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Climate-change resilience and positive scope for growth in wild adult Sydney rock oysters, *Saccostrea glomerata* (Gould, 1850)

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ABSTRACT

Context. Oysters have ecological and economic importance worldwide because they provide ecosystem services and sustain profitable aquaculture industries. Calcifying bivalves including oysters have been found to be sensitive to ocean warming and acidification caused by anthropogenic climate change. **Aims.** This study tested whether adult wild Sydney rock oysters, *Saccostrea glomerata*, have resilience and can maintain sufficient scope for growth or are pushed into a suboptimal state. **Methods.** Oysters were exposed to elevated $p\mathrm{CO}_2$ (335 and 857 µatm) and temperature (24 and 28°C) in an orthogonal design for 5 weeks. At the end of the exposure, growth, condition index, clearance, ingestion and absorption efficiency and rates were measured and scope for growth calculated. **Key results.** Sydney rock oysters responded to elevated $p\mathrm{CO}_2$ and temperature with no change in overall growth or condition index, but with significantly increased metabolic, clearance, ingestion, and absorption rates and positive scope for growth. **Conclusions.** Our results indicated that adult *S. glomerata* can cope with the moderate level of climate-change stress predicted for 2100, through increased standard metabolic rate and increased energetic processes. **Implications.** If food availability becomes limiting, and other environmental stressors interact with climate change stressors, then resilience thresholds maybe breached for this economically, ecologically and indigenous significant and iconic oyster species.

Keywords: bivalves, climate change, ocean acidification, ocean warming, oysters, resilience, scope for growth, stress.

Introduction

Anthropogenic disturbance to the earth's climate system is causing alterations to the physical and chemical properties of the world's oceans, habitats and biodiversity (Arias *et al.* 2021; Fox-Kemper *et al.* 2021; Lee *et al.* 2021; Pörtner *et al.* 2023). Climate change has altered seawater chemistry and surface-ocean pH has decreased by ~0.1 units compared with that in pre-industrial times in a process known as ocean acidification (OA) (Doney *et al.* 2009; Hoegh-Guldberg and Bruno 2010). Alterations of the partial pressure of CO_2 ($p\mathrm{CO}_2$), have directly influenced the concentration of carbonate ions, and calcite and aragonite saturation states and pH (Doney *et al.* 2009).

Impacts of OA on marine life have been widely reported (Kroeker *et al.* 2010; Riebesell and Gattuso 2015; Ross *et al.* 2023, 2024), including on feeding (Fernández-Reiriz *et al.* 2011; Ross *et al.* 2011; Vargas *et al.* 2013), homeostasis and acid–base status (Melzner *et al.* 2009), energy budgets and basal metabolism (Parker *et al.* 2015, 2024; Pereira *et al.* 2019) and growth and calcification (Ries *et al.* 2009; Chan *et al.* 2013; Gazeau *et al.* 2013; Wright *et al.* 2014; Byrne and Fitzer 2019; Ross *et al.* 2023, 2024). In addition to OA, emissions of CO_2 are causing ocean warming (OW), a pervasive stressor that will also affect marine organisms in many ways (Schulte 2015; Hobday *et al.* 2016, 2023). Studies evaluating the effect of OW predicted for the end of this century have reported impacts on feeding behaviour, growth, metabolism, biomineralisation and survivorship of a range of species (Ivanina *et al.* 2013; Ramajo *et al.* 2016*a*, 2016*b*; Wernberg *et al.* 2016, 2024; Pereira *et al.* 2020, 2024) or no impact (Lemasson *et al.* 2017; Ewere *et al.* 2021), implying resilience to OW in short term exposures.

When combined, OA and OW are predicted to interact in synergistic, antagonistic or additive ways (Folt *et al.* 1999; Parker *et al.* 2009; Byrne 2011; Byrne and Przeslawski 2013; Przeslawski *et al.* 2015; Riebesell and Gattuso 2015) or have little impact (Lemasson *et al.* 2017; Ewere *et al.* 2021). Synergistic impacts are when the combined effect of stressors is greater than the sum of individual impacts, whereas antagonistic impacts are when the combined impact is less than the sum of individual impacts. By contrast, additive impacts are when the combined impact is equal to the sum of individual impacts. In an early meta-analysis, Byrne and Przeslawski (2013) found that additive or antagonistic effects of OA and OW were the most common in 16 of 20 species studied. However, a later, more robust meta-analysis suggested that synergistic impacts (65% of individual tests) were more common than additive (17%) or antagonistic (17%) interactions in vulnerable early life-history stages (Przeslawski *et al.* 2015). Understanding how OA and OW will interact together and whether they will be synergistic and increase, be additive or be antagonistic and decrease to ameliorate the severity of impacts on marine species requires further investigation (Somero 2010; Byrne and Przeslawski 2013; Ewere *et al.* 2021; Ross *et al.* 2023).

It is known that bivalves, such as mussels and oysters, are at 'very high risk' to the impacts of climate change (Kroeker *et al.* 2010, 2013; Ross *et al.* 2011, 2024; Gattuso *et al.* 2015; Neokye *et al.* 2024*a*, 2024*b*). Several meta-analyses have reported studies with negative effects of OA and OW on calcifying bivalves, with oysters being identified as particularly vulnerable (Kroeker *et al.* 2013; Leung *et al.* 2022; Ross *et al.* 2023, 2024). Climate change has been found to decrease the growth and calcification and increase the metabolic rate of adult oysters (Beniash *et al.* 2010; Wright *et al.* 2014; Lemasson *et al.* 2017; Parker *et al.* 2024), and increase the abnormality, mortality and metabolic rates of larval oysters (Parker *et al.* 2012, 2015, 2017). Such changes are a concern because many bivalves have key ecological and foundational roles in coastal areas, being habitat and reef-forming species and providing important ecosystem services (Coen *et al.* 2007; Grabowski and Peterson 2007; Beck *et al.* 2009, 2011; Lemasson *et al.* 2017; Wernberg *et al.* 2024). In many countries, bivalves are also important aquaculture species with indigenous significance (Treviño *et al.* 2020; Peng *et al.* 2021; Valenti *et al.* 2021; Gibbs *et al.* 2023, 2024).

Studies have also found that OA as a sole stressor can alter a range of physiological processes to reduce the feeding rates of bivalves (Clements and Darrow 2018), increase standard metabolic rate (SMR) (Beniash *et al.* 2010, *Crassostrea virginica*; Parker *et al.* 2015 and Scanes *et al.* 2017, *S. glomerata*) and alter immune response (Wu *et al.* 2016, *Mytilus coruscus*). For example, OA reduced the feeding rates and nutrient intake of the grooved carpet clam (*Ruditapes decussatus*) a species also under pressure from harvesting, loss of habitat, pollution and hypoxia (Fernández-Reiriz *et al.* 2011). Similarly, when the oyster (*Crassostrea gigas*) was exposed to OA in Sanggou Bay, China, a decrease in their scope for growth was observed (Jiang *et al.* 2021). Sokolova *et al.* (2011) proposed the concept of energy-limited tolerance to stress to explain and predict the long-term persistence of species exposed to multiple climate-change stressors. Sokolova *et al.* (2011) described that the aerobic scope of species can decrease from an optimal state where the aerobic scope is at its maximum, covering basal energetic costs, growth and reproduction, to a suboptimal (pejus range), close to null (pessimum range) and then, ultimately, to a state where aerobic scope becomes negative at increasing levels of environmental stress. Using this energetic framework, the aerobic scope of populations during exposure to moderate stress can be conceived to exist at suboptimal or pejus level, when the aerobic scope is positive, but lower than optimal conditions (Sokolova 2013). Sokolova (2013) stated a reduction in aerobic scope from four areas, including (1) an increased cost of basal metabolism, (2) activation of mechanisms for protection and repair, (3) reduced food assimilation, and (4) impacts on ATP production (Sokolova 2013, p. 597). When environmental stress remains long enough, the aerobic scope of the organism can disappear as they enter the pessimum range, which prevents consistent growth and reproduction.

To maintain basal metabolism, marine organisms depend on food, which is captured, absorbed and converted to stored energy (Kooijman 2009). When OA and OW affect feeding, including ingestion and digestion, this can negatively affect marine organisms and potentially provide less capacity to withstand stress (Clements and Darrow 2018). How much an organism can metabolise will also directly influence how much individuals grow, invest in gametes, compete and endure adverse conditions. Whereas reduced absorption of food can push bivalves into the pejus range (Sokolova 2013), faster and more efficient feeding may balance energetic demands (Pörtner and Farrell 2008; Melzner *et al.* 2009, 2011; Hettinger *et al.* 2013; Thomsen *et al.* 2013).

An iconic, indigenous, culturally significant bivalve along the south-eastern Australian coast is the native Sydney rock oyster (*Saccostrea glomerata*), where it forms extensive biogenic reefs (Gillies *et al.* 2018) and supports an aquaculture industry and secondary sector worth A$430,000,000 year^{-1} and 1758 full-time jobs (Barclay *et al.* 2016). There are reasonable concerns about whether *S. glomerata* will survive as an aquacultural species until the end of the century. Studies have found that early life stages of this species are highly vulnerable to climate-change stressors, including OA and OW (Parker *et al.* 2009, 2010; Ross *et al.* 2024), but that parental exposure to OA can improve their response (Parker *et al.* 2012; Ross *et al.* 2024). Recent studies on the impact of both OA and OW on the resilience of selectively bred family lines of *S. glomerata* found that some family lines had resilience and a capacity to maintain their aerobic scope (Parker *et al.* 2024). However, it is not known whether wild oysters, which have not been selectively bred, have a capacity to maintain aerobic scope and energetic demands in response to OA and OW.

The aim of this study was to determine the combined impact of OA and OW on the scope for growth (SFG) as a measure of the energy available for growth and other fitness-sustaining processes, for example, reproduction (Parker *et al.* 2024) of non-selectively bred, i.e. naturally occurring or wild adult *S. glomerata* oysters, including whether OA and OW affect in synergistic, additive or antagonistic ways. Previous studies have mainly focused on the impact of OA and OW on larvae or adult *S. glomerata*, which have been selectively bred to have resilience to environmental stress. This study tested whether levels of OA and OW predicted for 2100 will push wild adult oysters beyond optimal physiological performance into a suboptimal pejus state. We have no knowledge of climate-change resilience, scope for growth (SFG), and overall physiological impact on wild, naturally occurring adult Sydney rock oysters. This is alarming, given the ecosystem-services role of oysters and oyster reefs and that any physiological impairment will have cascading impacts on estuarine water quality, fisheries productivity, and coastal climate resilience.

