unit (SSU) of a 300m buffer around our sampling points to derive measures of seascape configuration/composition (e.g., measures such as landscape fragmentation index, total amount of the various habitats within the seascape; Chapter 4 - Table 1). This choice was based on the scale at which the relevant organisms are likely to integrate the seascape (Wiens 1989; Schneider 2017), in this case representing 95% of the home ranges of many adult species found within the sampled assemblages (See **Chapter 1** –Section 1.3.2.2.4; **Chapters 3 & 4** Methods). This is a conservative SSU given that most of the fish sampled throughout both **Chapters 3 & 4** were juvenile fish which often exhibit smaller home ranges and greater site fidelity. Despite this, it is possible that the assemblages' characteristics are more associated with seascape characteristics measured on broader or smaller scales.

Sampling constraints in **Chapter 4** (loss of all samples in the upper estuary due to poor visibility) prevented coverage of the full estuarine gradient as planned. Future studies should address this gap by ensuring complete spatial coverage across estuarine gradients particularly in lower visibility areas (perhaps using sonar based methods like DIDSONs), as fish-seascape relationships may differ substantially between lower, middle, and upper estuarine zones due to varying environmental conditions, habitat configurations, and species present (Basset et al. 2013; Baillie et al. 2015; Bradley et al. 2020). Complete coverage of the estuarine gradient would provide a more comprehensive understanding of how seascape relationships vary across environmental contexts.

#### 6.6.1.2 Consideration of temporal scale

Temporal variability occurs across multiple time scales (hours, days, months, years, decades etc.), from seasonal changes driven by spawning periods and recruitment pulses (Pichler et al. 2017; Brosset et al. 2020; Arevalo et al. 2023), to annual and decadal variation in community structure (Colombano et al. 2022; van der Sleen et al. 2022; Receveur et al. 2024). An important next step would be to replicate this research across seasons to examine how relationships between fish assemblage metrics and seascape characteristics shift throughout the year. This seasonal sampling should then be extended across multiple years to assess consistency of these relationships over broader temporal scales. This temporal variability becomes particularly relevant given the context-dependent nature of seascape relationships (Schneider 2017; Bradley et al. 2020), as seasonal changes in environmental conditions and recruitment may further modulate how fish communities respond to seascape and focal patch characteristics, adding another layer of complexity to our ecological understanding and restoration planning.

Moreover, most current ecological understanding remains limited to daytime fish assemblages, as nighttime communities are rarely studied due to inherent limitations of sampling at night with RUV methodologies (Cooke et al. 2017) alongside general logistical challenges. However, distinct day-night community shifts are well-documented , involving changes not only in structure but also in behaviour (Helfman 1986; Myers et al. 2016; Yeoh et al. 2017; Cardoso et al. 2020). Capturing these nighttime assemblages is therefore essential for a comprehensive seascape understanding. This becomes particularly important when developing predictive models for restoration applications (**Chapter 5**), as neglecting the nighttime communities could compromise model reliability and restoration outcomes and may miss critical ecological impacts of unmeasured nighttime communities, potentially resulting in restoration designs that fail to support the full suite of species utilising seagrass habitats across day-night cycles. There is also evidence that suggests artificial light is associated with additional changes in behaviour and community composition during nighttime hours (Weschke et al. 2024). This indicates that potentially seascape-level relationships may shift not only between day and night but may also depend upon the presence and strength of artificial light in the seascape, suggesting that data layers quantifying the spatial extent and magnitude of artificial light at nighttime may need to be included within the restoration framework described in **Chapter 5**.

### *6.6.2 Limitations in testing complex seascape relationships*

Although I initially intended to test interactive effects among various seascape and focal patch characteristics, sample size limitations in **Chapter 4** due to poor visibility and weather prevented robust analysis of these higher-order relationships. Moreover, the small sample size necessitated using a full subsets approach, with models limited to a maximum of two predictors to avoid overfitting. This is important to note, as when multiple variables are included simultaneously in a model, one may account for some of the variance attributed to the other, potentially modifying the strength, direction, magnitude of the relationship or remove it entirely (Graham 2003; Dormann et al. 2013). A well-documented example of this in landscape ecology is the debate around the positive, negative, or neutral effect of landscape fragmentation, where apparent influence of fragmentation often disappears when habitat loss is properly accounted for within the models (Fahrig 2003; 2017; Fahrig et al. 2019). This is well argued by Pittman (2017a) where they state that *"both continuous spatial gradients and discrete patch mosaics may together explain more variability in response than either type used in isolation,".* Consequently, some of the relationships outlined in **Chapter 4** may be influenced by unmeasured covariates. Larger sample sizes enable the inclusion of more predictors simultaneously without the cost of potential overfitting and error, allowing for more accurate assessment of observed ecological relationships.

While I was able to identify important individual effects of seascape connectivity, composition, and configuration on fish assemblages, the potential for interactive and synergistic effects remains largely unexplored. There is growing recognition in landscape and seascape ecology that ecological relationships are often context dependent (Pittman 2017b; Bradley et al. 2020). For example, smaller seagrass patches with limited local resources might benefit more from mangrove connectivity due to increased access to resource pools than a larger seagrass patch with intrinsically more resources (Tilman 1982; Werner et al. 1983; Dunning et al. 1992). Similarly, the influence of artificial structure connectivity observed in **Chapter 3** may vary depending on other seascape characteristics such as total habitat area, seagrass patch density, or proximity to other habitat types. The non-linear relationships identified in **Chapter 3 & 4** may hint at such complexity, but explicit testing of higher-order interactions requires substantially larger sample sizes than were feasible within this thesis given the available time and personnel. Testing these multi-dimensional relationships represents an important next step for seascape research. Such studies would provide deeper understanding of the potential synergistic and antagonistic interactions among seascape and focal patch characteristics, potentially revealing further threshold effects or context-dependent relationships that could better inform restoration planning. Understanding when and where certain seascape characteristics matter most – and how different characteristics combine to influence associated communities would enable more nuanced understanding and effective restoration site selection that accounts for the full complexity of seascape ecology.

### *6.6.3 Developing mechanistic understanding of seascape-fish relationships through experimental approaches*

Though the correlative and observational studies I conducted throughout this thesis (**Chapter 3 & 4**) represent a first step to furthering our understanding of seagrass fish seascape ecology in these temperate estuarine systems, the observations I made raise questions that require more manipulative experimental approaches to test. Moving beyond purely correlative observational studies towards more controlled experiments would help in developing a more mechanistic understanding of observed associations and enable more robust predictive models that could be integrated into restoration workflows like the one outlined in **Chapter 5**. For example, many of the posited explanations for the relationships observed throughout this thesis are associated with perception of risk related to predation-pressures within a particular patch (**Chapter 3 & 4**). Manipulative studies using giving-up-density (GUD) experiments across seascape gradients would directly measure how risk perception varies with connectivity levels, patch characteristics, and seascape configuration. Such experiments would provide mechanistic insight into behavioural drivers of seascape-fish relationships I've observed here.

Understanding larval supply, settlement, and recruitment patterns across seascapes represents another critical research direction. High resolution temporal sampling of fish demography combined with larval sampling at equivalent spatial and temporal scales would reveal whether abundance patterns I've observed in this thesis result from differential mortality, larval supply, or greater growth opportunities. Complementary benthic surveys of prey items alongside stable isotope and gut content analysis across seascape gradients, would be able to assess whether observed associations reflect food abundance or food accessibility patterns as observed in some other seascape studies (Staveley et al. 2017). These experimental approaches would build directly upon the seascape relationships I've identified to develop a more complete mechanistic understanding of how seascape structure influences fish assemblages.

## 6.7 | Concluding remarks

My thesis represents an important step forward in developing our understanding of the relationships between the seascape and seagrass associated fish communities, alongside developing the ways that this understanding could be applied practically to restoration. I have further contributed to the methodological side of fish surveys that underpin this type of work, facilitating improvements to the cost-effectiveness and efficiency of fish video analysis. The contributions I have made within this thesis are timely given the accelerating pace of coastal development and impacts of climate change on marine ecosystems worldwide. As we face an unprecedented global crisis of habitat loss and ecosystem degradation, the need for both deeper ecological understanding and more effective restoration approaches has never been more urgent. Importantly, this research has generated many key questions for future study, highlighting that each ecological insight gained opens new avenues of research that will further advance our understanding of these complex seascape systems.

The seagrass meadows and their fish communities examined in this thesis represent some of our planet's most productive and threatened ecosystems - critical nurseries and fish habitat embedded within complex seascapes that support both marine biodiversity and human livelihoods. By advancing both our fundamental understanding of seascape ecology and our ability to apply this knowledge to restoration practice, this work contributes to enhancing coastal management with additional scientific tools that complement existing knowledge and experience. I hope that through these contributions, we can move toward more effective stewardship of marine systems, ensuring these remarkable seascapes continue to support the intricate web of life they have sustained for millennia; and most importantly, so that future generations can still be able to experience the wonder and amazement I felt exploring beneath the waves for the first time as a kid.

