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Resilience against the impacts of climate change in an ecologically and economically significant native oyster

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ABSTRACT

Climate change is acidifying and warming our oceans, at an unprecedented rate posing a challenge for marine invertebrates vital across the globe for ecological services and food security. Here we show it is possible for resilience to climate change in an ecologically and economically significant oyster without detrimental effects to the energy budget. We exposed 24 pair-mated genetically distinct families of the Sydney rock oyster, *Saccostrea glomerata* to ocean acidification and warming for 4w and measured their resilience. Resilience was identified as the capacity to defend their acid-base balance without a loss of energy available for Scope for Growth (SFG). Of the 24 families, 13 were better able to defend their acid-base balance while eight had no loss of energy availability with a positive SFG. This study has found oyster families with reslience against climate change without a loss of SFG, is an essential mitigation strategy, in a critical mollusc.

1. Introduction

Climate change and biodiversity loss is impacting ecosystems across the globe (Pörtner et al., 2023). Continuing human-driven carbon dioxide (CO_2) emissions into our atmosphere are causing rapid ocean acidification and warming (Arias et al., 2021; Scanes et al., 2020b). Climate models predict that ocean acidification is *virtually certain*, and in the worst-case scenario will be −0.45 pH units lower than present day levels (shared socioeconomic pathway SSP5-8.5). Ocean warming is also v*irtually certain* and sea-surface temperatures (SSTs) will rise by 2.89 °C (SSP5–8.5 range 2.01 °C–4.07 °C) (Fox-Kemper et al., 2021; Lee et al., 2021). There are now grave concerns that the rate of climate change may outpace the intrinsic capacity for marine species to adapt and acclimate (Van Oppen et al., 2015) with serious consequences for marine ecosystems and the services they provide (Duarte et al., 2020).

Building resilience of marine species will be essential to ensure their persistence, but to do this has been a challenge across the globe (Van Oppen et al., 2015; Duarte et al., 2020). Resilience is broadly defined as the capacity of an organism or ecosystem to respond, recover and learn from stress and persist (Carpenter et al., 2001; Gunderson, 2000; Holling, 1996; Holling and Gunderson, 2002; Walker, 2019). Marine species can build resilience via acclimation and adaptation. Acclimation is a relatively rapid process. It is known that marine species can alter their morphology, physiology and/or behaviour quickly in response to stress through phenotypic plasticity (within or transgenerational), perhaps via epigenetic modifications, without changing their genotype Chakravarti et al., 2016; Ross et al., 2016; (Donelson et al., 2019, Leung et al., 2022; Ross et al., 2023). Adaptation by contrast, is typically a slower process. Without assistance marine species may take many generations to shift the mean phenotype towards a fitness peak through natural selection of more tolerant genotypes, gene modification, or genetic change through mutations or deletions (Van Oppen et al., 2015; Duarte et al., 2020; Chakravarti et al., 2016). Adaptation can also occur through assisted evolution which involves the speeding up of naturally occurring evolutionary processes through active human interventions, such as the selection of tolerant genotypes. The more "resilient" genotypes developed by these interventions can increase the tolerance and recovery capacity of key marine species and ecosystems (Van Oppen et al., 2015).

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Despite the obvious need to build resilience in a wide range of marine species to climate change, to date there has been largely an emphasis on reef building corals and their algal symbionts because of the dire threats they face (Van Oppen et al., 2015; van Oppen et al., 2018). Studies have investigated genetic variation of *Symbiodinium* to determine if it is possible to buy time for corals to adapt (Chakravarti et al., 2016; Chakravarti and Van Oppen, 2018). While these advances are encouraging, unfortunately, for corals and other marine species, improvement selection and success in one trait can come at the cost or trade-off in another that may ultimately limit resilience as measured by fitness, survival, and success (Thomsen et al., 2013, Chakravarti et al., 2016, Kelly et al., 2016, Stapp et al., 2018, Parker et al., 2017a, Parker et al., 2012). For example, while transgenerational exposure to ocean acidification in the polychaete *Ophryotrocha labronica* improved the growth rate of juveniles exposed to elevated CO_2, there was a trade-off of reduced egg volume (Thomsen et al., 2013). Also, Kelly et al. (2016), found when populations of the copepod *Tigriopus californicus* were exposed to ocean warming, heat selected lines had greater heat tolerance but lower fecundity indicating an energetic trade-off. Similarly, Parker et al. (2012, 2015, 2017a) and others (Diaz et al., 2018; Zhao et al., 2019; Spencer et al., 2020) have found in oysters that resilience to ocean acidification in one trait comes with trade-offs in size and survival.