Materials and methods

It was hypothesised that elevated $p\mathrm{CO}_2$ (867 μatm) and temperature (+4°C) will have a synergistic and negative impact on growth, condition index and SFG of wild adult Sydney rock oysters. Concentrations of elevated $p\mathrm{CO}_2$ and temperature in this study were selected for sea-surface temperatures (SSTs) that are predicted to rise by 2.01–4.07°C (shared socio-economic pathway SSP5–8.5) and for water pH to be 0.45 pH units lower than the present-day levels by the Year 2100 (Fox-Kemper *et al.* 2021; Lee *et al.* 2021).

Animals and laboratory set-up

Naturally caught, wild adult *Saccostrea glomerata* (mean shell height 84.99 ± s.e. 7.27 mm, $n = 180$) were sourced from Holbert's (32.7221°S, 152.0676°E) and Diemer's (32.724°S, 152.065°E) oyster farms in Port Stephens, New South Wales (NSW), Australia during Austral winter 2017. Both suppliers grow oysters in Cromarty Bay, Port Stephens, NSW, Australia. Oysters were transported to the Department of Primary Industries and Regional Development (DPIRD) Port Stephens Fisheries Institute (PSFI), Taylors Beach, NSW (32.7460°S, 152.0595°E).

On arrival, oysters were cleaned of epifauna, divided, and placed in 12 40-L tubs with 1-μm-filtered seawater ($\mathrm{pH}_{\mathrm{NBS}}$, 8.3; ambient temperature, 18°C) supplied by an aquarium pump from a 750-L header tank for 2 weeks. Oysters were fed *ad libitum* two times per day, with a mixture of four species of microalgae, namely, *Tisochrysis lutea* (25%), *Tetraselmis chui* (25%), *Diacronema lutheri* (25%) and *Chaetoceros muelleri* (25%), at a concentration of 2×10^9 cells oyster^{-1} day^{-1} (Leica 400×). Algae were cultivated at the facilities of PSFI and feeding commenced from Day 1 until the end of the experiment. To determine the combined impact of OA and OW on *S. glomerata*, there were two temperatures and two $p\mathrm{CO}_2$ treatments. The temperature treatments were control at 24°C and elevated at 28°C and $p\mathrm{CO}_2$ concentrations were control 335 μatm and elevated $p\mathrm{CO}_2$ of 857 μatm, in an orthogonal design with a total of 12 tanks (three replicates per treatment). These treatments (24°C; 335 μatm) were based on the condition currently experienced by *S. glomerata* in Port Stephens (15–26°C) in Australia (natural) (Wolf and Collins 1979) and elevated temperatures predicted for oceanic change in temperature and pH (Hobday *et al.* 2006; Lee and Romero 2023).

Oysters were placed into 12 independent tanks, with seawater supplied by header tanks with a volume of 750 L by using an aquarium pump to smaller 40-L tanks at a flow rate of 3 L min^{-1} in a recirculating system. Fifteen oysters were randomly allocated to each of 12 tanks (total of 180 oysters, Table 1). The seawater was changed every 2 days. To reach the desired elevated $p\mathrm{CO}_2$ treatment (857 μatm), a negative feedback system consisting of a pH controller (Aqua Medic, Aqacenta Pty Ltd, Kingsgrove, Sydney, NSW, Australia; accuracy ±0.01 pH units), connected to a pH probe dipped into the header tank and to a solenoid valve (Aqua Medic Electronic shut-off valve for CO_2-standard), was used. The solenoid valve was connected to a food-grade CO_2 cylinder (BOC Australia) and CO_2 gas was introduced through an air stone into the tank accordingly with the pre-set pH value on the pH controller. This CO_2 system has been used previously by Parker *et al.* (2012, 2015) for OA experiments.

Oysters were acclimated to temperature and pH treatments to reach the desired levels across two weeks. The pH of seawater was reduced by 0.05 units per day for 8 days (final pH 7.94, ~857 μatm) to reach the desired elevated $p\mathrm{CO}_2$ conditions. Once the pH reached the desired value, the temperature of the tanks was gradually changed to reach the control temperature of 24°C and elevated temperature of 28°C, by placing waterproof heaters with thermostats (Titan heavy duty aquarium heater 1500 W) in the header tank. For both control and elevated temperature treatments, temperature

Table 1. Number of oysters used in each experiment.

Variable	Oysters per replicate tank	Oysters per treatment	Oysters total
Growth	3	9 (Day 1) + 9 (Day 35)	36 (Day 1) + 36 (Day 35)
Condition index	6	18	72
SMR	3	9	36
Clearance and ingestion rates	3	9	36
Absorption rates	2	6	24
Subtotal			168
SFG	2	6	24
Total oysters in experiment			180

was increased from 18 to 20°C by increasing 1°C day^{-1}. Following this, for control temperature replicates, an increase of 0.5°C day^{-1} was used to reach 24°C. For elevated temperature replicates, temperature was increased 1°C per day to reach 28°C, resulting in tanks reaching treatment conditions at the same time. This took 11 days in total for each treatment. From this date, oysters were exposed to treatments for 5 weeks. Temperature and pH were monitored daily. All oysters were photographed at the beginning of the experiment for individual identification.

Seawater chemistry

Samples of seawater were collected once a week for total alkalinity (TA) and pH total measurements (n = 5). Total alkalinity was measured in triplicate by Gran titration (for more details, see Parker *et al.* 2012). The values for TA, pH and salinity were entered in the program *CO2SYS* (ver. 1.04, see https://www.ncei.noaa.gov/access/ocean-carbon-acidification-data-system/oceans/CO2SYS/co2rprt.html#aboutco2sys; Lewis and Wallace 1998) for calculation of other parameters of carbonate system ($p\mathrm{CO_2}$, Ωcalcite, Ωaragonite, DIC). The pH ($\mathrm{pH_{NBS}}$) of the tanks was measured daily by using a hand-held pH probe (pH electrode Sentix 940-3 pH2 12/0-80C WTW) and pH was also measured in the total scale by using Tris buffer, following recommendations from Dickinson *et al.* (2012) for data reporting (Table 2).

Shell growth and condition index

At the start (Day 1) and end of the experiment (Day 35), three oysters per tank were collected randomly from each tank and treatment, and shell height was measured with digital callipers (±0.01 mm). To determine shell growth, the initial mean shell height per tank was subtracted from the final mean height (three oysters per tank; total of 9 oysters per treatment and 36 oysters overall at Days 1 and 35 of the experiment (Table 1). The condition index (CI) of oysters was determined at the end of the experiment after 5 weeks. Six oysters per tank were used (18 oysters per treatment, total of 72) to calculate means. The body mass and shell of oysters were dried separately (60°C for 3 days) and weighed using a digital scale (±0.0001 g; Analytical Balance Sartorius Research). CI was calculated by the following formula (Lucas and Beninger 1985; Rainer and Mann 1992):

$$\mathrm{CI} = \frac{(\text{Dry body tissue weight})}{(\text{Dry shell weight})} \times 100$$

Standard metabolic rate (SMR)

The standard metabolic rate (SMR) of three oysters in each tank (9 oysters per treatment and 36 overall, Table 1) was measured after 5 weeks of experimental exposure following the methods used in Parker *et al.* (2012). To calculate SMR, oxygen consumption was measured by a closed respirometry system (OXY-10 PreSens, AS1 Ltd, Regensburg, Germany). One individual was placed in a sealed container (830-mL volume) of filtered seawater (1 μm) adjusted to the treatment conditions that oyster was kept in. Each container had a fibre optic O_2 probe attached on top (PreSens dipping probe DP-PSt3, AS1 Ltd). The probe was previously calibrated using two O_2 concentration points (0 and 100% oxygen saturation of seawater). Twenty-four hours before individual respiration trials, oysters were gently cleaned and placed in filtered seawater without food (1 μm; adjusted to the corresponding treatment levels) to avoid noise from digestion processes. The time that individuals took to lower the oxygen concentration by 20% (1.29–1.38 mg O_2 L^{-1}) was recorded. A 'blank' container with only FSW was set up for each treatment to test for bacterial respiration; however, because the change in this chamber was negligible, it was not included in the VO_2 calculation. Containers were kept inside a water bath over the measurement period to maintain experimental temperatures (24 and 28°C). Following the procedure of Parker *et al.* (2012, 2024), only the time that oysters are open and actively respiring was used to calculate SMR. At the end of trials, each oyster was then removed from the container and shucked to separate body tissues and shell. The tissue was then dried in an oven at 60°C for 3 days to measure their constant dry body tissue and shell weight

Table 2. Seawater chemistry results of laboratory exposure to elevated $p\mathrm{CO_2}$ (335 and 857 μatm) and temperature (24 and 28°C), separately and combined, over 5 weeks.

Item	Control	Temperature	$p\mathrm{CO_2}$	Combined temperature and $p\mathrm{CO_2}$
$p\mathrm{CO_2}$ (μatm)	340.28 ± 1.65	331.51 ± 10.14	866.78 ± 3.70	848.82 ± 9.70
Temperature (°C)	24 ± 0.5	28 ± 0.5	24 ± 0.5	28 ± 0.5
Total alkalinity (μmol kg^{-1})	2449.10 ± 63.97	2471.74 ± 59.99	2482.31 ± 58.42	2467.48 ± 50.55
pH total	8.12 ± 0.01	8.13 ± 0.01	7.78 ± 0.0097	7.79 ± 0.0097
Salinity (ppm)	34.08 ± 0.15	34.08 ± 0.15	34.08 ± 0.15	34.08 ± 0.15
DIC (μmol kg^{-1})	2096.57 ± 50.53	2069.97 ± 49.85	2313.66 ± 51.84	2269.02 ± 43.90
ΩCa	6.09 ± 0.27	6.98 ± ± 0.26	3.28 ± 0.14	3.78 ± 0.14
ΩAr	4.00 ± 0.18	4.64 ± 0.17	2.15 ± 0.09	2.51 ± 0.09

Values are means and standard errors (s.e.) for the four tested treatments. Seawater was collected weekly for analysis.

in grams (±0.0001 g, Analytical Balance Sartorius Research). The following calculation for SMR was used:

$$\mathrm{SMR} = \frac{\mathrm{Vr} \times \Delta \mathrm{CwO_2}}{\Delta t \times \mathrm{bw}}$$

where SMR is the oxygen consumption normalised to 1 g of dry tissue mass (mg O_2 g^{-1} dry tissue mass h^{-1}), Vr is the volume of the respirometry chamber minus the volume of the oyster (L), ΔCwO_2 is the change in water oxygen concentration measured (mg O_2 L^{-1}), Δt is measuring time (h) and bw is the dry tissue mass (g) of the oyster.