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# Appendix A | FL50 values used to determine the life stage of each fish species observed throughout this thesis

**Table A1 –** Table of the length at maturity either determined by literature or 33% of the total length (as found on FishBase) for each species observed throughout this thesis

| Common Name | Genus | Species | Measure Used | Maturity Length (mm) | References Used |
|---|---|---|---|---|---|
| Yellowfin Bream | *Acanthopagrus* | *australis* | FL50 | 190 | (Roelofs et al. 2020) |
| Black Bream | *Acanthopagrus* | *butcheri* | FL50 | 240 | (Sarre and Potter 1999) |
| Eastern Smooth Boxfish | *Anoplocapros* | *inermis* | 33% of TL | 122 | FishBase (Froese and Pauly 2021) |
| Australasian Snapper | *Chrysophrys* | *auratus* | FL50 | 220 | (Stewart, Roelofs, et al. 2020) |
| Threebar Porcupinefish | *Dicotylichthys* | *punctulatus* | 33% of TL | 132 | FishBase (Froese and Pauly 2021) |
| Gunns Leatherjacket | *Eubalichthys* | *gunnii* | 33% of TL | 198 | FishBase (Froese and Pauly 2021) |
| Smooth Flutemouth | *Fistularia* | *commersonii* | FL50 | 55 | (Bariche et al. 2013) |
| Silverbiddy | *Gerres* | *subfasciatus* | 33% of TL | 66 | FishBase (Froese and Pauly 2021) |
| Luderick | *Girella* | *tricuspidata* | FL50 | 280 | (Broadhurst et al. 2020) |
| Rock Blackfish | *Girella* | *elevata* | FL50 | 360 | (Stocks 2015) |
| Goldspot Mullet | *Liza* | *argentea* | 33% of TL | 148.5 | FishBase (Froese and Pauly 2021) |
| Banded Toadfish | *Marilyna* | *pleurosticta* | 33% of TL | 44.55 | FishBase (Froese and Pauly 2021) |
| Yellowfin Leatherjacket | *Meuschenia* | *trachylepis* | 33% of TL | 132 | FishBase (Froese and Pauly 2021) |
| Brownstriped Leatherjacket | *Meuschenia* | *australis* | 33% of TL | 99 | FishBase (Froese and Pauly 2021) |
| Fanbelly Leatherjacket | *Monacanthus* | *chinensis* | 33% of TL | 125.4 | FishBase (Froese and Pauly 2021) |
| Sea Mullet | *Mugil* | *cephalus* | FL50 | 300 | (Stewart, Pidd, et al. 2020) |
| Ocean Leatherjacket | *Nelusetta* | *ayraudi* | FL50 | 350 | (Miller and Stewart 2013) |
| Rotund Blenny | *Omobranchus* | *rotundiceps* | 33% of TL | 16.5 | FishBase (Froese and Pauly 2021) |
| Striped Cardinalfish | *Ostorhinchus* | *fasciatus* | 33% of TL | 4.158 | FishBase (Froese and Pauly 2021) |
| Horned Blenny | *Parablennius* | *intermedius* | 33% of TL | 39.6 | FishBase (Froese and Pauly 2021) |
| Southern Grubfish | *Parapercis* | *australis* | 33% of TL | 33 | FishBase (Froese and Pauly 2021) |
| Blacksaddle Goatfish | *Parupeneus* | *spilurus* | FL50 | 160 | (Mellin et al. 2007) |
| Eastern Striped Grunter | *Pelates* | *sexlineatus* | FL50 | 50 | (Veale et al. 2015) |
| Silvery Trevally | *Pseudocaranx* | *georgianus* | FL50 | 190 | (Chick et al. 2020) |

| | | | | | |
|---|---|---|---|---|---|
| Gunthers Wrasse | *Pseudolabrus* | *guentheri* | 33% of TL | 59.4 | FishBase (Froese and Pauly 2021) |
| Striped Scat | *Selenotoca* | *multifasciata* | 33% of TL | 132 | FishBase (Froese and Pauly 2021) |
| Yellowtail Kingfish | *Seriola* | *lalandi* | FL50 | 800 | (Hughes et al. 2020) |
| Sand Whiting | *Sillago* | *ciliata* | FL50 | 170 | (Ochwada-Doyle et al. 2014) |
| Striped Barracuda | *Sphyraena* | *obtusata* | FL50 | 211 | (Meshram et al. 2021) |
| Moon Wrasse | *Thalassoma* | *lunare* | FL50 | 90 | (Ackerman 2004) |
| Weeping Toadfish | *Torquigener* | *pleurogramma* | 33% of TL | 69.3 | FishBase (Froese and Pauly 2021) |
| Stout Longtom | *Tylosurus* | *gavialoides* | 33% of TL | 247.5 | FishBase (Froese and Pauly 2021) |
| Bluestriped Goatfish | *Upeneichthys* | *lineatus* | 33% of TL | 132 | FishBase (Froese and Pauly 2021) |
| Australian Goatfish | *Upeneus* | *australiae* | FL50 | 65 | (Uiblein and Gledhill 2015) |
| Eastern Shovelnose Ray | *Aptychotrema* | *rostrata* | Estimated length at maturity for Ray species is measured as the disc width (DW50). I could not measure disc width in the stereo-videos. As such, I could not categorise these species into juveniles or adults and were not included within the juvenile analysis | | |
| Estuary Stingray | *Hemitrygon* | *fluviorum* | | | |
| Bluespotted Maskray | *Neotrygon* | *australiae* | | | |
| Common Stingaree | *Trygonoptera* | *testacea* | | | |
| Eastern Fiddler Ray | *Trygonorrhina* | *fasciata* | | | |

# Appendix B | Supplementary material for Chapter 3

## Appendix B1 - Tables describing the results of the statistical models in Chapter 3

**Table B1** - Final statistical models used to analyse the effect of proximity to jetties alongside focal patch and seascape characteristics on various fish community responses.

| Response | Model Type | Distribution Family | Final Parsimonious Model |
|---|---|---|---|
| Abundance (MeanCount) | GLM | gaussian(link=sqrt) | ~ Treatment + (1\|BlockID) |
| Species Richness | GLM | gaussian(link=identity) | ~ Treatment + (1\|BlockID) |
| Diversity (Shannon H) | GLM | gaussian(link=log) | ~ Treatment + (1\|BlockID) |
| Proportion of Juveniles | GLM | binomial(link=logit) | ~ Treatment + (1\|BlockID) |
| Behaviour | GAM | betar(link=logit) | ~ Treatment + s(Total Area of Zostera within the Seascape, k =3) + s(Focal Patch Shape, k=3) + (Site\|BlockID) |
| Length Frequency Distribution of Yellowfin Bream | GAMLSS | gamma(link=log) | ~ Treatment + (1\|BlockID) |

**Table B2** – Results of the statistical tests analysing the effect of proximity to jetties alongside focal patch and seascape characteristics on various fish assemblage metrics.

| **Abundance (MeanCount)** | | | |
|---|---|---|---|
| | Chisq | Df | Pr(>Chisq) |
| Treatment | 9.7737 | 1 | 0.00177 |
| **Species Richness** | | | |
| | Chisq | Df | Pr(>Chisq) |
| Treatment | 1.00E-04 | 1 | 0.9926 |
| **Diversity** | | | |
| | Chisq | Df | Pr(>Chisq) |
| Treatment | 2.2527 | 1 | 0.1334 |
| **Proportion of Juveniles** | | | |
| | Chisq | Df | Pr(>Chisq) |
| Treatment | 5.4293 | 1 | 0.0198 |

**Table B3** - Results of the statistical tests analysing the effect of proximity to jetties alongside focal patch and seascape characteristics on the behaviour of all fish observed throughout the stereo-RUVs. A) Comparison of proportion of behaviour observed between jetty-adjacent seagrass and seagrass far from jetties. B) Comparison between rates of behaviour within each treatment. C) Relationships between behaviour and continuous predictors.