It is becoming increasingly clear that we do not understand the capacity of marine organisms to build resilience to climate change and this is critical if we are to protect the essential ecological and economic services they provide, and adequately secure the persistence of marine organisms over this century.

Molluscs, especially oysters, are one group of organisms that appear to be vulnerable to climate change. Evidence from laboratory and field trials suggests that climate change including ocean acidification and warming will interact to have negative impacts on oysters across each life-history stage (Gazeau et al., 2013; Parker et al., 2013; Ross et al., 2011; Ross et al., 2023; Leung et al., 2022). However, the response of oysters and other bivalves to climate change can vary among species, and among genotypes within species (Parker et al., 2011; Scanes et al., 2020a; Stapp et al., 2017). As vital ecosystem engineers, oysters provide a habitat and nursery ground for other marine organisms and birds, are important at maintaining water quality and preventing shoreline erosion, and yet like corals are under significant threat from climate change and other factors (Beck et al., 2011; Grabowski and Peterson, 2007; McAfee et al., 2022).

Oysters are also a source of protein for people across the globe and form a global aquaculture industry valued at close to 7 billion USD annually (FAO, 2021). Oysters have been selectively bred to reduce disease and increase growth (Dégremont et al., 2015; Dove et al., 2020). Climate change, however, poses a "global threat to food security and nutrition" (FAO, 2022). The effects of climate change have already plunged millions of people into acute food and water insecurity (IPCC, 2022). In many coastal regions, declines in fish and shellfish attributed to climate change have resulted in reduced fisheries catches, disproportionally affecting vulnerable communities in close connection with coastal environments e.g. small islands (including Small Island Developing States), and polar areas (IPCC, 2022). In order to reverse these threats urgent adaptation and mitigation measures are required. One such measure may be the building of resilience in high value marine species which are seafood products.

The Sydney rock oyster, *Saccostrea glomerata*, are found in coastal bays and estuaries across much of Australia and forms the oldest and largest aquaculture industry (Raelene Trenaman, 2022). *S. glomerata* are also the focus of extensive restoration efforts to re-establish lost oyster reefs ((La Peyre et al., 2014, Grabowski et al., 2005, McAfee and Connell, 2020, Brumbaugh and Coen, 2009, Scanes et al., 2016). Building resilience of the Sydney rock oyster to climate change, however, comes with challenges. Previous attempts to build resilience of *S. glomerata* to climate change through transgenerational plasticity (TGP) have led to oysters that grow and develop faster, which have fewer shell abnormalities and are better able to maintain acid-base balance when exposed to ocean acidification (Parker et al., 2012, 2015, 2017a, 2017b). An ability to defend key extracellular acid-base balance parameters (i.e. extracellular pH {pH_e} and partial pressure of CO_2 {P_eCO_2}) close to control levels is one important indicator of resilience to ocean acidification, with a reduction in pH_e and increase in P_eCO_2 being a common feature among molluscs and other marine organisms when exposed to ocean acidification (Melzner et al., 2009; Gazeau et al., 2013). If left uncompensated, this change in acid-base balance parameters can have flow-on consequences for other physiological processes, including but not limited to increased energetic costs for acid-base and ion-regulatory processes (Melzner et al., 2009; Stapp et al., 2018), metabolic depression (Michaelidis et al., 2005; Reipschläger and Pörtner, 1996; Melzner et al., 2009), and acidification at the site of calcification (Ramesh et al., 2017).

Oysters with resilience to climate change, however, also have a higher standard metabolic rate (SMR) and the cost of this resilience is a loss in the available energy budget (Parker et al., 2018). Parker et al. (2017a) also found that oysters with high SMR when exposed to ocean acidification and one or more other stressor (ocean warming, reduced salinity and/or reduced food supply) had significantly reduced survival (Parker et al., 2017a). Similar increases in SMR have been found in the mussel, *Mytilus edulis* that were resilient to ocean acidifcation (Stapp et al., 2017). While a high SMR is thought to be beneficial for organisms during exposure to elevated CO_2, potentially allowing for higher ion and acid-base regulation, growth, and protein synthesis (Pörtner and Farrell, 2008; Melzner et al., 2009) there can also be non-beneficial consequences of a high SMR which reduce aerobic scope and place an organism closer to its tolerance limits (DeWitt, 1998; Pörtner and Farrell, 2008; Sokolova, 2013).