Clearance and ingestion rates

The clearance rates of three oysters per tank were measured ($n = 9$ oysters per treatment, Table 1). Oysters were selected at random from tanks, placed individually in a container with 3 L of filtered seawater (1 μm) and left undisturbed for 30 min before microalgae (*T. lutea*) were added. A small air stone bubbling air was added to the container to ensure mixing of algae. Microalgae were added to the container by using a pipette to reach an initial concentration of 10×10^4 cells mL^{-1}. Samples of seawater (5 mL) from the experimental container were collected in duplicate at times of 0, 30 and 60 min after the addition of microalgae. Samples (5 mL) were collected with a micropipette and placed in a 120-mL vial with 4% formalin for quantification of microalgae concentration. Utmost care was taken to ensure the mixing of samples and microalgae cells were counted under a microscope by using a Neubauer chamber (Leica, 400×). The counting for total cell concentration was performed in duplicates and averaged. No pseudofaeces were observed during this experiment. A control container with no oyster was sampled to measure differences between initial concentration and final concentrations of microalgae over trials. Only measurements from oysters that were visibly open during this experiment were used. Clearance rate (CR), being the volume of water cleared of algal cells per hour (L h^{-1}), was calculated using an adaptation of the method of Coughlan (1969), as follows:

$$\mathrm{CR} = \frac{[\ln C_{\mathrm{final}} - \ln C_{\mathrm{initial}}] \times V}{t} - \mathrm{Blank}$$

where C_{final} is the final concentration of microalgae quantified after 60 min (L) and C_{initial} is the initial concentration at quantified time zero (L); V is the volume of the container (L), t is the duration of the trial (h) and *Blank* is the difference in concentration of microalgae between time zero and time 60 min. Only linear measurements (plot of food concentration over time) were used for statistical analysis. Ingestion rates (mg h^{-1}) were calculated by multiplying clearance rate by food concentration in the experimental containers, following the methods of Bayne *et al.* (1999*a*) (n = 9). To remove any weight-dependent effects on physiological traits, clearance and respiration rate measurements were converted to a standard body size by applying the following formula and allometric exponents from Bayne *et al.* (1999*b*):

$$V_{\mathrm{stand}} = \left(\frac{W_{\mathrm{stand}}}{W_{\mathrm{meas}}}\right)\beta \times V_{\mathrm{meas}}$$

where V_{stand} is the converted rate (g; for CR, L g^{-1} h^{-1}; for rate of oxygen consumption, mg O_2 g^{-1} h^{-1}), W_{stand} is the standard weight (1.38 g), W_{meas} is the weight measured (g), β is the appropriate allometric exponent (CR = 0.641; rate of oxygen consumption = 0.536) and V_{meas} is the rate measured experimentally.

Absorption efficiency (AE) and absorption rate (AR)

To quantify the absorption efficiency of oysters, the efficiency with which organic matters from the food is injested and absorbed faeces produced during the clearance rate trials were carefully collected with a pipette from two oysters per replicate tank and six oysters per treatment, and filtered in pre-washed, dried and weighted GF/C filter papers. Filters containing samples were washed with 0.5 M of ammonium formate to remove sea salts. The filters containing the faeces were dried in an oven for 3 days at 60°C for measurement of the dry weight of faeces. The weight of pre-weighed filter papers was then subtracted from the total dry weight so as to have individual faeces dry weight. For the calculation of the ash-free dry weight (AFDW) of faeces, filters were dried in a muffle furnace at 450°C for 2 h and re-weighted (n = 6, N = 24). The food (microalga *T. lutea*) added for this experiment was also filtered in pre-weighed GF/C filter papers at different concentrations (n = 50), dried for 3 days at 60°C and processed using the same method to calculate the ash-free dry weight of faeces samples. Specific values of organic content of different amounts of food were calculated through regression equations (dry weight, $r^2 = 0.9283$; and for AFDW, $r^2 = 0.83$). Absorption efficiency was calculated following the method of Conover (1966):

$$\mathrm{AE} = \frac{(F - E)}{[(1 - E) \times F]}$$

where F is the ratio of AFDW and dry weight of food and E is the ratio of AFDW and dry weight of faeces. Corrections with blanks were used over calculations as recommended by Widdows and Staff (2006). Absorption rates (AR, mg h^{-1}) were calculated by multiplying values of absorption efficiency and the mean of ingestion rates per treatment.

Scope for growth (SFG)

The aerobic scope or Scope for Growth (SFG) was calculated using the following formula:

$$\mathrm{SFG} = (\mathrm{IR} \times \mathrm{AE}) - \mathrm{RR}$$

where IR is ingestion rate (mg g^{-1} h^{-1}), AE is assimilation efficiency (%) and RR (mg O_2 g^{-1} h^{-1}) is respiration rate (on the basis of the methods used by Widdows 1985, Widdows and Johnson 1988, Widdows and Staff 2006 and Le Moullac *et al.* 2016). Physiological rates were converted to energy equivalents (J g^{-1} h^{-1}) to allow the calculation of SFG. The conversions used were as follows: 14.1 J for 1 mg O_2 and 20.3 J for 1 mg of particulate organic matter (Bayne and Newell 1983; Gnaiger 1983; Bayne *et al.* 1987). SFG (J g^{-1} h^{-1}) was calculated for two oysters per tank, for a total of six individual oysters per treatment ($n = 2$, $N = 24$).

Data analysis

Data analyses were performed using *R* software (ver. 4.6.0, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/) using the aov() function from the base *R* package. Response variables were analysed using either a two-way (for growth) or three-way (for all other variables) mixed-model ANOVA, following Underwood (1997), with $p\mathrm{CO_2}$ and temperature as fixed factors and tank as a random factor nested within these treatments. Model assumptions were assessed using residual diagnostics, and all tests were evaluated at $\alpha = 0.05$. Data were analysed by a three-way ANOVA for condition index, SMR, clearance rates, ingestion rates, absorption rate and SFG. In all analyses, tank was not significant, and *post hoc* procedure of pooling was performed to increase the capacity of the analysis to detect differences among the main sources of variation or treatments (Underwood 1997, p. 268). When an interaction between the main factors was detected, a Tukey test was performed to determine significant differences among the means.

Results

Shell growth and condition index

Oyster shell growth was not significantly different among treatments after 5 weeks of exposure (Table 3, Fig. 1). The greatest mean growth of oysters was in controls (2.77 ± 0.58 mm) and the least at elevated temperature (2.11 ± 0.40 mm, mean ± s.e.). Oyster condition index also was not significantly different among treatments (Table 3, Fig. 2). The greatest condition index was in controls (3.47 ± 0.16) and smallest at elevated $p\mathrm{CO_2}$, and the combined elevated $\mathrm{pCO_2}$ and temperature treatments 3.63 ± 0.20 and 3.63 ± 0.18 (mean ± s.e.) respectively (Fig. 2).

Standard metabolic rates (SMR)

The SMR of oysters was significantly different among treatments, with a significant interaction between elevated $p\mathrm{CO_2}$ and temperature treatments after 5 weeks of exposure (Table 3, Fig. 3). *Post hoc* analysis indicated that SMR of oysters was greatest at elevated temperature (3.20 ± 0.55 mg O_2 g^{-1} dry tissue h^{-1}), and significantly lower in the other three treatments, which were similar to each other whether at elevated $p\mathrm{CO_2}$ (2.89 ± 0.53 mg O_2 g^{-1} dry tissue^{-1} h^{-1}), elevated temperature and $p\mathrm{CO_2}$ (2.44 ± 0.49 mg O_2 g^{-1} dry tissue h^{-1}), or in controls (1.66 ± 0.25 mg O_2 g^{-1} dry tissue tissue h^{-1}) (Table 3, Fig. 3).

Clearance and ingestion rates

Oyster clearance and ingestion rates were significantly greater at elevated $p\mathrm{CO_2}$ and temperature treatments than in the controls (Table 4, Fig. 4, 5). Clearance rates were nearly double at the combined elevated $p\mathrm{CO_2}$ and temperature treatments compared with the controls, being 3.31 ± 0.46 and 1.79 ± 0.32 L g^{-1} h^{-1} respectively (mean ± s.e.) for the combined and control treatments. Ingestion rates of oysters were from 5.80 ± 1.03 mg g^{-1} h^{-1} in the controls to 10.72 ± 1.49 mg g^{-1} h^{-1} in the combined elevated $p\mathrm{CO_2}$ and temperature treatment (Fig. 5).

Absorption efficiency (AE) and absorption rates (AR)

Oyster absorption efficiency data were heterogenous and could not be transformed (Barlett test, $P = 0.0195$). The greatest oyster absorption efficiency was at elevated temperature (77% ± 6.0, mean ± s.e.), and least in the controls (55% ± 12.89) (Fig. 6). Oyster absorption rates followed a

Table 3. Two- and three-way ANOVA results for shell growth, condition index and SMR of *Saccostrea glomerata* exposed to control and elevated $p\mathrm{CO_2}$ (335 and 857 μatm) and control and elevated temperature (24 and 28°C) for 5 weeks.

Source	Growth				Condition index				SMR			
	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
$p\mathrm{CO_2}$	1	0.009	0.02	0.896	1	0.05	0.11	0.786	1	0.51	0.44	0.524
Temperature	1	0.75	1.48	0.260	1	0.25	0.59	0.535	1	2.67	2.28	0.169
$p\mathrm{CO_2}$ × Temperature	1	0.08	0.16	0.696	1	0.23	0.56	0.545	1	8.78	7.51	0.025*
Tank ($p\mathrm{CO_2}$ × Temperature)	n/a	n/a	n/a		8	0.41	0.65	0.73	8	1.17	0.64	0.737
Residuals	8	0.51			60	0.63			24	2.27		
Total	11				71				35			

Growth, $n = 12$; condition index, $n = 72$; and SMR, $n = 36$. The random factor 'Tank' was included in the analyses. Probabilities are significant at ***, $P < 0.001$; **, $P < 0.01$; and *, $P < 0.05$.

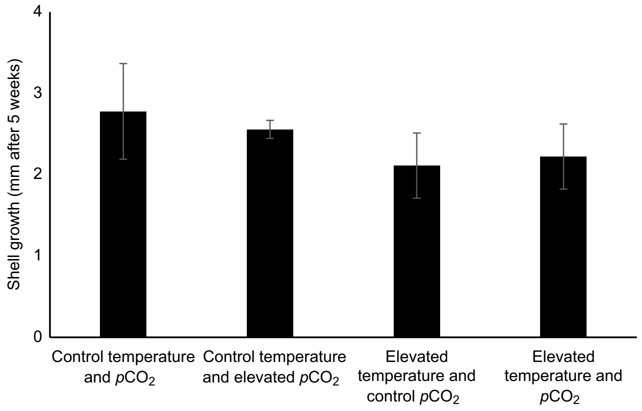

Fig. 1. Mean shell growth ± s.e. of *S. glomerata* to control and elevated pCO_2 (335 and 857 µatm) and control and elevated temperature (24 and 28°C) after 5 weeks of exposure ($n = 3$, $N = 36$).