**A)**

| Behaviour | Contrast | Estimate | SE | df | t.ratio | p.value |
|---|---|---|---|---|---|---|
| Feeding | Jetty-Adjacent Seagrass – Seagrass Far from Jetties | -0.7289 | 0.365 | 68.8 | -1.999 | 0.0495 |
| Passing | Jetty-Adjacent Seagrass - Seagrass Far from Jetties | 0.0639 | 0.309 | 68.8 | 0.207 | 0.8365 |
| Foraging | Jetty-Adjacent Seagrass - Seagrass Far from Jetties | 0.1524 | 0.302 | 68.8 | 0.505 | 0.6152 |

**B)**

| Treatment | Contrast | Estimate | SE | df | t.ratio | p.value |
|---|---|---|---|---|---|---|
| Jetty-Adjacent Seagrass | Feeding - Passing | -2.6027 | 0.436 | 68.8 | -5.964 | <.0001 |
| Jetty-Adjacent Seagrass | Feeding - Scavenging | -2.7464 | 0.415 | 68.8 | -6.615 | <.0001 |
| Jetty-Adjacent Seagrass | Passing - Foraging | -0.1437 | 0.33 | 68.8 | -0.436 | 0.9622 |
| Seagrass Far from Jetties | Feeding - Passing | -1.8098 | 0.384 | 68.8 | -4.711 | <.0001 |
| Seagrass Far from Jetties | Feeding - Foraging | -1.865 | 0.372 | 68.8 | -5.007 | <.0001 |
| Seagrass Far from Jetties | Passing - Foraging | -0.0552 | 0.317 | 68.8 | -0.174 | 0.9974 |

**C)**

| **Behaviour of Fish** | | | | |
|---|---|---|---|---|
| Predictor | edf | Ref.df | Chi.sq | p-value |
| s(Total area of *Zostera* meadows in the seascape):Feeding | 0.84 | 22.00 | 5.1840 | 0.0124 |
| s(Total area of *Zostera* meadows in the seascape):Passing | 0.00 | 2.00 | 0.0000 | 0.6438 |
| s(Total area of *Zostera* meadows in the seascape):Foraging | 0.00 | 2.00 | 0.0000 | 0.9065 |
| s(Focal Patch Shape Index):Feeding | 1.76 | 2.00 | 14.1070 | 0.0003 |
| s(Focal Patch Shape Index):Passing | 0.64 | 2.00 | 1.7160 | 0.1020 |
| s(Focal Patch Shape Index):Foraging | 0.00 | 2.00 | 0.0000 | 0.9727 |

**Table B4** – Results of the GAMLSS model of the length frequency distribution of Yellowfin Bream

**Length-Frequency Distribution of Yellowfin Bream**

**Mu Coefficients**

| | Estimate | Std. Error | t value | Pr(>\|t\|) |
|---|---|---|---|---|
| (Intercept) | 4.95753 | 0.01248 | 397.382 | < 2e-16 |
| TreatmentS | -0.08876 | 0.01895 | -4.685 | 3.13E-06 |

**Sigma Coefficients**

| | Estimate | Std. Error | t value | Pr(>\|t\|) |
|---|---|---|---|---|
| (Intercept) | -1.22723 | 0.02762 | -44.43 | <2e-16 |
| TreatmentS | 0.4077 | 0.04062 | 10.04 | <2e-16 |

**Table B5** – Results of the multivariate PERMANOVA analysis looking at the differences in community composition between treatments.

**PERMANOVA**

| | Df | SumOfSqs | R2 | F | Pr(>F) |
|---|---|---|---|---|---|
| Treatment | 1 | 0.1689 | 0.03947 | 0.8831 | 0.525 |
| Landscape Fragmentation Index | 1 | 0.1191 | 0.02784 | 0.6229 | 0.386 |
| Total area of *Zostera* meadows within the seascape | 1 | 0.045 | 0.01051 | 0.2353 | 0.901 |
| Focal Patch Shape | 1 | 0.1104 | 0.02581 | 0.5775 | 0.792 |
| Total area of *Posidonia* meadows within the seascape | 1 | 0.0777 | 0.01815 | 0.4062 | 0.745 |
| Residual | 19 | 3.633 | 0.8491 | | |
| Total | 25 | 4.2787 | 1 | | |

**Table B6** – Influence of the area of jetties within the seascape on only the seagrass meadows adjacent to jetties. Statistical analysis was only run in the presence of a significant treatment effect (Table B2)

**Abundance**

| Predictor | Chisq | Df | Pr(>Chisq) |
|---|---|---|---|
| Total area of jetties within the seascape | 0.1212 | 1 | 0.7277 |

**Proportion of Juveniles**

| Predictor | Chisq | Df | Pr(>Chisq) |
|---|---|---|---|
| Total area of jetties within the seascape | 0.2291 | 1 | 0.6322 |

**Behaviour of Fish**

| Predictor | edf | Ref.df | Chi.sq | p-value |
|---|---|---|---|---|
| s(Total area of jetties within the seascape):Feeding | 6.31E-01 | 2.00E+00 | 1.848 | 0.087 |
| s(Total area of jetties within the seascape):Passing | 1.59E-01 | 2.00E+00 | 0.211 | 0.249 |
| s(Total area of jetties within the seascape):Foraging | 6.82E-06 | 2.00E+00 | 0 | 0.389 |

# Appendix B2 - Diagnostic plots for each of the statistical models

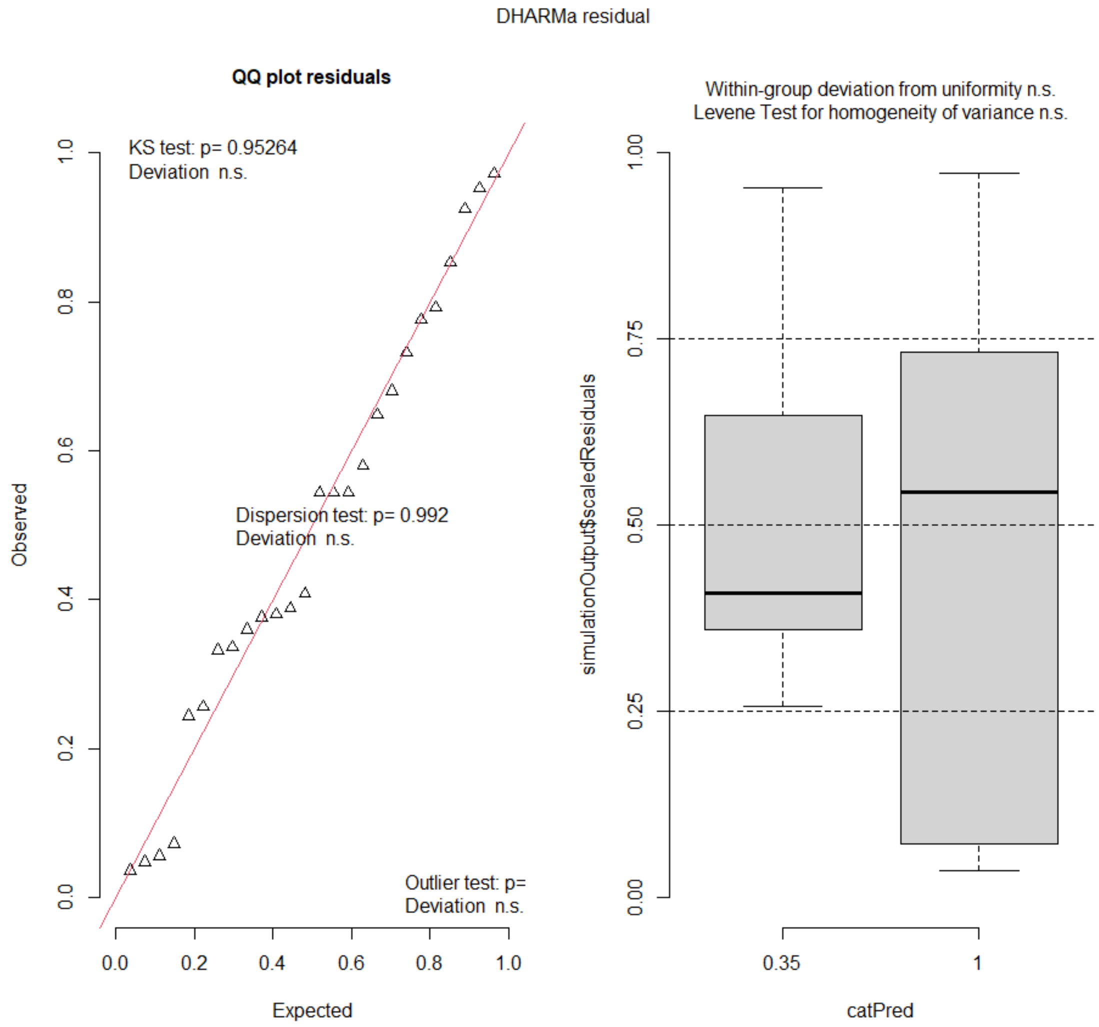

**Figure B1** – *DHARMa* scaled residual diagnostics for the Total Abundance (MeanCount) statistical model. All diagnostic tests (deviation, dispersion, outliers, and homogeneity of variance) were non-significant, indicating the model meets statistical assumptions