In this study, we assessed whether it is possible for an ecologically and economically significant habitat forming native Sydney rock oyster, *S. glomerata* to have resilience to climate change without negative impacts previously observed in their energy budget via the selection of genotypes. To do this, we exposed 24 genetically distinct pair-mated families of *S. glomerata*, selected for fast growth and disease resistance to ocean acidification and warming in the laboratory and measured their ability to defend extracellular acid-base balance and energy budget. After we identified families that defended their acid-base balance we then measured their Scope for Growth (SFG) to assess whether there was loss of available energy. SFG is a measure of the energy available for growth and other fitness sustaining processes e.g., reproduction.

2. Methods

As part of a wider oyster breeding program run by the NSW Department of Primary Industries, families of *S. glomerata* have been selectively bred for nine-generations at the Port Stephens Fisheries Institute (PSFI) (Dove et al., 2020). The purpose of creating selectively bred families was to increase the growth rate and build resistance to disease of oysters to improve aquaculture profitability (Dove and O'Connor, 2007). Previous research has also shown that oyster families differ in their response to climate change (Parker et al., 2015; Parker et al., 2012; Parker et al., 2011; Scanes et al., 2020a). Adult oysters (20 mo. old) were obtained from each of 24 distinct families of *S. glomerata.* The 24 families were designated all the letters of the alphabet except Y and Z: A, B, C, D, E, F, G, H, I, J, K, L, M, N, O, P, Q, R, S, T, U, V, W & X, for this study. Each family was created by "pair mating" a male and female oyster from families with known pedigree and traits. When juvenile oysters reached a shell length of 5 mm, they were transferred to purpose built commercial bags (SEAPA Co. Edwardstown South Australia, 600 × 250 × 100 mm) and cultured on intertidal leases in Cromarty Bay, Port Stephens (152° 4′0.69″E, 32°43′19.69″S) where they remained for 18 mo. until the beginning of the experiment.

2.1. Oyster husbandry, acclimation, and experimental exposure

All seawater used in acclimation and experimental exposure was collected from Little Beach, Port Stephens, NSW (152°9′30.00″E, 32°42′43.03″S), filtered through canister filters to a nominal 1 μm, and stored onsite in 38,000 L polyethylene tanks as a stock of filtered seawater (FSW).

120 individual *S. glomerata,* from each of the 24 families (A-X) were collected for experiments from intertidal leases in Cromarty Bay, Port Stephens, NSW (152° 4′0.69″E, 32°43′19.69″S) in July 2019. Once collected, oysters were transported to the laboratory at PSFI and gently cleaned of any fouling organisms before being placed into two 1500 L fibreglass tanks containing aerated FSW.

Oysters were maintained in the 1500 L fibreglass tanks for two weeks to acclimate to laboratory conditions at 24 °C, salinity at 34.6 ppt and ambient pCO_2 (400 μatm) were selected for the study based on the present-day temperature range of *S. glomerata* in Port Stephens (15–26 °C) (Wolf and Collins, 1979) and based on previous studies (Parker et al., 2017b). The optimal salinity range of the Sydney rock oyster being 25 to 35 ppt and temperature 25 °C and 30 °C (Nell and Dunkley, 1984; Ertl et al., 2019). These are also optimal salinities and temperatures for filtration rates, larval and spat development (Dove and O'Connor, 2007).

During all acclimation and experimental exposure, tanks containing oysters received a full water change every second day. This involved removing all oysters from the tank, gently rinsing them with freshwater to remove solid waste and un-eaten food and placing them into a new tank of FSW pre-equilibrated to their pCO_2 and temperature treatment. During all acclimation and experimental exposures, oysters were fed live algae cultured on site comprising of 50 % *Chaetoceros muelleri*, 25 % *Diacronema lutheri*, and 25 % *Tisochrysis lutea* at a rate of 1×10^9 cells oyster^{-1} day^{-1}.