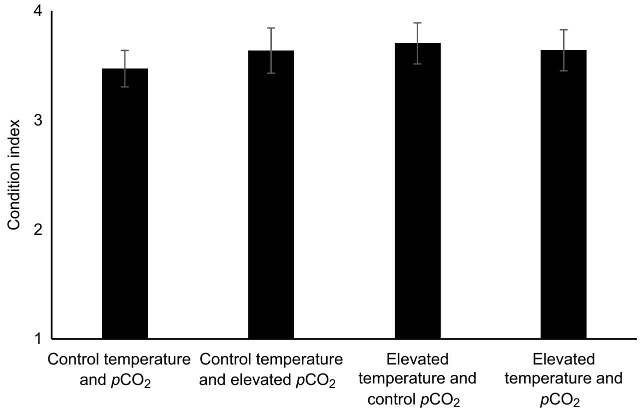

Fig. 2. Mean condition index ± s.e. of *S. glomerata* to control and elevated pCO_2 (335 and 857 µatm) and control and elevated temperature (24 and 28°C) after 5 weeks of exposure ($n = 6$; $N = 72$).

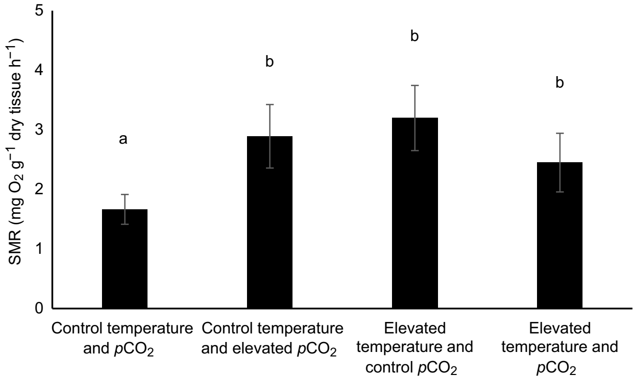

Fig. 3. Mean standard metabolic rates (±s.e.) of *S. glomerata* in the four experimental treatments: control (340 µatm, 24°C), elevated pCO_2 (867 µatm, 24°C), elevated temperature (331 µatm, 28°C) and combined elevated pCO_2 and temperature (849 µatm, 28°C) after 5 weeks of exposure. The letters above bars represent significant differences as determined by *post hoc* tests among treatments ($P < 0.05$) ($n = 3$; $N = 36$).

Table 4. Three-way ANOVA results for the clearance rates and ingestion rates standardised by dry bodyweight of *Saccostrea glomerata* exposed in the laboratory to control and elevated pCO_2 (335 and 857 µatm) treatments and control and elevated temperature (24 and 28°C) treatments or 5 weeks.

Item	**Clearance rate (L g^{-1} dry tissue h^{-1})**				**Ingestion rate (mg g^{-1} dry tissue h^{-1})**			
	d.f.	**MS**	***F***	***P***	**d.f.**	**MS**	***F***	***P***
pCO_2	1	5.87	21.27	0.0017**	1	61.57	21.31	0.0017**
Temperature	1	4.58	16.59	0.0035**	1	47.93	16.59	0.0036**
pCO_2 × Temperature	1	0.36	1.30	0.286	1	3.72	1.29	0.2891
Tank (pCO_2 × Temperature)	8	0.27	0.21	0.986	8	2.89	0.21	0.986
Residuals	24	1.26			24	13.21		
Total	35				35			

Clearance and ingestion rates, $n = 3$; and absorption rates, $n = 2$. The random factor 'Tank' was included in the analyses. Probabilities are significant at ***, $P < 0.001$; **, $P < 0.01$; and *, $P < 0.05$.

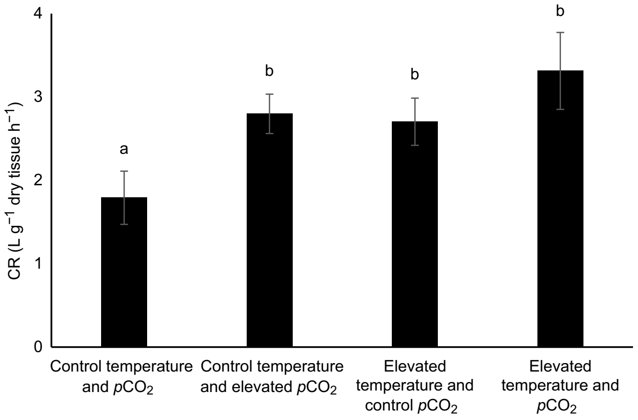

Fig. 4. Mean clearance rates standardised by dry bodyweight (L g^{-1} dry tissue h^{-1}, mean ± s.e.) of *S. glomerata* in the four experimental treatments: control (340 µatm, 24°C), elevated pCO_2 (857 µatm, 24°C), elevated temperature (331 µatm, 28°C) and combined elevated temperature and pCO_2 (849 µatm, 28°C) after 5 weeks of exposure ($n = 9$). Different letters above bars represent significant differences as determined by *post hoc* tests among treatments ($P < 0.05$) ($n = 3$; $N = 36$).

similar pattern, but were significantly greater at both elevated pCO_2 and temperature, although there was no interaction between these factors (Table 5, Fig. 7). The greatest absorption rate of oysters was at elevated pCO_2 and temperature (7.94 ± 0.27 mg h^{-1}) almost double compared to controls (3.19 ± 0.75 mg h^{-1}).

Scope for growth (SFG)

Overall oyster SFG was significantly greater at both elevated pCO_2 and temperature than in the controls (Table 5, Fig. 8).

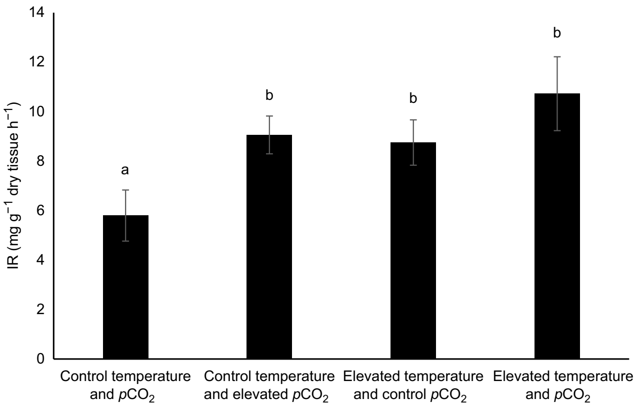

Fig. 5. Mean ingestion rates standardised to dry bodyweight (mg g $^{-1}$ h^{-1}) ± s.e of *S. glomerata* in the four experimental treatments: control (340 µatm, 24°C), elevated pCO$_2$ (857 µatm, 24°C), elevated temperature (331 µatm, 28°C) and combined elevated pCO$_2$ and temperature (849 µatm, 28°C) after 5 weeks of exposure ($P < 0.05$) ($n = 3$; $N = 36$).

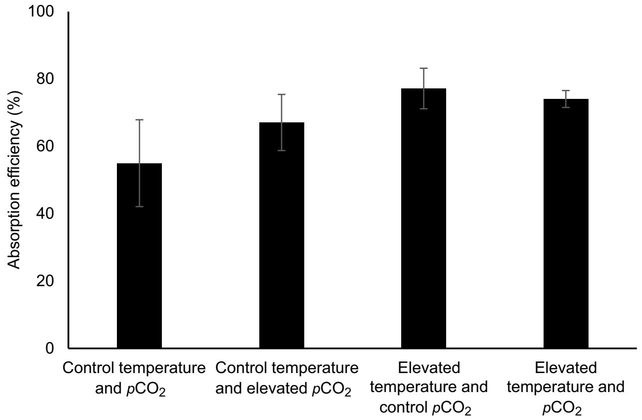

Fig. 6. Mean absorption efficiency (AE %) ±s.e. of *S. glomerata* in the four treatments: control (340 µatm, 24°C), elevated pCO$_2$ (857 µatm, 24°C), elevated temperature (331 µatm, 28°C) and combined elevated pCO$_2$ and temperature (849 µatm, 28°C) after 5 weeks of exposure ($n = 2$; $N = 24$).

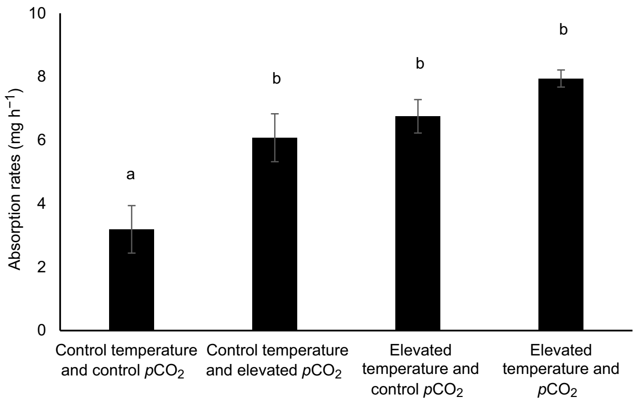

Fig. 7. Mean absorption rates of *Saccostrea glomerata* from control and elevated pCO$_2$ (335 and 857 µatm) and control and elevated temperature (24 and 28°C) treatments after 5 weeks of exposure.

SFG was positive and almost more than three times higher in the combined treatment (145.19 ± 24.83 J g^{-1} h^{-1}) than in the control (46.41 ± 10.81 J g^{-1} h^{-1}) (Fig. 8).

Discussion

At the levels of elevated pCO$_2$ and temperature used this study, we did not find a significant negative synergistic effect of pCO$_2$ and temperature on the growth or condition index of *S. glomerata* over an exposure period of 5 weeks. There were some additive impacts of elevated pCO$_2$ and temperature on *S. glomerata*, with a significant increase in SMR and a significant increase in clearance and ingestion rate, absorption rate and an overall positive SFG compared with the controls. These results suggest that adult *S. glomerata* individuals were able to compensate for the impacts of elevated pCO$_2$ and temperature at the levels used in this study, to have a net positive energy budget.

Despite a net positive energy budget, *S. glomerata* individuals that were exposed to stress of elevated pCO$_2$ and temperature, either singly or in combination, also had

Table 5. Two-way ANOVA results for the absorption rate and scope for growth of *Saccostrea glomerata* exposed to elevated pCO$_2$ (335 and 857 µatm) and temperature (24 and 28°C) for 5 weeks.

Source	**Absorption rate (mg g^{-1} dry tissue h^{-1})**				**Scope for growth (J g^{-1} h^{-1})**			
	d.f.	**MS**	***F***	***P***	**d.f.**	**MS**	***F***	***P***
pCO$_2$	1	24.97	11.27	0.00289**	1	12,560	8.99	0.0171*
Temperature	1	44.23	19.95	0.000497***	1	16,875	12.07	0.0084**
pCO$_2$ × Temperature	1	4.30	3.074	0.11764	8	113	0.81	0.7837
Tank (pCO$_2$ × Temperature)	8	1.40	0.61	0.754		1398	0.41	0.894
Residuals	12	2.27			12	3386		
Total	23				23			

The random factor 'Tank' was included in the analyses. Probabilities are significant at: ***, $P < 0.001$; **, $P < 0.01$; and *, $P < 0.05$.