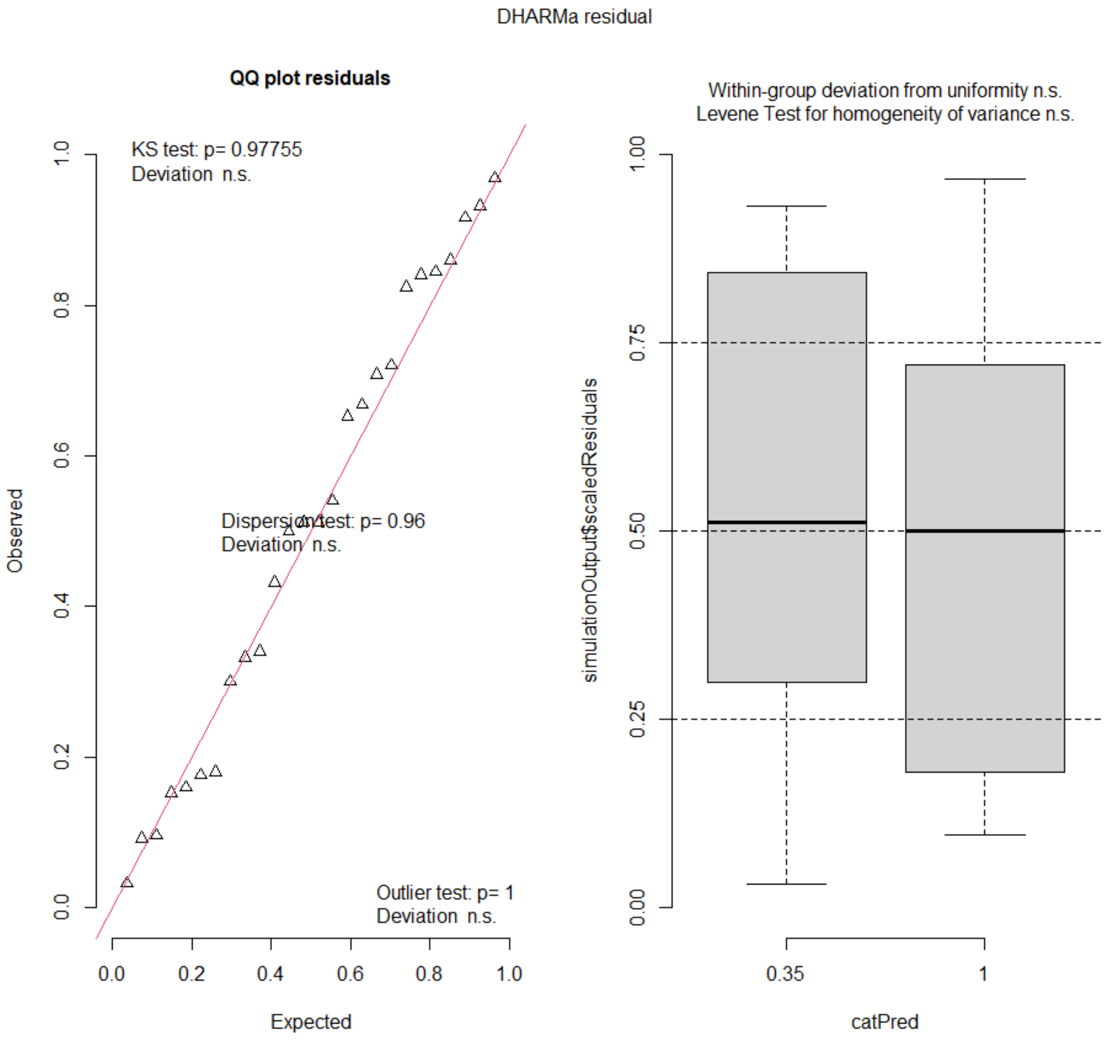

**Figure B2** – *DHARMa* scaled residual diagnostics for the species richness statistical model. All diagnostic tests (deviation, dispersion, outliers, and homogeneity of variance) were non-significant, indicating the model meets statistical assumptions

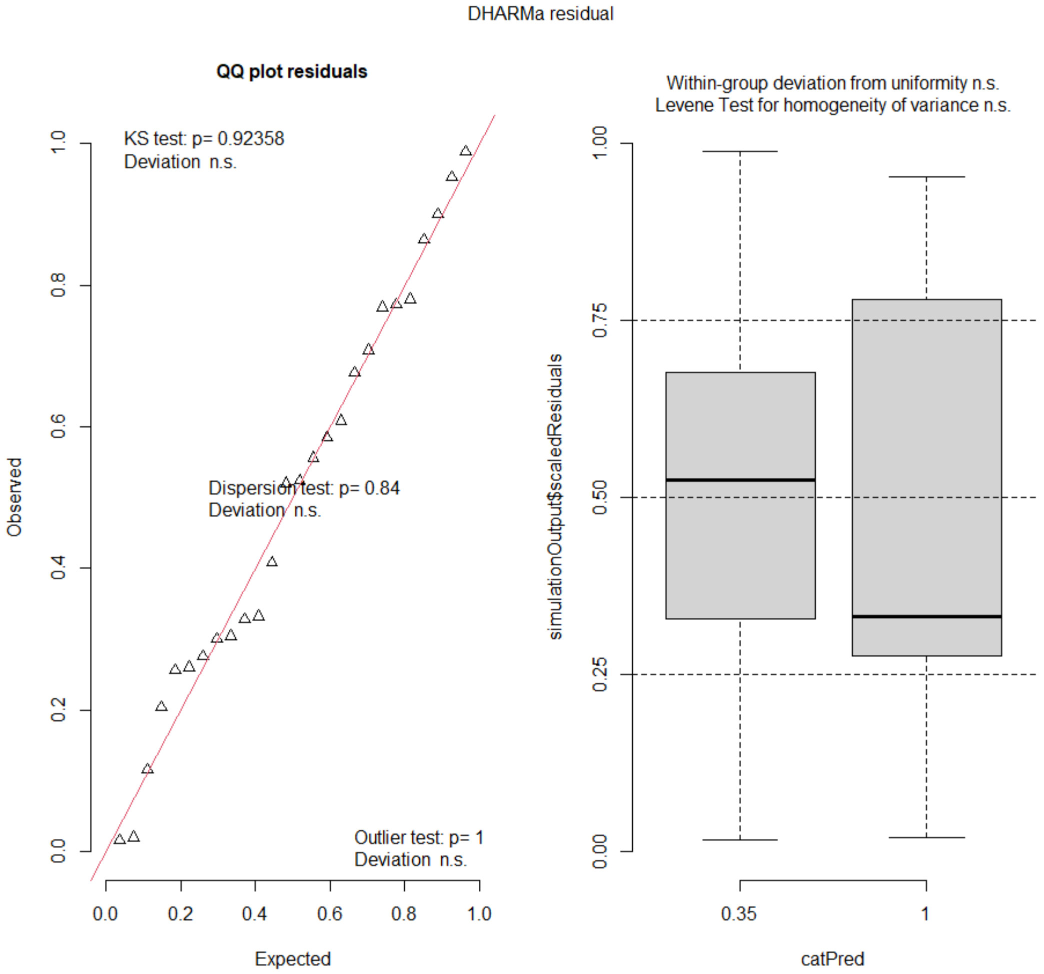

**Figure B3** – *DHARMa* scaled residual diagnostics for the diversity statistical model. All diagnostic tests (deviation, dispersion, outliers, and homogeneity of variance) were non-significant, indicating the model meets statistical assumptions

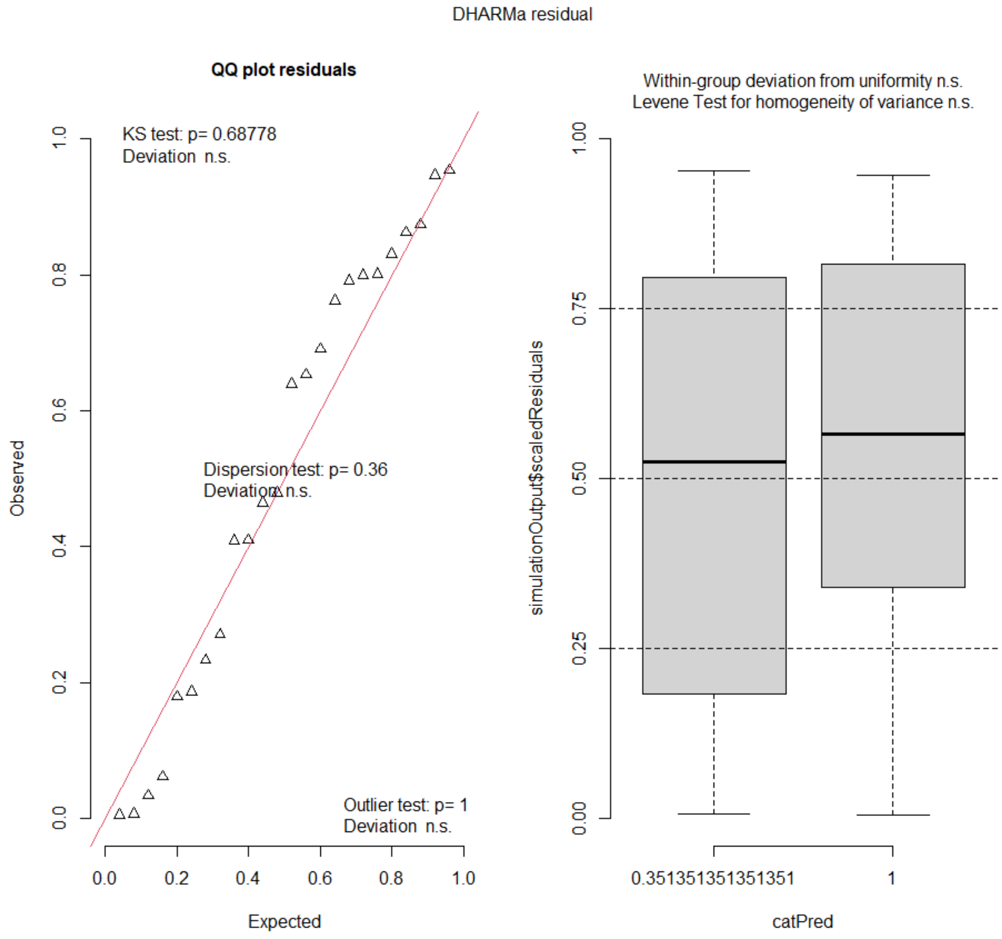

**Figure B4** – *DHARMa* scaled residual diagnostics for the proportion of juvenile fish within the assemblage statistical model. All diagnostic tests (deviation, dispersion, outliers, and homogeneity of variance) were non-significant, indicating the model meets statistical assumptions