Following acclimation, oysters from each family were placed in 24 netted bags, with 5 oysters per bag. At this time, twelve bags from each family were divided among twelve 750 L polyethylene tanks filled with 500 L FSW. These oysters were used to measure extracellular acid-base balance (see below). As measurements of Scope for Growth take a considerable amount of time, the addition of the remaining 12 bags was staggered over a period of 4 w, to ensure that all oysters had 4 w of exposure at the time of the Scope for Growth sampling. Briefly, each week, six families were added to each experimental tank until all 24 families were in the experimental treatments. Treatments consisted of fully orthogonal combinations of two pCO_2 concentrations (ambient [400 μatm]; elevated [1000 μatm]) and two temperature treatments (ambient [24 °C] and elevated [28 °C]). Each combination was replicated across three tanks and physicochemical variables of seawater in each treatment are described in Table 1. Treatments were selected to represent pCO_2 and temperature concentrations predicted for 2080-2100 by the Intergovernmental Panel on Climate Change (IPCC) (Arias et al., 2021) with respect to current ambient conditions in south-eastern Australia (Scanes et al., 2020b). Oysters remained in experimental treatments for four weeks and checked daily for mortality; no dead oysters were found in any tanks during the four-week exposure period.

The two pCO_2 levels used in this study of 400 μatm and 1000 μatm corresponded to a mean ambient pH_{NBS} of 8.17–8.18 ± 0.01 and pH_{NBS} of 7.83–7.84 ± 0.01, respectively. The elevated pCO_2 level was maintained using a pH-negative feedback system (Aqua Medic, Aqacenta Pty Ltd., Kingsgrove, NSW, Australia; accuracy ±0.01 pH units) that controls the pH level in each tank. To determine the set pH level corresponding to the desired experimental elevated pCO_2 level, total alkalinity (TA) was quantified at each water change using triplicate Gran-titration (Gran, 1952), and entered into a CO_2 system calculation program (CO2 SYS) (Lewis et al., 1998), using the dissociation constants of (Mehrbach et al., 1973) (NBS buffers, WTW 3400i). Temperature and salinity were measured daily and were also entered into the program (Table 1). Food grade CO_2 (BOC Australia) was bubbled directly into independent tanks to reduce pH. A pH probe connected to a controlling computer was placed within each tank with each elevated CO_2 tank was controlled by its own independent pH-controlling system.

The start date of experimental tanks was staggered over a 4-week period to accommodate for the time needed to measure scope for growth (SFG) parameters and ensure that all oysters received the same time in treatments prior to sampling. Oysters were slowly acclimated to the elevated pCO_2 and temperature treatments at the beginning of the experiment to minimise acute stress. To do this, pH was decreased by 0.05 units per day and temperature was increased by 1 °C every second day, in the elevated pCO_2 and/or temperature exposure tanks, respectively, until the experimental treatment levels were reached. Separate acclimation tanks were set up for oysters that experienced a staggered start date, and these oysters were added to the experimental tanks once the experimental treatment levels were reached. Oysters were then exposed to their respective treatments for a further four weeks. Specifically, a subset of all oysters was placed into the experimental tanks on day 1.

2.2. Extracellular acid-base balance

The level of resilience of each family under ocean acidification and warming was defined as the ability of oysters to defend their extracellular acid-base balance. Measurements of pH_e were taken from two oysters from each family in each tank (following methods of (Parker et al., 2018, Parker et al., 2012, Scanes et al., 2017). Oysters were observed prior to removing from tank to ensure that they were open and filtering at the time of sampling and were immediately opened without rupturing the pericardial cavity. Haemolymph samples were drawn from the extracellular fluid filling the pericardial cavity chamber using a sealed 1 mL needled syringe. A 0.5 mL sample was drawn carefully to avoid aeration of the haemolymph. 0.4 mL of the sample was then immediately transferred to an Eppendorf tube where pH_e of the sample was measured using a micro pH probe (Metrohm 827 biotrode). The remaining 100 μL of the haemolymph was transferred to a gas analyser (CIBA Corning 965) to determine total CO_2 (CCO_2). The micro pH probe was calibrated prior to use with NBS standards at the experimental temperature that the sampled oysters were held at and the gas analyser was calibrated. Partial pressure of CO_2 in haemolymph (P_eCO_2) was calculated from the CCO_2 concentration using the modified Henderson-Hasselbalch equation (Eq. (1)) according to Heisler (Heisler, 1984; Heisler, 1986) as found in (Pörtner et al., 2010) where molarity of dissolved species = 1.033 M^{-1} L^{-1} (seawater; Hammer et al., 2011), [Na^+]

Table 1
Mean (±S.E.) physicochemical variables of seawater in each treatment over the 4-week experimental exposure period ($n = 3$).