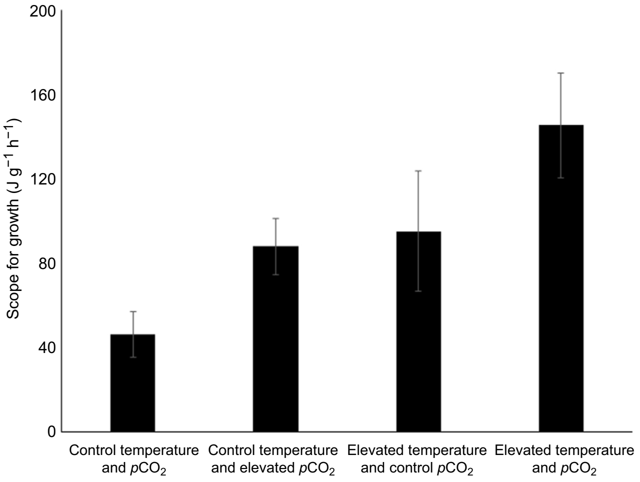

Fig. 8. Mean (± s.e.) scope for growth (J g^{-1} h^{-1}) of *Saccostrea glomerata* from control and elevated pCO$_2$ (335 and 857 µatm) and control and elevated temperature (24 and 28°C) treatments after 5 weeks of exposure ($n = 2$; $N = 24$).

significantly greater SMR than did oysters in controls. A greater SMR suggests that it is more energetically costly for *S. glomerata* to live in a more acidic and warmer environment, but they compensate by an increase in clearance, ingestion and absorption rates. Previous studies have found increased SMR of oysters exposed to elevated pCO$_2$ or temperature (Lannig *et al.* 2010; Parker *et al.* 2012, 2015, 2024; Scanes *et al.* 2017). In a series of studies, Parker *et al.* (2012, 2015, 2024) found increased SMR of *S. glomerata* in response to pCO$_2$ and warming in wild and selectively bred lines. Similarly, Lannig *et al.* (2010) found an increased SMR of *C. gigas* exposed to chronic elevated pCO$_2$ and acute warming. An increase in SMR indicates higher costs of basal maintenance, which means that oysters will require more energy through food to sustain basic physiological functions under even moderate stressful conditions.

The higher basal maintenance costs of oysters exposed to elevated pCO$_2$ and temperature appear to be offset by increased rates of feeding, ingestion and absorption. For example, clearance and ingestion rates of algae were nearly doubled in oysters exposed to the combined effects of elevated pCO$_2$ and temperature compared with the controls. Greater clearance and ingestion rates in marine organisms and bivalves in response to climate-change stress have been found in a range of studies (Hutchinson and Hawkins 1992; Pernet *et al.* 2008; Burnell *et al.* 2013; Navarro *et al.* 2016; Ramajo *et al.* 2016*a*; Parker *et al.* 2024). For example, in juvenile scallops, *Argopecten purpuratus*, exposure to low pH (7.6) led to an increase in ingestion rates compared with scallops in the control treatment (Ramajo *et al.* 2016*a*). In the sea urchin, *Amblypneustes pallidus*, exposure to elevated pCO$_2$ (~650 µatm) has been shown to lead to an increase in grazing on seagrass (*Amphibolis antarctica*) (Burnell *et al.* 2013). Similarly, an increase in clearance rates in response to elevated temperature was observed in *Ostrea edulis* (Hutchinson and Hawkins 1992) and *C. virginica* (Pernet *et al.* 2008). In Parker *et al.* (2024), clearance rates of *S. glomerata* were between 2.35 ± 0.91 and 19.57 ± 5.94 L g^{-1} h^{-1} and, as in this study, greater at elevated 28°C than at control temperature of 24°C. In the real world of an estuary, a framework similar to that discussed by Neokye *et al.* (2024*a*) is useful to determine any loss or gain in estuarine services from Sydney rock oysters and set the future research directions (Lemasson *et al.* 2017; Neokye *et al.* 2024*a*, 2024*b*).

Other studies have found that an abundant food supply can compensate for the negative effects of decreased pH (Li and Gao 2012; Sanders *et al.* 2013; Ramajo *et al.* 2016*b*). Ramajo *et al.* (2016*b*), in their meta-analysis, highlighted that there was a need for more studies on the mediating influence of food abundance, conferring resilience on calcifying species to the adverse effects of OA. In our study, the food concentration and quality were high, and oysters were fed to satiation. Our study also found increased feeding rates of *S. glomerata* in response to the exposure to elevated pCO$_2$ and temperature, which appear to indicate the capacity of *S glomerata* to compensate for increased energetic demands. In the real world, where OA affects the coastline (Cai *et al.* 2011), there may not be sufficient food for oysters of sufficient nutritional quality to compensate for higher basal maintenance costs. Limited food may lead to less energy being available for other fitness-sustaining processes, such as investment in gamete production (Boulais *et al.* 2017). Already, it is known that food availability for bivalves naturally varies spatially and temporally (Fernandes *et al.* 2012; Winder and Sommer 2012). Furthermore, bivalves feed on a range of suspended particles, including phytoplankton, zooplankton, detritus and bacteria (Langdon and Newell 1990; Lehane and Davenport 2002; Arapov *et al.* 2010), which may be altered by climate-change stressors (Winder and Sommer 2012; Henson *et al.* 2021). Even with optimal food concentration, not all molluscs will have the capacity to increase clearance, ingestion and absorption rates in response to elevated pCO$_2$ and temperature. For many mollusc species tested, studies have found that exposure to elevated pCO$_2$ and temperature resulted in no change, and even led to a depression of feeding (Navarro *et al.* 2016; Clements and Darrow 2018). For example, in the mussel *M. chilensis*, exposure to elevated pCO$_2$ at 700 µatm had no effect on clearance rates. By contrast, in the mussel *M. coruscus*, exposure to elevated temperature of 30°C depressed clearance rates (Wang *et al.* 2015). Further, in the mussel, *M. edulis* collected from the CO$_2$-enriched Kiel Fjord, there was no change in clearance rates observed when exposed to an intermediate level of pCO$_2$ of 1120 µatm and a reduction in clearance rates at the extreme level of pCO$_2$ of 2240 µatm (Stapp *et al.* 2018). Causes of reduced feeding of oysters in response to exposure to elevated pCO$_2$ and temperature have been explained by decreased ciliary movement essential for food capture, altered sensitivity of the neuroreceptor GABA to elevated pCO$_2$ (Clements and Darrow 2018), and prolonged periods of valve closure as a coping mechanism to suboptimal conditions (Wang *et al.* 2015). Reduced clearance and ingestion rates can also indicate that bivalves have passed their threshold tolerance limits (Sokolova *et al.* 2011).

It is important to emphasise that oysters in this study had plentiful food and were fed *ad libitum* to satiation, so as to avoid any impact of food limitation. However, this might not reflect natural conditions in the real world and coastal areas, where *S. glomerata* occurs and where this species is farmed for aquaculture and given climate change is predicted to alter the regime of abiotic factors that affect plankton dynamics (Winder and Sommer 2012; Meunier *et al.* 2025). In general, the influence of food availability and the combined stress of elevated $p\mathrm{CO}_2$ and temperature on SFG of adult oysters is less well known and requires further investigation (Parker *et al.* 2015). Aligned with our results, a recent study found food to be a key aspect for oysters to cope with climate-change stress (Caillon *et al.* 2025). Understanding oyster responses is critical to prepare the aquaculture sector for the warming, acidifying and freshening predicted for the south-eastern coastline of Australia, the location also of the distribution of *S. glomerata* (Scanes *et al.* 2020).

The results of this study suggest that an elevated temperature of 28°C is within the thermal tolerance range of *S. glomerata* when food is optimal. This is similar to the pattern found for *M. chilensis* exposed to warming, with the highest scope for growth observed at the elevated temperature treatment of 16°C, because this temperature level was within naturally experienced levels in their habitat (Navarro *et al.* 2016). Like this study, other studies using similar $p\mathrm{CO}_2$ and temperature have also found a positive SFG in 8 of 13 selectively bred *S. glomerata* family lines exposed to temperatures of 28°C and pH of 1000 μatm, suggesting that energy was available for other processes such as growth and condition (Parker *et al.* 2024). The novelty of this study is that positive SFG was found in naturally recruiting wild adult oysters. Whereas the elevated temperature used in this study represents a +4°C warming of the mean summer temperature of *S. glomerata* from the collection location of Port Stephens, NSW, on the south-eastern coast of Australia, the upper geographic range of *S. glomerata* in Australia extends as far north as Hervey Bay in Queensland, where mean summer water temperatures reach as high as the elevated temperature treatment used in this study.

The growth and condition index of *S. glomerata* in this study was not significantly affected by the elevated $p\mathrm{CO}_2$ and temperature treatments compared with the controls. The observed result for shell growth might be related to the adult-sized oysters used in the study, which have slower growth than do juveniles. This result contrasts with many other studies on bivalves, which have found a significant reduction in growth or condition index at elevated $p\mathrm{CO}_2$ and temperature. However, the results of this study are within the range of previous studies on selectively bred lines of *S. glomerata* (Parker *et al.* 2024). Parker *et al.* (2024) found that selectively bred lines of *S. glomerata* ranged in scope for growth from negative -9.18 ± 3.67 to positive 608.80 ± 192.09 J g^{-1} h^{-1}. Whereas several selectively bred families had negative or no scope for growth in response to climate-change stress, others had positive and high scope for growth. In this study, clearance and absorption rates of wild oysters were all positive in response to climate-change stress, resulting in a positive scope for growth. The results of this study suggest that the energy budget of adult wild *S. glomerata* had resilience to the climate-change stressors of OA and OW at levels tested.

As indicated earlier, our results also suggest that under optimal food concentrations, the elevated concentration of $p\mathrm{CO}_2$ and temperature used in this study (857 μatm and 28°C) might be within the optimal range for *S. glomerata* because a suboptimal pejus state was not observed (Sokolova *et al.* 2011). The SFG of *S. glomerata* remained positive even under the combined stress of elevated $p\mathrm{CO}_2$ and temperature, indicating that they had sufficient energy for other fitness-sustaining processes after meeting basal energy demands (Bayne *et al.* 1999*b*; Widdows and Staff 2006). Optimistically, the capacity of *S. glomerata* to alter metabolic, clearance and absorption rates in response to stress may indicate significant phenotypic plasticity (Ross *et al.* 2016; Parker *et al.* 2024), although this capacity will also come at a higher cost of basal metabolism (Solan and Whiteley 2016). In the natural environment, other stressors such as pollution and lower salinity, can make it difficult for oysters to maintain elevated SMR and may push them across a threshold into the pessimum or lethal range (Lannig *et al.* 2006; Sokolova *et al.* 2011; Dickinson *et al.* 2012; Sokolova 2013; Glencross *et al.* 2025). The strategy of increased metabolic rates in response to climate-change stress may provide a mechanism to survive, but as stated, this will be highly dependent on food supply (Ramajo *et al.* 2016*a*). Maintenance of greater metabolic rates may be possible only in marine habitats that also have a high abundance of phytoplankton (e.g. Parker *et al.* 2012). If we are to predict species responses to global change, more experiments are needed that modify the availability of food and the interactions with the impact of multiple stressors.