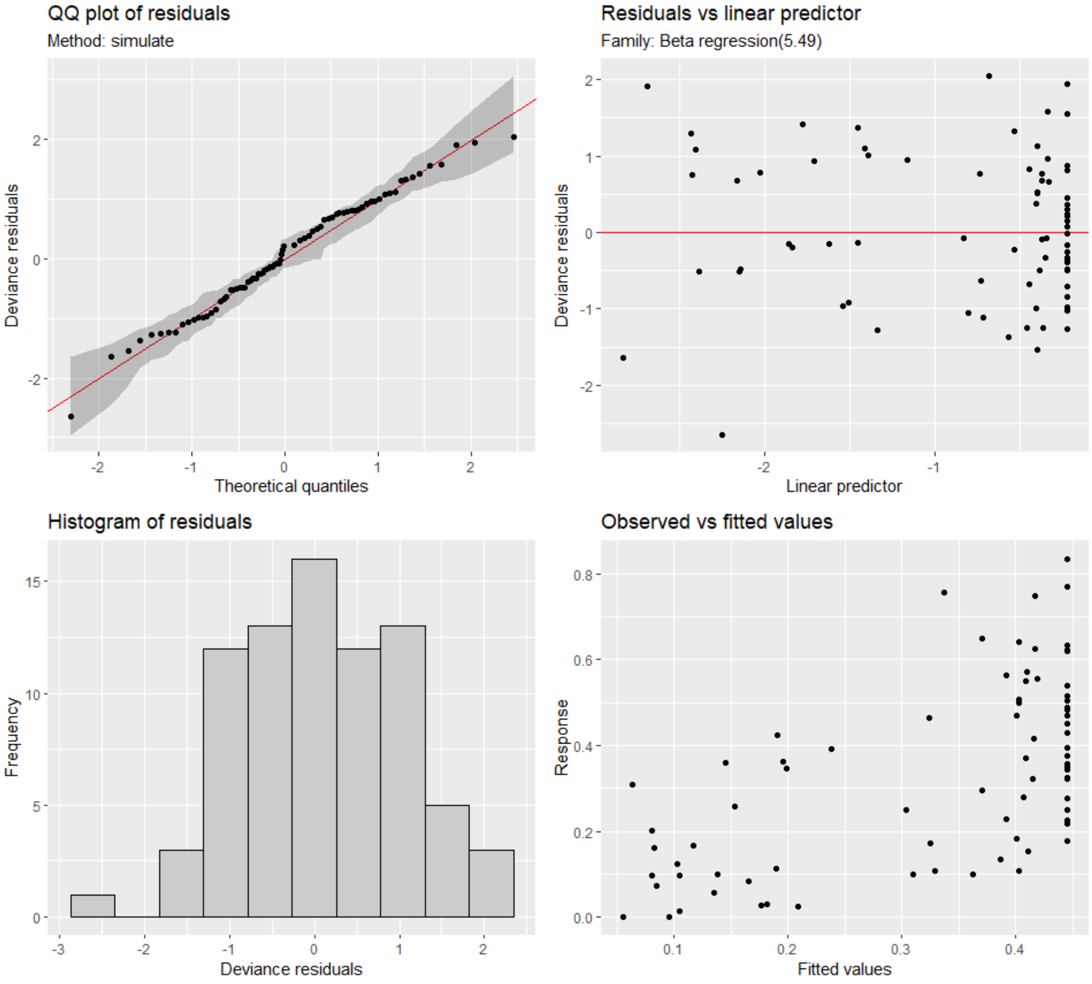

**Figure B5** – Diagnostic plots for the beta regression model looking at fish behaviour. Plots include Q-Q plot with simulation envelope, residuals versus linear predictor, histogram of deviance residuals, and observed versus fitted values, all indicating adequate model fit

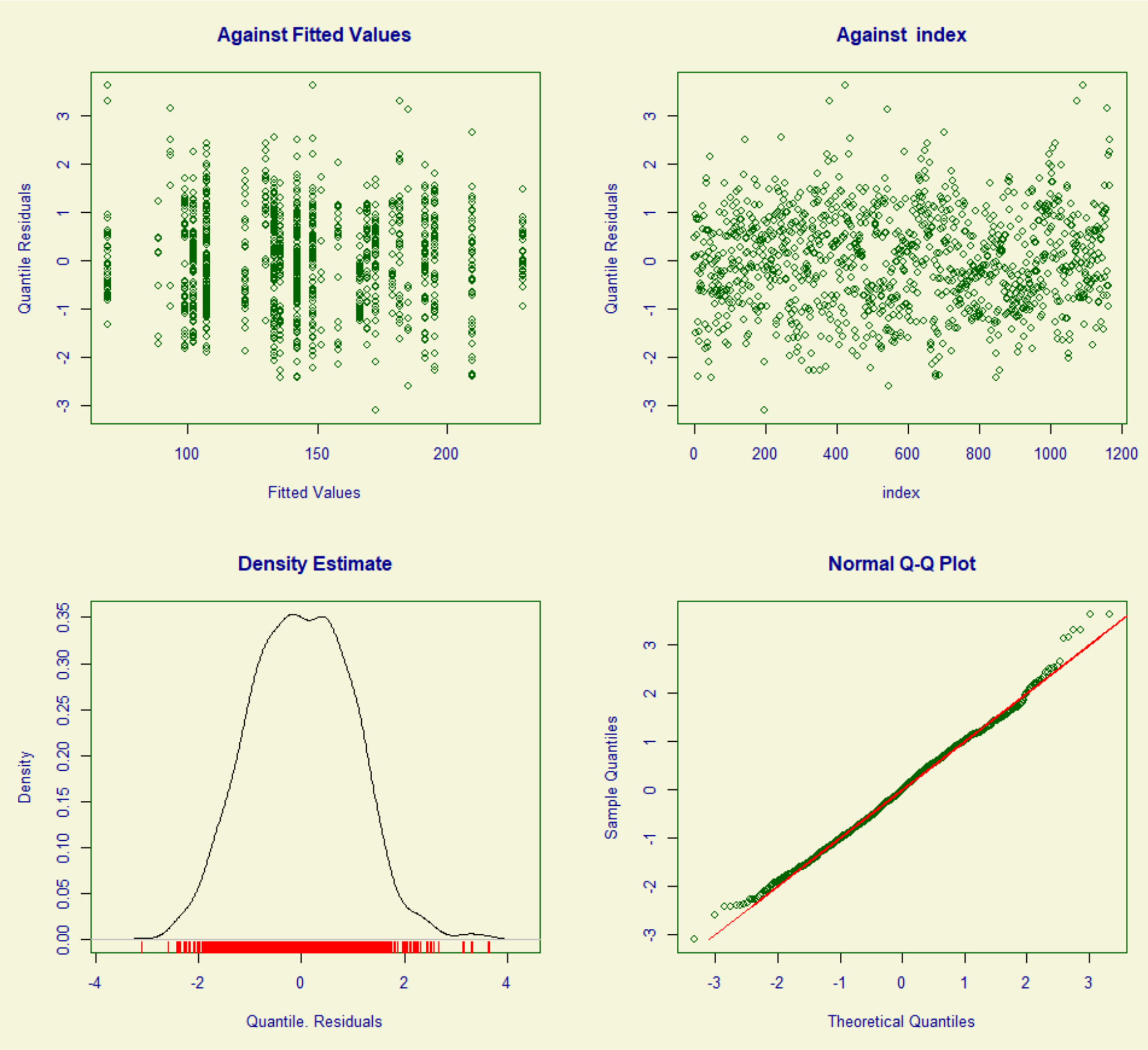

**Figure B6** – Diagnostic plots for the GAMLSS model of length frequency distribution of yellowfin bream. Panels display quantile residuals against fitted values and index, density estimate of residuals, and normal Q-Q plot, indicating the model meets distributional assumptions