Exp. treatment	Salinity	Temp. (°C)	pHNBS	TA (μmol kg^{-1})	Pco2 (μatm)	DIC (μmol kg^{-1})	Ωcalcite	Ωaragonite
24 °C								
Ambient *p*CO2	34.6 ± 0.2	24 ± 0.5	8.17 ± 0.01	2330 ± 5.08	417 ± 1.7	2045 ± 8.4	4.95 ± 0.02	3.25 ± 0.01
Elevated *p*CO2	34.6 ± 0.2	24 ± 0.5	7.83 ± 0.01	2330 ± 5.08	1033.4 ± 4.2	2206.7 ± 8.9	2.56 ± 0.01	1.68 ± 0.01
28 °C								
Ambient *p*CO2	34.6 ± 0.2	28 ± 0.5	8.18 ± 0.01	2330 ± 5.08	412.2 ± 1.7	2009.2 ± 8.3	5.57 ± 0.02	3.71 ± 0.02
Elevated *p*CO2	34.6 ± 0.2	28 ± 0.5	7.84 ± 0.01	2330 ± 5.08	1037.8 ± 4.2	2183.8 ± 8.9	2.93 ± 0.01	1.95 ± 0.01

Values for partial pressure of CO2 (*p*CO2), Dissolved Inorganic Carbon (DIC), Ωcalcite and Ωaragonite calculated from salinity, temperature, pH(NBS) and total alkalinity (TA). Ω = saturation state.

= 0.55 M (measured previously), and protein concentration of *S. glomerata* = 0.05 g^{-1} L^{-1} (Peters and Raftos, 2003).

$$P_eCO_2 = CCO_2 \times \left(10^{pH_e - pK'''} \times \alpha + \alpha\right)^{-1}$$

where P_eCO_2 = partial pressure of CO_2 in haemolymph as calculated (mM), CCO_2 = total CO_2 concentration in haemolymph as measured (mM), α = the physical solubility of CO_2, and pK‴ is the apparent dissociation constant of carbonic acid in body fluids after Heisler (1986).

Families that displayed no significant difference in pH_e and/or P_eCO_2 under ocean acidification and warming compared to control levels were identified as having resilience.

2.3. Scope for growth

Energy budget was measured by assessing the scope for growth (SFG) of all families that were able to defend their extracellular acid-base balance and identified as having resilience. To determine the SFG of each family, two oysters were measured for clearance rate, absorption efficiency, oxygen respiration rate and ammonia-nitrogen excretion from each family, treatment and replicate combination following the modified methods of Widdows (1985). Measurements on all 24 families for SFG were taken and data from the 13 families are included here. These families were able to defend their extracellular acid-base balance, with no significant difference in pH_e when exposed to elevated CO_2 and temperature, were identified with a potentially higher level of resilience.

Clearance rate (CR). CR was defined as the "volume of water cleared of algal cells per hour" (Lh^{-1}) (Bayne, 1999), and measured the number of algal cells removed from flow-through chambers containing individual oysters. A flow-through system was set up consisting of a header tank, set at the specific pCO_2 and temperature level, and dosed with an algal concentration of 100,000 cells mL^{-1} (*Tisochrysis lutea*). Water was pumped from the header tank to 13 flow-through chambers at a flow rate of 300 mL min^{-1}. An individual oyster was placed in each of 12 chambers with the 13th chamber acting as the blank. The inflow tube into each chamber was at the bottom and the outflow was at the top. A baffle in each chamber ensured uni-directional flow of seawater. Oysters were placed in the chambers and allowed to acclimate from the stress of handling and resume feeding for 2 h prior to sampling.