Conclusions

In this study, adult wild Sydney rock oyster (*S. glomerata*) displayed resilience in its response to the combined stress of elevated $p\mathrm{CO}_2$ and temperature at the levels tested and the food provided, and was able to maintain positive SFG. Oysters were able to adjust clearance, ingestion and absorption rates to meet increased energetic demand. Although there was no indication of synergistic effects of elevated $p\mathrm{CO}_2$ and temperature, when *S. glomerata* and other oysters are exposed in the wild to multiple stressors, including variable levels of food supply, impacts are probably more severe for this economically, ecologically iconic and indigenous culturally iconic oyster species.

References

Arapov J, Ezgeta-Balić D, Peharda M, Ninčević Gladan Ž (2010) Bivalve feeding – how and what they eat? *Croatian Journal of Fisheries* **68**, 105–116.

Arias PAN, Bellouin E, Coppola RG, Jones G, Krinner J, Marotzke V, Naik MD, Palmer Plattner GK, Rogelj J (2021) Technical summary. In 'Climate Change 2021: the Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change'. (Eds V Masson-Delmotte, P Zhai, A Pirani, SL Connors, C Péan, S Berger, N Caud, Y Chen, L Goldfarb, MI Gomis, *et al.*) pp. 33–144. (Cambridge University Press: Cambridge, UK, and New York, NY, USA) doi:10.1017/9781009157896.002

Barclay K, McIlgorm A, Mazur N, Voyer M, Schnierer S, Payne AM (2016) Social and economic evaluation of NSW Coastal Aquaculture. Fisheries Research and Development Corporation (FRDC 2015/302). (University of Technology Sydney) Available at https://www.uts.edu.au/globalassets/sites/default/files/fass-report-social-economic-evaluation-nsw-coastal-aquaculture.pdf

Bayne BL, Newell RC (1983) Physiological energetics of marine molluscs. *The Mollusca* **4**, 407–515. doi:10.1016/B978-0-12-751404-8.50017-7

Bayne BL, Hawkins AJS, Navarro E (1987) Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. *Journal of Experimental Marine Biology and Ecology* **111**, 1–22. doi:10.1016/0022-0981(87)90017-7

Bayne BL, Hedgecock D, McGoldrick D, Rees R (1999*a*) Feeding behaviour and metabolic efficiency contribute to growth heterosis in Pacific oysters [*Crassostrea gigas* (Thunberg)]. *Journal of Experimental Marine Biology and Ecology* **233**, 115–130. doi:10.1016/S0022-0981(98)00125-7

Bayne BL, Svensson S, Nell JA (1999*b*) The physiological basis for faster growth in the Sydney rock oyster, *Saccostrea commercialis*. *The Biological Bulletin* **197**, 377–387. doi:10.2307/1542792

Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay M, Lenihan H, Luckenbach MW, Toropova CL, Zhang G, Conservancy TN (2009) Shellfish at risk: a global analysis of problems and solutions. The Nature Conservancy, Arlington, VA, USA.

Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay MC, Lenihan HS, Luckenbach MW, Toropova CL, Zhang G, Guo X (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience* **61**, 107–116. doi:10.1525/bio.2011.61.2.5

Beniash E, Ivanina A, Lieb NS, Kurochkin I, Sokolova IM (2010) Elevated level of carbon dioxide affects metabolism and shell formation in oysters *Crassostrea virginica*. *Marine Ecology Progress Series* **419**, 95–108. doi:10.3354/meps08841

Boulais M, Chenevert KJ, Demey AT, Darrow ES, Robison MR, Roberts JP, Volety A (2017) Oyster reproduction is compromised by acidification experienced seasonally in coastal regions. *Scientific Reports* **7**, 13276. doi:10.1038/s41598-017-13480-3

Burnell OW, Russell BD, Irving AD, Connell SD (2013) Eutrophication offsets increased sea urchin grazing on seagrass caused by ocean warming and acidification. *Marine Ecology Progress Series* **485**, 37–46. doi:10.3354/meps10323

Byrne M (2011) Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanography and Marine Biology: An Annual Review* **49**, 1–42.

Byrne M, Fitzer S (2019) The impact of environmental acidification on the microstructure and mechanical integrity of marine invertebrate skeletons. *Conservation Physiology* **7**, coz062. doi:10.1093/conphys/coz062

Byrne M, Przeslawski R (2013) Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories. *Integrative and Comparative Biology* **53**, 582–596. doi:10.1093/icb/ict049

Cai W-J, Hu X, Huang W-J, Murrell MC, Lehrter JC, Lohrenz SE, Chou W-C, Zhai W, Hollibaugh JT, Wang Y, Zhao P, Guo X, Gundersen K, Dai M, Gong G-C (2011) Acidification of subsurface coastal waters enhanced by eutrophication. *Nature Geoscience* **4**, 766–770. doi:10.1038/ngeo1297

Caillon C, Fleury E, Di Poi C, Gazeau F, Pernet F (2025) Food availability, but not tidal emersion, influences the combined effects of ocean acidification and warming on oyster physiological performance. *Aquaculture* **604**, 742459. doi:10.1016/j.aquaculture.2025.742459

Chan VBS, Thiyagarajan V, Lu XW, Zhang T, Shih K (2013) Temperature dependent effects of elevated CO_2 on shell composition and mechanical properties of *Hydroides elegans*: insights from a multiple stressor experiment. *PLoS ONE* **8**, e78945. doi:10.1371/journal.pone.0078945

Clements JC, Darrow ES (2018) Eating in an acidifying ocean: a quantitative review of elevated CO_2 effects on the feeding rates of calcifying marine invertebrates. *Hydrobiologia* **820**, 1–21. doi:10.1007/s10750-018-3665-1

Coen LD, Brumbaugh RD, Bushek D, Grizzle R, Luckenbach MW, Posey MH, Powers SP, Tolley SG (2007) Ecosystem services related to oyster restoration. *Marine Ecology Progress Series* **341**, 303–307. doi:10.3354/meps341303

Conover RJ (1966) Assimilation of organic matter by zooplankton. *Limnology and Oceanography* **11**, 338–345. doi:10.4319/lo.1966.11.3.0338

Coughlan J (1969) The estimation of filtering rate from the clearance of suspensions. *Marine Biology* **2**, 356–358. doi:10.1007/BF00355716

Dickinson GH, Ivanina AV, Matoo OB, Pörtner HO, Lannig G, Bock C, Beniash E, Sokolova IM (2012) Interactive effects of salinity and elevated CO_2 levels on juvenile eastern oysters, *Crassostrea virginica*. *The Journal of Experimental Biology* **215**, 29–43. doi:10.1242/jeb.061481

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science* **1**, 169–192. doi:10.1146/annurev.marine.010908.163834

Ewere EE, Rosic N, Bayer PE, Ngangbam A, Edwards D, Kelaher BP, Mamo LT, Benkendorff K (2021) Marine heatwaves have minimal influence on the quality of adult Sydney rock oyster flesh. *Science of The Total Environment* **795**, 148846. doi:10.1016/j.scitotenv.2021.148846

Fernandes LDA, Quintanilha J, Monteiro-Ribas W, Gonzalez-Rodriguez E, Coutinho R (2012) Seasonal and interannual coupling between sea surface temperature, phytoplankton and meroplankton in the subtropical south-western Atlantic Ocean. *Journal of Plankton Research* **34**, 236–244. doi:10.1093/plankt/fbr106

Fernández-Reiriz MJ, Range P, Álvarez-Salgado XA, Labarta U (2011) Physiological energetics of juvenile clams *Ruditapes decussatus* in a high CO_2 coastal ocean. *Marine Ecology Progress Series* **433**, 97–105. doi:10.3354/meps09062

Folt CL, Chen CY, Moore MV, Burnaford J (1999) Synergism and antagonism among multiple stressors. *Limnology and Oceanography* **44**, 864–877. doi:10.4319/lo.1999.44.3_part_2.0864

Fox-Kemper B, Hewitt H, Xiao C, Aolgeirsdottir G, Driihout S, Edwards T, Golledge N, Hemer M, Kopp R, Krinner G, Mix A, Notz D, Nowicki S, Nrrhati I, Ruiz JJ, Sallee JB, Slangen A, Yu AY, Alakkat U, Horton B, Marsland S (2021) Ocean, cryosphere, and sea level change. In 'Climate Change 2021: the Physical Science Basis. Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change'. (Eds V Masson-Delmotte, P Zhal, A Pirani, SL Connors, C Pean, Y Chen, L Goldfarb, MI Gomis, JBR Matthnews, S Berge, M Hurang, O Yelekci, R Yu, B Zhou, L Lonnoy, TK Maycock, T Waterfield, K Leitzell, N Caud) pp. 1211–1362. (Cambridge University Press: Cambridge, UK, and New York, NY, USA) doi:10.1017/9781009157896

Gattuso J-P, Magnan A, Billé R, Cheung WWL, Howes EL, Joos F, Allemand D, Bopp L, Cooley SR, Eakin CM, Hoegh-Guldberg O, Kelly RP, Pörtner H-O, Rogers AD, Baxter JM, Laffoley D, Osborn D, Rankovic A, Rochette J, Sumaila UR, Treyer S, Turley C (2015) Contrasting futures for ocean and society from different anthropogenic CO_2 emissions scenarios. *Science* **349**, aac4722. doi:10.1126/science.aac4722

Gazeau F, Parker LM, Comeau S, Gattuso J-P, O'Connor WA, Martin S, Pörtner H-O, Ross PM (2013) Impacts of ocean acidification on marine shelled molluscs. *Marine Biology* **160**, 2207–2245. doi:10.1007/s00227-013-2219-3

Gibbs M, Ross P, Scanes E, Gibbs J, Rotolo-Ross R, Parker L (2023) Extending conservation of coastal and oyster reef restoration for First Nations cultural revitalization. *Conservation Biology* **37**, e14158. doi:10.1111/cobi.14158

Gibbs MC, Parker LM, Scanes E, Ross PM (2024) Recognising the importance of shellfish to First Nations peoples, Indigenous and Traditional Ecological Knowledge in aquaculture and coastal management in Australia. *Marine and Freshwater Research* **75**, MF23193. doi:10.1071/MF23193

Gillies CL, McLeod IM, Alleway HK, Cook P, Crawford C, Creighton C, Diggles B, Ford J, Hamer P, Heller-Wagner G, Lebrault E, Le Port A, Russell K, Sheaves M, Warnock B (2018) Australian shellfish ecosystems: past distribution, current status and future direction. *PLoS ONE* **13**, e0190914. doi:10.1371/journal.pone.0190914