# Appendix B3 – List of Species Observed in Chapter 3 (Lake Macquarie *Zostera capricorni* meadows)

| **Common Name** | **Genus** | **Species** |
|---|---|---|
| Yellowfin Bream | *Acanthopagrus* | *australis* |
| Australasian Snapper | *Chrysophrys* | *auratus* |
| Silverbiddy | *Gerres* | *subfasciatus* |
| Luderick | *Girella* | *tricuspidata* |
| Rock Blackfish | *Girella* | *elevata* |
| Goldspot Mullet | *Gracilimugil (formerly Liza)* | *argenteus (formerly argentea)* |
| Yellowfin Leatherjacket | *Meuschenia* | *trachylepis* |
| Brownstriped Leatherjacket | *Meuschenia* | *australis* |
| Fanbelly Leatherjacket | *Monacanthus* | *chinensis* |
| Sea Mullet | *Mugil* | *cephalus* |
| Rotund Blenny | *Omobranchus* | *rotundiceps* |
| Eastern Striped Grunter | Pelates | sexlineatus |
| Gunthers Wrasse | *Pseudolabrus* | *guentheri* |
| Sand Whiting | *Sillago* | *ciliata* |
| Striped Barracuda | *Sphyraena* | *obtusata* |
| Moon Wrasse | *Thalassoma* | *lunare* |
| Stout Longtom | *Tylosurus* | *gavialoides* |
| Australian Goatfish | *Upeneus* | *australiae* |

# Appendix C | Supplementary material for Chapter 4

## Appendix C1 – Supplementary material for the statistics in Chapter 4

**Figure C1** – Correlation Matrix for all the focal patch and seascape characteristics calculated

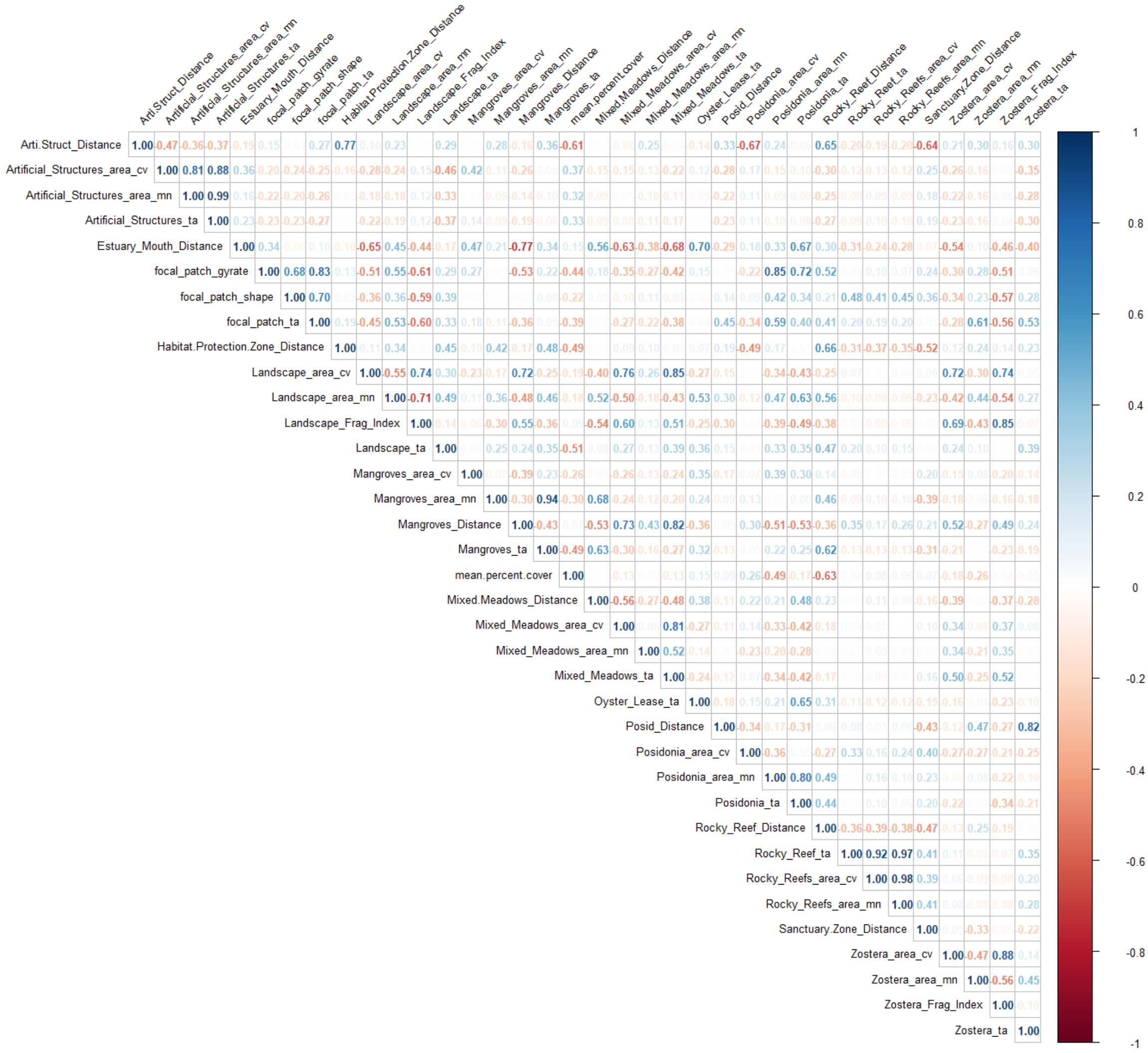

**Table C1** - List of variables not included for the analysis due to low number of unique variables observed (less than or equal to 5), done prior to removal of colinear variables

| Variable | Reason |
|---|---|
| Total area of Mangroves within the Seascape | Less than 5 unique variables |
| Total area of Artificial structures within the Seascape | Less than 5 unique variables |
| Total area of Rocky Reefs within the Seascape | Less than 5 unique variables |
| Total area of oyster leases within the Seascape | Less than 5 unique variables |

**Table C2** – Best statistical models predicting the various fish metrics assessed in Chapter 4; A) Total Abundance (MeanCount); B) Species Richness; C) Diversity (Shannon H Index); D) Proportion of Juveniles within the Assemblage. All models within +/- 2 AICc values are presented here.

**A)**

**Total Abundance (MeanCount)**

| Model Structure | AICc | BIC | r2.vals | edf | delta.AICc | delta.BIC | wi.AICc | wi.BIC |
|---|---|---|---|---|---|---|---|---|
| Total area of Posidonia within the Seascape | 63.05 | 64.56 | 0.08 | 2.28 | 0.00 | 0.43 | 0.11 | 0.08 |
| Distance from the Estuary Mouth | 63.37 | 65.04 | 0.07 | 2.00 | 0.32 | 0.91 | 0.10 | 0.06 |
| Mean Percent Cover+Distance from Posidonia Meadows | 63.91 | 64.19 | 0.17 | 3.87 | 0.86 | 0.06 | 0.07 | 0.09 |
| Total area of Mixed Seagrass Meadows within the Seascape | 64.04 | 65.30 | 0.21 | 2.74 | 0.99 | 1.17 | 0.07 | 0.05 |
| Distance from Rocky Reefs | 64.31 | 65.54 | 0.12 | 2.86 | 1.26 | 1.41 | 0.06 | 0.05 |
| Distance from the Estuary Mouth+Distance from Rocky Reefs | 64.83 | 65.15 | 0.19 | 3.79 | 1.78 | 1.01 | 0.05 | 0.06 |
| Distance from Posidonia Meadows | 64.98 | 66.23 | 0.11 | 2.78 | 1.93 | 2.10 | 0.04 | 0.03 |

**B)**

**Species Richness**

| Model Structure | AICc | BIC | r2.vals | edf | delta.AICc | delta.BIC | wi.AICc | wi.BIC |
|---|---|---|---|---|---|---|---|---|
| Total Amount of Habitat within the Seascape+Distance from Posidonia Meadows | 106.37 | 107.69 | 0.53 | 3.85 | 0.00 | 0.00 | 0.38 | 0.32 |
| Total Amount of Habitat within the Seascape+Distance from Mixed Seagrass Meadows+Distance from Posidonia Meadows | 108.53 | 107.84 | 0.64 | 5.66 | 2.16 | 0.15 | 0.13 | 0.30 |
| Mean Percent Cover | 109.60 | 111.32 | 0.27 | 2.00 | 3.23 | 3.64 | 0.08 | 0.05 |
| Total Amount of Habitat within the Seascape | 110.32 | 112.07 | 0.30 | 2.55 | 3.95 | 4.38 | 0.05 | 0.04 |
| Mean Percent Cover+Distance from Posidonia Meadows | 111.28 | 112.96 | 0.31 | 3.00 | 4.92 | 5.28 | 0.03 | 0.02 |
| Mean Percent Cover+Distance from Mixed Seagrass Meadows | 111.59 | 113.27 | 0.30 | 3.00 | 5.22 | 5.58 | 0.03 | 0.02 |

**C)**

**Diversity (Shannon's H)**

| Model Structure | AICc | BIC | r2.vals | edf | delta.AICc | delta.BIC | wi.AICc | wi.BIC |
|---|---|---|---|---|---|---|---|---|
| Focal Patch Size+Distance from Marine Sanctuary Zones | 27.78 | 29.06 | 0.47 | 3.91 | 0.00 | 0.00 | 0.18 | 0.18 |
| Distance from Marine Sanctuary Zones | 28.43 | 30.13 | 0.35 | 2.88 | 0.65 | 1.08 | 0.13 | 0.10 |
| Total area of Posidonia within the Seascape | 29.84 | 31.56 | 0.21 | 2.00 | 2.06 | 2.51 | 0.06 | 0.05 |
| Total Amount of Habitat within the Seascape+Distance from Marine Sanctuary Zones | 29.96 | 31.25 | 0.41 | 3.89 | 2.18 | 2.19 | 0.06 | 0.06 |
| Distance from Mixed Seagrass Meadows+Distance from Marine Sanctuary Zones | 30.41 | 31.27 | 0.46 | 4.45 | 2.63 | 2.22 | 0.05 | 0.06 |
| Mean Percent Cover+Distance from Marine Sanctuary Zones | 30.43 | 31.33 | 0.46 | 4.41 | 2.66 | 2.27 | 0.05 | 0.06 |

**D)**

**Juvenile Proportion**

| Model Structure | AICc | BIC | r2.vals | edf | delta.AICc | delta.BIC | wi.AICc | wi.BIC |
|---|---|---|---|---|---|---|---|---|
| Distance from Mixed Seagrass Meadows | -1.95 | -1.25 | 0.33 | 3.86 | 0.00 | 0.00 | 0.40 | 0.28 |
| Focal Patch Shape Index+Distance from Rocky Reefs | 0.60 | 0.23 | 0.47 | 4.67 | 2.56 | 1.48 | 0.11 | 0.14 |
| Total Amount of Habitat within the Seascape+Distance from Mixed Seagrass Meadows | 1.69 | 1.10 | 0.36 | 4.89 | 3.64 | 2.35 | 0.06 | 0.09 |
| Distance from Mixed Seagrass Meadows+Distance from Posidonia Meadows | 2.03 | 1.56 | 0.34 | 4.85 | 3.98 | 2.81 | 0.05 | 0.07 |
| Distance from Rocky Reefs | 2.04 | 3.52 | 0.15 | 2.00 | 3.99 | 4.77 | 0.05 | 0.03 |
| Distance from Mixed Seagrass Meadows+Distance from Marine Sanctuary Zones | 2.05 | 1.60 | 0.35 | 4.82 | 4.01 | 2.85 | 0.05 | 0.07 |

## Appendix C2 – List of Species Observed in Chapter 4 (Port Stephens *Zostera capricorni* meadows)

| Common Name | Genus | Species |
|---|---|---|
| Yellowfin Bream | *Acanthopagrus* | *australis* |
| Black Bream | *Acanthopagrus* | *butcheri* |
| Eastern Smooth Boxfish | *Anoplocapros* | *inermis* |
| Eastern Shovelnose Ray | *Aptychotrema* | *rostrata* |
| Australasian Snapper | *Chrysophrys* | *auratus* |
| Australasian Snapper | *Chrysophrys* | *auratus* |
| Threebar Porcupinefish | *Dicotylichthys* | *punctulatus* |
| Gunns Leatherjacket | *Eubalichthys* | *gunnii* |
| Smooth Flutemouth | *Fistularia* | *commersonii* |
| Silverbiddy | *Gerres* | *subfasciatus* |
| Luderick | *Girella* | *tricuspidata* |
| Estauary Stingray | *Hemitrygon* | *fluviorum* |
| Sandy Sprat | *Hyperlophus* | *vittatus* |
| Banded Toadfish | *Marilyna* | *pleurosticta* |
| Yellowfin Leatherjacket | *Meuschenia* | *trachylepis* |
| Fanbelly Leatherjacket | *Monacanthus* | *chinensis* |
| Sea Mullet | *Mugil* | *cephalus* |
| Ocean Leatherjacket | *Nelusetta* | *ayraudi* |
| Bluespotted Maskray | *Neotrygon* | *australiae* |
| Rotund Blenny | *Omobranchus* | *rotundiceps* |
| Striped Cardinalfish | *Ostorhinchus* | *fasciatus* |
| Horned Blenny | *Parablennius* | *intermedius* |
| Southern Grubfish | *Parapercis* | *australis* |
| Blacksaddle Goatfish | *Parupeneus* | *spilurus* |
| Eastern Striped Grunter | Pelates | sexlineatus |
| Silvery Trevally | *Pseudocaranx* | *georgianus* |
| Gunthers Wrasse | *Pseudolabrus* | *guentheri* |
| Striped Scat | *Selenotoca* | *multifasciata* |
| Yellowtail Kingfish | *Seriola* | *lalandi* |
| Sand Whiting | *Sillago* | *ciliata* |
| Striped Barracuda | *Sphyraena* | *obtusata* |
| Weeping Toadfish | *Torquigener* | *pleurogramma* |
| Common Stingaree | *Trygonoptera* | *testacea* |
| Eastern Fiddler Ray | *Trygonorrhina* | *fasciata* |
| Bluestriped Goatfish | *Upeneichthys* | *lineatus* |
| Australian Goatfish | *Upeneus* | *australiae* |

# Appendix D | Supplementary material for Chapter 5

**Table S1** – Percent contribution of predictors to the *Zostera capricorni* MaxENT habitat suitability model. Higher percentages indicate that a particular variable was used more often to predict habitat suitability.

| Variable | Importance (%) |
|---|---|
| Depth (m) | 91.22 |
| Distance from Posidonia meadows | 1.99 |
| Mean Yearly Turbidity (NDTI) | 1.78 |
| Distance from Mangroves (m) | 1.45 |
| Mean Yearly Salinity | 1.22 |
| Distance from Estuary Mouth (m) | 1.05 |
| Mean_Wave_Height | 0.63 |
| Tidal_Max (m) | 0.53 |
| Distance from Sanctuary Zones (m) | 0.12 |

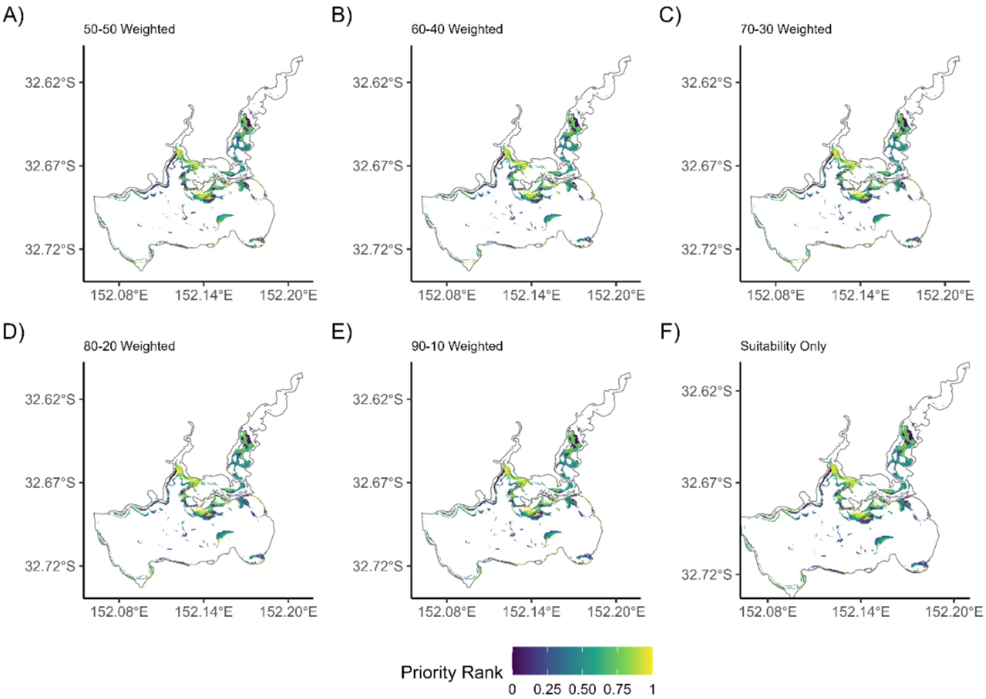

**Figure D1** - Priority rank maps for all the various prioritisation scenarios with different weightings of seagrass habitat suitability to all other fish assemblage metrics. The rank of a cell (0-1) indicates the priority/order in which the cell should be restored.

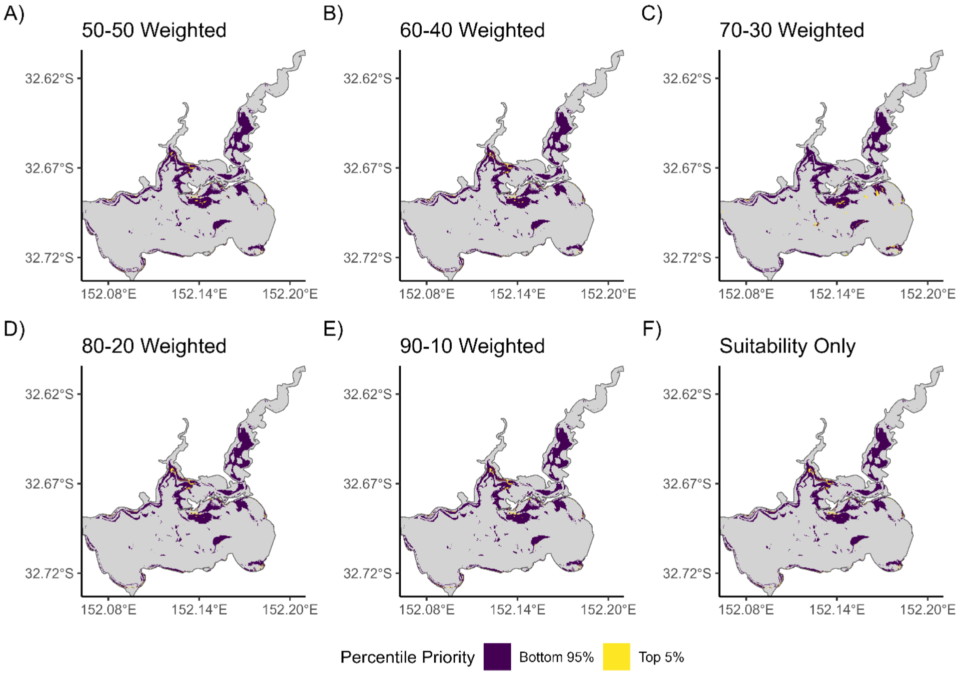

**Figure D2** - Restoration Solutions as Determined by the top 5th percentile priority ranks for all the various prioritisation scenarios with different weightings of seagrass habitat suitability to all other fish assemblage metrics. Purple Areas represent areas selected. Yellow areas represent areas not selected.