Glencross J, Scanes E, Byrne M, Ross PM (2025) Responses of Sydney rock oyster juveniles vary with marine heatwaves and freshening. *Discover Oceans* **2**, 28. doi:10.1007/s44289-025-00071-8

Gnaiger E (1983) Calculation of energetic and biochemical equivalents of respiratory oxygen consumption. In 'Polarographic oxygen sensors: aquatic and physiological applications'. (Eds E Gnaiger, H Forstner) pp. 337–345. (Springer)

Grabowski JH, Peterson CH (2007) Restoring oyster reefs to recover ecosystem services. *Theoretical Ecology Series* **4**, 281–298. doi:10.1016/S1875-306X(07)80017-7

Henson SA, Cael BB, Allen SR, Dutkiewicz S (2021) Future phytoplankton diversity in a changing climate. *Nature Communications* **12**, 5372. doi:10.1038/s41467-021-25699-w

Hettinger A, Sanford E, Hill TM, Hosfelt JD, Russell AD, Gaylord B (2013) The influence of food supply on the response of Olympia oyster larvae to ocean acidification. *Biogeosciences* **10**, 6629–6638. doi:10.5194/bg-10-6629-2013

Hobday AJ, Okey TA, Poloczanska ES, Kunz TJ, Richardson AJ (2006) (Eds) Impacts of climate change on Australian marine life: Part C. Literature review. Report to the Australian Greenhouse Office. (CSIRO Marine and Atmospheric Research: Canberra, ACT, Australia) Available at https://www.reefwatch.asn.au/fishforum/forum4_cc/Hobday_etal_2006.pdf

Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver ECJ, Benthuysen JA, Burrows MT, Donat MG, Feng M, Holbrook NJ, Moore PJ, Scannell HA, Sen Gupta A, Wernberg T (2016) A hierarchical approach to defining marine heatwaves. *Progress in Oceanography* **141**, 227–238. doi:10.1016/j.pocean.2015.12.014

Hobday AJ, Burrows MT, Filbee-Dexter K, Holbrook NJ, Sen Gupta A, Smale DA, Smith KE, Thomsen MS, Wernberg T (2023) With the arrival of El Niño, prepare for stronger marine heatwaves. *Nature* **621**, 38–41. doi:10.1038/d41586-023-02730-2

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science* **328**, 1523–1528. doi:10.1126/science.1189930

Hutchinson S, Hawkins LE (1992) Quantification of the physiological responses of the European flat oyster *Ostrea edulis* L. to temperature and salinity. *Journal of Molluscan Studies* **58**, 215–226. doi:10.1093/mollus/58.2.215

Ivanina AV, Dickinson GH, Matoo OB, Bagwe R, Dickinson A, Beniash E, Sokolova IM (2013) Interactive effects of elevated temperature and CO_2 levels on energy metabolism and biomineralization of marine bivalves *Crassostrea virginica* and *Mercenaria mercenaria*. *Comparative Biochemistry and Physiology – A. Molecular & Integrative Physiology* **166**, 101–111. doi:10.1016/j.cbpa.2013.05.016

Jiang W, Wang X, Rastrick SPS, Wang J, Zhang Y, Strand Ø, Fang J, Jiang Z (2021) Effects of elevated pCO$_2$ on the physiological energetics of Pacific oyster, *Crassostrea gigas*. *ICES Journal of Marine Science* **78**, 2579–2590. doi:10.1093/icesjms/fsab139

Kooijman SALM (2009) 'Dynamic energy budget theory for metabolic organization', 3rd edn. (Cambridge University Press)

Kroeker KJ, Kordas RL, Crim RN, Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* **13**, 1419–1434. doi:10.1111/j.1461-0248.2010.01518.x

Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, Singh GS, Duarte CM, Gattuso J-P (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology* **19**, 1884–1896. doi:10.1111/gcb.12179

Langdon CJ, Newell RIE (1990) Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. *Marine Ecology Progress Series* **58**, 299–310. doi:10.3354/meps058299

Lannig G, Flores JF, Sokolova IM (2006) Temperature-dependent stress response in oysters, *Crassostrea virginica*: pollution reduces temperature tolerance in oysters. *Aquatic Toxicology* **79**, 278–287. doi:10.1016/j.aquatox.2006.06.017

Lannig G, Eilers S, Pörtner HO, Sokolova IM, Bock C (2010) Impact of ocean acidification on energy metabolism of oyster, *Crassostrea gigas* – changes in metabolic pathways and thermal response. *Marine Drugs* **8**, 2318–2339. doi:10.3390/md8082318

Le Moullac G, Soyez C, Latchere O, Vidal-Dupiol J, Fremery J, Saulnier D, Lo Yat A, Belliard C, Mazouni-Gaertner N, Gueguen Y (2016) *Pinctada margaritifera* responses to temperature and pH: acclimation capabilities and physiological limits. *Estuarine, Coastal and Shelf Science* **182**, 261–269. doi:10.1016/j.ecss.2016.04.011

Lee H, Romero J (Eds) (2023) 'Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.' (Intergovernmental Panel on Climate Change: Geneva, Switzerland) doi:10.59327/IPCC/AR6-9789291691647

Lee J-Y, Bellouin E, Coppola RG, Jones G, Krinner J, Marotzke V, Naik MD, Palmer GK, Plattner J, Rogelj M, *et al.* (2021) Future global climate: scenario-based projections and near-term information. In 'Climate Change 2021: the Physical Science Basis. Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change'. (Ed. V Masson-Delmotte, *et al.*) pp. 553–672. (Cambridge University Press: Cambridge, UK, and New York, NY, USA) doi:10.1017/9781009157896.006

Lehane C, Davenport J (2002) Ingestion of mesozooplankton by three species of bivalve; *Mytilus edulis*, *Cerastoderma edule* and *Aequipecten opercularis*. *Journal of the Marine Biological Association of the United Kingdom* **82**, 615–619. doi:10.1017/S0025315402005957

Lemasson AJ, Kuri V, Hall-Spencer JM, Fletcher S, Moate R, Knights AM (2017) Sensory qualities of oysters unaltered by a short exposure to combined elevated pCO$_2$ and temperature. *Frontiers in Marine Science* **4**, 352. doi:10.3389/fmars.2017.00352

Leung JYS, Zhang S, Connell SD (2022) Is ocean acidification really a threat to marine calcifiers? A systematic review and meta-analysis of 980+ studies spanning two decades. *Small* **18**, e2107407. doi:10.1002/smll.202107407

Lewis E, Wallace D (1998) Program developed for CO_2 system calculations. Environmental Sciences Division number 4735, ORNL/CDIAC-105. (Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA) Available at https://www.ncei.noaa.gov/access/ocean-carbon-acidification-data-system/oceans/CO2SYS/co2rprt.html

Li W, Gao K (2012) A marine secondary producer respires and feeds more in a high CO_2 ocean. *Marine Pollution Bulletin* **64**, 699–703. doi:10.1016/j.marpolbul.2012.01.033

Lucas A, Beninger PG (1985) The use of physiological condition indices in marine bivalve aquaculture. *Aquaculture* **44**, 187–200. doi:10.1016/0044-8486(85)90243-1

Melzner F, Gutowska MA, Langenbuch M, Dupont S, Lucassen M, Thorndyke MC, Bleich M, Pörtner H-O (2009) Physiological basis for high CO_2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences* **6**, 2313–2331. doi:10.5194/bg-6-2313-2009

Melzner F, Stange P, Trübenbach K, Thomsen J, Casties I, Panknin U, Gorb SN, Gutowska MA (2011) Food supply and seawater pCO$_2$ impact calcification and internal shell dissolution in the blue mussel *Mytilus edulis*. *PLoS ONE* **6**, e24223. doi:10.1371/journal.pone.0024223

Meunier CL, Schmidt J, Ahme A, Balkoni A, Berg K, Blum L, Boersma M, Brüwer JD, Fuchs BM, Gimenez L, Guignard M, Schulte-Hillen R, Krock B, Rick J, Stibor H, Stockenreiter M, Tulatz S, Weber F, Wichels A, Wiltshire KH, Wohlrab S, Kirstein IV (2025) Plankton communities today and tomorrow – potential impacts of multiple global change drivers and marine heatwaves. *Limnology and Oceanography* **70**, S225–S241. doi:10.1002/lno.70042

Navarro JM, Duarte C, Manríquez PH, Lardies MA, Torres R, Acuña K, Vargas CA, Lagos NA (2016) Ocean warming and elevated carbon dioxide: multiple stressor impacts on juvenile mussels from southern Chile. *ICES Journal of Marine Science* **73**, 764–771. doi:10.1093/icesjms/fsv249

Neokye EO, Wang X, Thakur KK, Quijon P, Nawaz RA, Basheer S (2024*a*) Climate change impacts on oyster aquaculture – part I: identification of key factors. *Environmental Research* **251**(Part 1), 118561. doi:10.1016/j.envres.2024.118561

Neokye EO, Wang X, Thakur KK, Quijón PA, Nawaz RA (2024*b*) Climate change impacts on oyster aquaculture – part II: impact assessment and adaptation measures. *Environmental Research* **259**, 119535. doi:10.1016/j.envres.2024.119535

Parker LM, Ross PM, O'Connor WA (2009) The effect of ocean acidification and temperature on the fertilization and embryonic development of the Sydney rock oyster *Saccostrea glomerata* (Gould, 1850). *Global Change Biology* **15**, 2123–2136. doi:10.1111/j.1365-2486.2009.01895.x

Parker LM, Ross PM, O'Connor WA (2010) Comparing the effect of elevated pCO_2 and temperature on the fertilization and early development of two species of oysters. *Marine Biology* **157**, 2435–2452. doi:10.1007/s00227-010-1508-3

Parker LM, Ross PM, O'Connor WA, Borysko L, Raftos DA, Pörtner H-O (2012) Adult exposure influences offspring response to ocean acidification in oysters. *Global Change Biology* **18**, 82–92. doi:10.1111/j.1365-2486.2011.02520.x

Parker LM, O'Connor WA, Raftos DA, Pörtner H-O, Ross PM (2015) Persistence of positive carryover effects in the oyster, *Saccostrea glomerata*, following transgenerational exposure to ocean acidification. *PLoS ONE* **10**, e0132276. doi:10.1371/journal.pone.0132276

Parker LM, O'Connor WA, Byrne M, Coleman RA, Virtue P, Dove M, Gibbs M, Spohr L, Scanes E, Ross PM (2017) Adult exposure to ocean acidification is maladaptive for larvae of the Sydney rock oyster *Saccostrea glomerata* in the presence of multiple stressors. *Biology Letters* **13**(2), 20160798. doi:10.1098/rsbl.2016.0798

Parker LM, Scanes E, O'Connor WA, Dove M, Elizur A, Pörtner H-O, Ross PM (2024) Resilience against the impacts of climate change in an ecologically and economically significant native oyster. *Marine Pollution Bulletin* **198**, 115788. doi:10.1016/j.marpolbul.2023.115788

Peng D, Zhang S, Zhang H, Pang D, Yang Q, Jiang R, Lin Y, Mu Y, Zhu Y (2021) The oyster fishery in China: trend, concerns and solutions. *Marine Policy* **129**, 104524. doi:10.1016/j.marpol.2021.104524

Pereira RRC, Scanes E, Parker LM, Byrne M, Cole VJ, Ross PM (2019) Restoring the flat oyster *Ostrea angasi* in the face of a changing climate. *Marine Ecology Progress Series* **625**, 27–39. doi:10.3354/meps13047

Pereira RRC, Scanes E, Gibbs M, Byrne M, Ross PM (2020) Can prior exposure to stress enhance resilience to ocean warming in two oyster species? *PLoS ONE* **15**, e0228527. doi:10.1371/journal.pone.0228527

Pereira RRC, Ribeiro e Silva R, de Oliveira VP, Valentin JL (2024) Forecasting the impact of marine heat waves on farmed bivalves *Nodipecten nodosus* and *Magallana gigas*. *Regional Studies in Marine Science* **80**, 103883. doi:10.1016/j.rsma.2024.103883

Pernet F, Tremblay R, Redjah I, Sévigny J-M, Gionet C (2008) Physiological and biochemical traits correlate with differences in growth rate and temperature adaptation among groups of the eastern oyster *Crassostrea virginica*. *The Journal of Experimental Biology* **211**, 969–977. doi:10.1242/jeb.014639

Pörtner HO, Farrell AP (2008) Physiology and climate change. *Science* **322**, 690–692. doi:10.1126/science.1163156

Pörtner H-O, Scholes RJ, Arneth A, Barnes DKA, Burrows MT, Diamond SE, Duarte CM, Kiessling W, Leadley P, Managi S, McElwee P, Midgley G, Ngo HT, Obura D, Pascual U, Sankaran M, Shin YJ, Val AL (2023) Overcoming the coupled climate and biodiversity crises and their societal impacts. *Science* **380**, eabl4881. doi:10.1126/science.abl488

Przeslawski R, Byrne M, Mellin C (2015) A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. *Global Change Biology* **21**, 2122–2140. doi:10.1111/gcb.12833

Rainer JS, Mann RL (1992) A comparison of methods for calculating condition index in eastern oysters, *Crassostrea virginica* (Gmelin, 1791). *Journal of Shellfish Research* **11**, 55–58.

Ramajo L, Marbà N, Prado L, Peron S, Lardies MA, Rodriguez-Navarro AB, Vargas CA, Lagos NA, Duarte CM (2016*a*) Biomineralization changes with food supply confer juvenile scallops (*Argopecten purpuratus*) resistance to ocean acidification. *Global Change Biology* **22**, 2025–2037. doi:10.1111/gcb.13179

Ramajo L, Pérez-León E, Hendriks IE, Marbà N, Krause-Jensen D, Sejr MK, Blicher ME, Lagos NA, Olsen YS, Duarte CM (2016*b*) Food supply confers calcifiers resistance to ocean acidification. *Scientific Reports* **6**, 19374. doi:10.1038/srep19374

Riebesell U, Gattuso J-P (2015) Lessons learned from ocean acidification research. *Nature Climate Change* **5**, 12–14. doi:10.1038/nclimate2456

Ries JB, Cohen AL, McCorkle DC (2009) Marine calcifiers exhibit mixed responses to CO_2-induced ocean acidification. *Geology* **37**, 1131–1134. doi:10.1130/G30210A.1

Ross PM, Parker L, O'Connor WA, Bailey EA (2011) The impact of ocean acidification on reproduction, early development and settlement of marine organisms. *Water* **3**, 1005–1030. doi:10.3390/w3041005

Ross PM, Parker L, Byrne M (2016) Transgenerational responses of molluscs and echinoderms to changing ocean conditions. *ICES Journal of Marine Science* **73**(3), 537–549. doi:10.1093/icesjms/fsv254

Ross PM, Scanes E, Byrne M, Ainsworth TA, Doneslon JM, Foo SA, Hutchings P, Thiyagarajan V, Parker LM (2023) Surviving the Anthropocene: the resilience of marine animals to climate change. In 'Oceanography and marine biology: an annual review. Vol. 61'. (Eds SJ Hawkins, PA Todd, BD Russell, AJ Lemasson, AL Allcock, M Byrne, LB Fruth, CH Lucas, EM Marzinelli, PJ Mumby, J Sharples, IP Smith, SE Swearer) pp. 35–80. (Taylor & Francis) doi:10.1201/9781003363873-3

Ross PM, Pine C, Scanes E, Byrne M, O'Connor WA, Gibbs M, Parker LM (2024) Meta-analyses reveal climate change impacts on an ecologically and economically significant oyster in Australia. *iScience* **27**, 110673. doi:10.1016/j.isci.2024.110673

Sanders MB, Bean TP, Hutchinson TH, Le Quesne WJF (2013) Juvenile king scallop, *Pecten maximus*, is potentially tolerant to low levels of ocean acidification when food is unrestricted. *PLoS ONE* **8**, e74118. doi:10.1371/journal.pone.0074118

Scanes E, Parker LM, O'Connor WA, Stapp LS, Ross PM (2017) Intertidal oysters reach their physiological limit in a future high-CO_2 world. *Journal of Experimental Biology* **220**, 765–774. doi:10.1242/jeb.151365

Scanes E, Scanes PR, Ross PM (2020) Climate change rapidly warms and acidifies Australian estuaries. *Nature Communications* **11**, 1803. doi:10.1038/s41467-020-15550-z

Schulte PM (2015) The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. *The Journal of Experimental Biology* **218**, 1856–1866. doi:10.1242/jeb.118851

Sokolova IM (2013) Energy-limited tolerance to stress as a conceptual framework to integrate the effects of multiple stressors. *Integrative and Comparative Biology* **53**, 597–608. doi:10.1093/icb/ict028

Sokolova IM, Sukhotin AA, Lannig G (2011) Stress effects on metabolism and energy budgets in mollusks. In 'Oxidative stress in aquatic ecosystems'. (Eds D Abele, JP Vázquez-Medina, T Zenteno-Savín) pp. 261–280. (Wiley–Blackwell) doi:10.1002/9781444345988.ch19

Solan M, Whiteley N (2016) 'Stressors in the marine environment: physiological and ecological responses; societal implications.' (Oxford University Press)

Somero GN (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *The Journal of Experimental Biology* **213**, 912–920. doi:10.1242/jeb.037473

Stapp LS, Parker LM, O'Connor WA, Bock C, Ross PM, Pörtner HO, Lannig G (2018) Sensitivity to ocean acidification differs between populations of the Sydney rock oyster: role of filtration and ion-regulatory capacities. *Marine Environmental Research* **135**, 103–113. doi:10.1016/j.marenvres.2017.12.017

Thomsen J, Casties I, Pansch C, Körtzinger A, Melzner F (2013) Food availability outweighs ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. *Global Change Biology* **19**, 1017–1027. doi:10.1111/gcb.12109

Treviño L, Lodeiros C, Vélez-Falcones J, Chávez-Alcivar C, Isea-León F, Bermúdez-Medranda AE, Vélez-Chica JC, Cruz-Quintana Y, Leal D, Santana-Piñeros AM, Rodríguez-Pesantes D (2020) Suspended culture evaluation of Pacific oyster *Crassostrea gigas* in a tropical estuary. *Aquaculture Research* **51**, 2052–2061. doi:10.1111/are.14556

Underwood AJ (1997) 'Experiments in ecology : their logical design and interpretation using analysis of variance.' (Cambridge University Press) doi:10.1017/CBO9780511806407

Valenti WC, Barros HP, Moraes-Valenti P, Bueno GW, Cavalli RO (2021) Aquaculture in Brazil: past, present and future. *Aquaculture Reports* **19**, 100611. doi:10.1016/j.aqrep.2021.100611

Vargas CA, de La Hoz M, Aguilera V, Martín VS, Manríquez PH, Navarro JM, Torres R, Lardies MA, Lagos NA (2013) CO_2-driven ocean acidification reduces larval feeding efficiency and changes food selectivity in the mollusk *Concholepas concholepas*. *Journal of Plankton Research* **35**, 1059–1068. doi:10.1093/plankt/fbt045

Wang Y, Li L, Hu M, Lu W (2015) Physiological energetics of the thick shell mussel *Mytilus coruscus* exposed to seawater acidification and thermal stress. *Science of The Total Environment* **514**, 261–272. doi:10.1016/j.scitotenv.2015.01.092

Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* **353**, 169–172. doi:10.1126/science.aad8745

Wernberg T, Thomsen MS, Baum JK, Bishop MJ, Bruno JF, Coleman MA, Filbee-Dexter K, Gagnon K, He Q, Murdiyarso D, Rogers K, Silliman BR, Smale DA, Starko S, Vanderklift MA (2024) Impacts of climate change on marine foundation species. *Annual Review of Marine Science* **16**, 247–282. doi:10.1146/annurev-marine-042023-093037

Widdows J (1985) Physiological procedures. In 'The effects of stress and pollution on marine animals'. (Eds BL Bayne, DA Brown, K Burns, DR Dixon, A Ivanovici, DR Livingston, DM Lowe, MN Moore, ARD Stebbing, J Widdows) pp. 161–178. (Praeger: New York, NY, USA)

Widdows J, Johnson D (1988) Physiological energetics of *Mytilus edulis*: scope for growth. *Marine Ecology Progress Series* **46**, 113–121. doi:10.3354/meps046113

Widdows J, Staff F (2006) Biological effects of contaminants: measurement of scope for growth in mussels. ICES Techniques in Marine Environmental Science, Number 40. International Council for the Exploration of the Sea, Copenhagen, Denmark.

Winder M, Sommer U (2012) Phytoplankton response to a changing climate. *Hydrobiologia* **698**, 5–16. doi:10.1007/s10750-012-1149-2

Wolf PH, Collins A (1979) Summary of daily temperature and salinity records for major oyster-producing estuaries of New South Wales, 1965–1973. New South Wales State Fisheries Miscellaneous bulletin 2. NSW Department of Agriculture.

Wright JM, Parker LM, O'Connor WA, Williams M, Kube P, Ross PM (2014) Populations of Pacific oysters *Crassostrea gigas* respond variably to elevated CO_2 and predation by *Morula marginalba*. *The Biological Bulletin* **226**(3), 269–281. doi:10.1086/BBLv226n3p269

Wu F, Lu W, Shang Y, Kong H, Li L, Sui Y, Hu M, Wang Y (2016) Combined effects of seawater acidification and high temperature on hemocyte parameters in the thick shell mussel *Mytilus coruscus*. *Fish & Shellfish Immunology* **56**, 554–562. doi:10.1016/j.fsi.2016.08.012

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