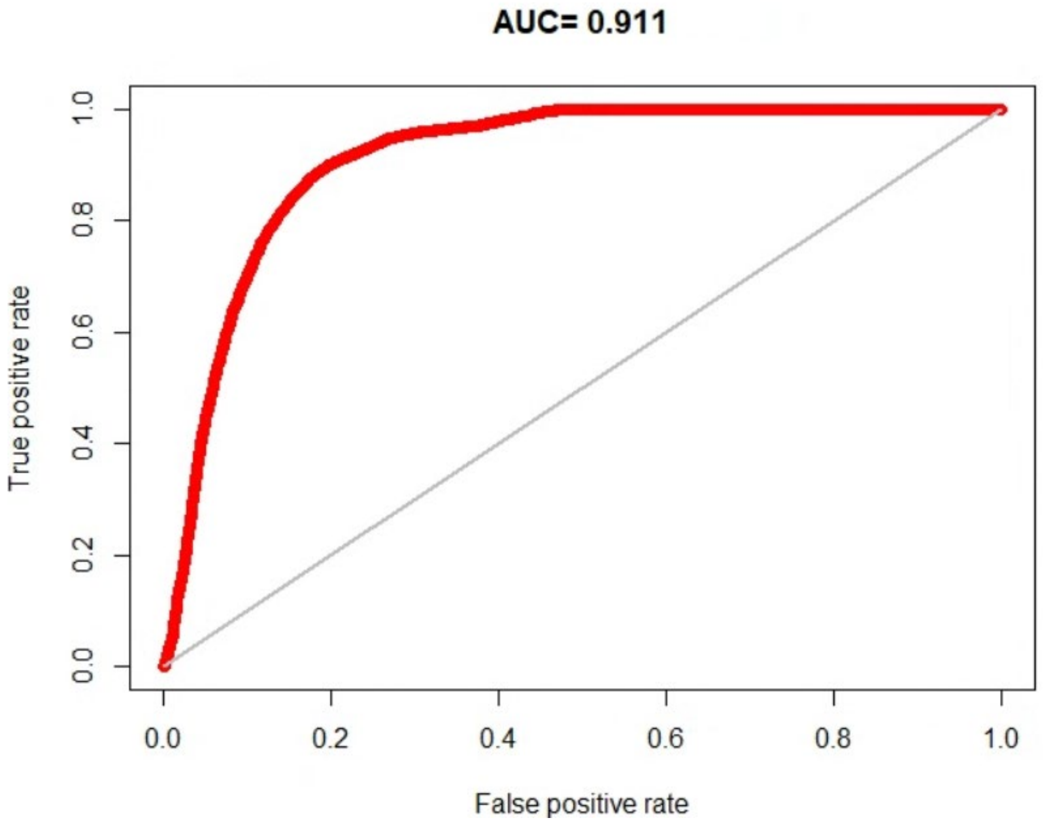

**Figure D3** – Area under the receiver operating curve (AUC-ROC) illustrating the accuracy of the *Zostera* habitat suitability model predictions over the 5-fold model cross validation. Red line represents the mean AUC curve. The black line represents the AUC curve if the model was as accurate as a random prediction. An AUC value of 0.5 indicates the model is as good as a 50/50 guess. An AUC value of 1 indicates that the model predicts all true presences with a 100% rate.

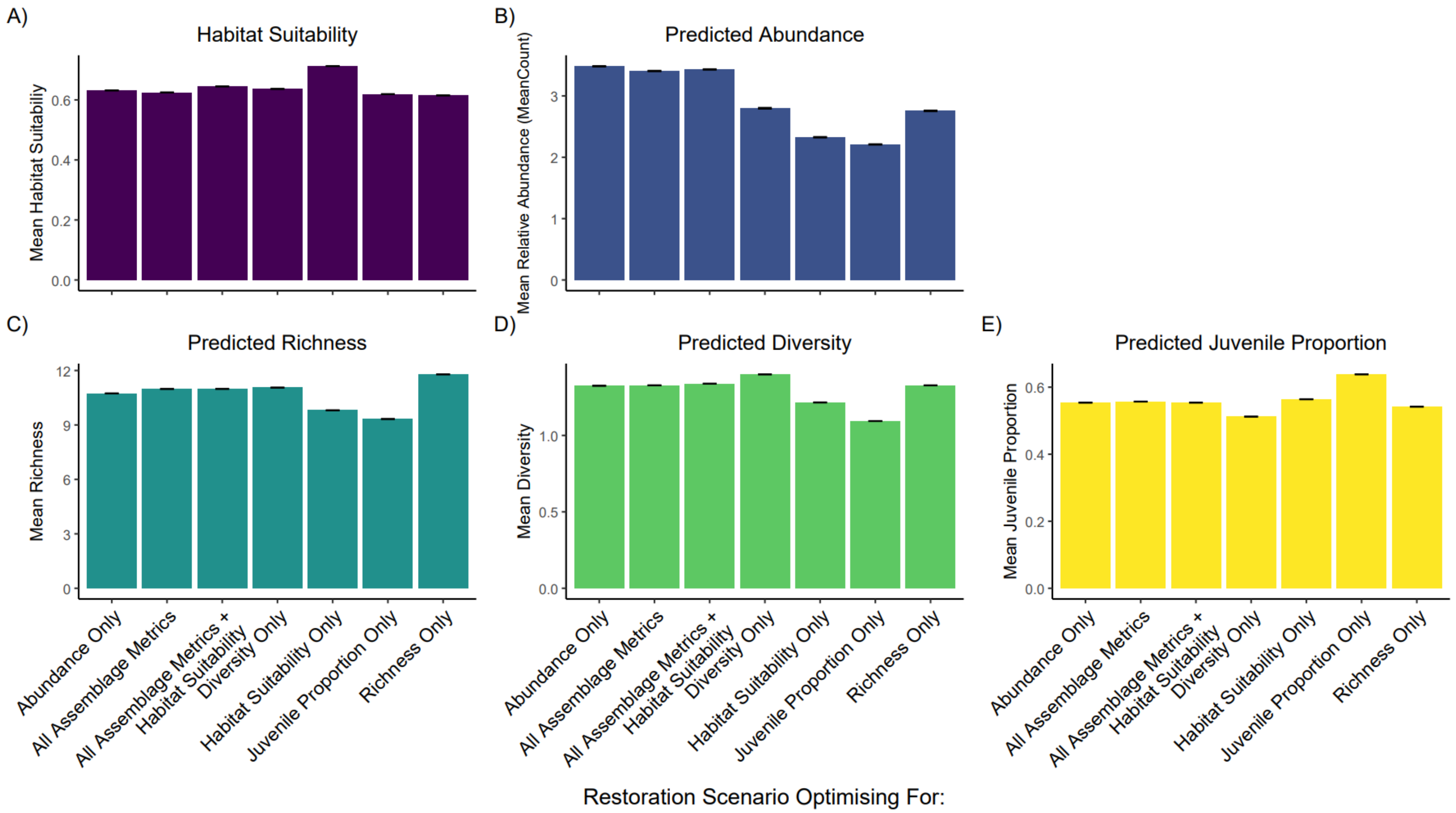

**Figure D4 -** Performance of restoration sites selected from different restoration prioritisation scenarios across multiple outcomes faceted by each ecological metric. A) *Zostera capricorni* habitat suitability. B) predicted fish abundance. C) Predicted species richness. D) Predicted diversity – Shannon H. E) Predicted proportion of juvenile fish within the assemblage. Error bars represent the standard error.

# Appendix E | Methodology for Deriving Seagrass Density (Percent Cover)

Seagrass percent cover was assessed using three spatially balanced $1m^2$ quadrats per patch (Heidelbaugh & Nelson, 1996). The spatially balanced sampling locations within each patch were generated using the spatially balanced algorithm (BAS) in the *MBHdesign* R package (Foster 2021). I employed a point intercept method using a 50x50 point grid and averaged the three quadrat measurements to obtain mean percent cover for each patch.