To estimate the clearance rate of oysters, the outflow algal cell concentration in each chamber was determined 1 and 2 h after acclimation. Water samples were collected simultaneously from the outflow tube of each chamber using a measuring cylinder and the flow rate was recorded. Algal cell concentration was measured using a light microscope (100×) and haemocytometer (n = 2 for each sample) and the timepoint of the maximum clearance rate used in the calculation. Clearance rate was calculated as:

$$CR = \frac{C_1 - C_0}{C_1} \text{x flow rate } \left(\text{L h}^{-1}\right)$$

where C_1 is the outflow algal cell concentration in the blank chamber and C_0 is the outflow algal cell concentration in each experimental chamber.

Absorption efficiency (AE). AE, the efficiency with which organic matter from the food is ingested and absorbed by oysters was measured following the method of (Conover, 1966) and (Widdows and Shick, 1985). Oysters were observed in the clearance rate experimental chambers and faeces were collected over a 2-hour period using a Pasteur pipette immediately following ejection. Faecal material from two oysters per family per replicate was pooled for analysis. Pooled samples were collected in 50 mL Falcon tubes and were stored in the freezer at −20 °C for later analysis.

Samples were thawed and filtered over a washed, ashed and pre-weighed 47 mm GF/C glass microfibre filter (Whatman, CAT No.1822-047) to remove salts (J, 1985). To determine the total dry weight of particulate matter, samples were then oven dried for 12 h at 90 °C and weighed. To determine the total ash free dry weight samples were ashed at 450 °C for 4 h and weighed. AE was calculated as:

$$AE = F - E/[(1 - E)\, x\, F]$$

where F is the ash-free dry weight: dry weight ratio of food (algae), and E is the ash-free dry weight: dry weight ratio of the faeces.

Oxygen consumption (VO_2). The rate of oxygen consumption was measured using a closed respiratory system (Parker et al., 2012). Following the CR measurements oysters were placed in individual 700 mL airtight chambers filled with FSW set to the corresponding pCO_2 and temperature treatment. Each chamber was fitted with a fibre-optic O_2 probe (PreSens dipping probe DP-PSt3, AS1 Ltd., Regensburg, Germany). The probes were calibrated using a two-point calibration (0 % and 100 % air saturated FSW). The time taken to reduce the percentage oxygen saturation of seawater in the chamber from 100 % to 80 % was recorded. A "blank" chamber containing only FSW was set up for each treatment to test for bacterial respiration, but as the change in this chamber was negligible it was not included in the VO_2 calculation. Time was measured only when oysters were actively respiring (time that oxygen levels were decreasing). Following the measurements, oysters were removed from the chambers, opened, and the tissue separated from shell. VO_2 was calculated as:

$$VO_2 = (V_r x\, \Delta C_w O_2)/\Delta t$$

where VO_2 is oxygen consumption (μmol O_2 h^{-1}), V_r is the volume of the respiratory chamber minus the volume of the oyster (L), $\Delta C_W O_2$ is the change in water oxygen concentration measured (μmoL O_2 L^{-1}), Δt is the measuring time (h) (Parker et al., 2012).

Excretion rate (VNH_4–N). Following measurements of oxygen consumption, the rate at which nitrogen was excreted as ammonia was measured. After 3 h in the chambers (Bayne, 1999), a 10 mL seawater sample was taken from each chamber containing oysters and filtered through a 0.45 μm membrane filter before being stored in the freezer at −20 °C. A sample was also taken from the blank chamber containing seawater only. The concentration of ammonia in a subset of samples was analysed at the Ecochemistry Services Laboratory at the University of Canberra. Samples were pre-digested using persulfate. Concentrations of ammonia were then determined using flow-injection spectrometry (Lachat Quickchem 8500) according to standard methods (APHA, 1998). VNH_4–N (μg N L^{-1}) and calculated as:

$$\text{VNH4–N} = \left(\text{Conc}_{\text{expt1}} - \text{Conc}_{\text{blank}}\right) \text{x}\ Vol/t$$

where $\text{Conc}_{\text{expt1}}$ is the concentration of ammonia in the experiment chamber and $\text{Conc}_{\text{blank}}$ is the concentration in the blank chamber, Vol is the volume of water in the chamber (L) and t is the incubation time (3 h).

Conversion of physiological rates to a standard body size. To determine the dry tissue weight of oysters, oysters were shucked, the tissue removed from the shell and then they were oven dried to a constant weight at 80 °C for 48 h and weighed using an electronic balance (± 0.001 g). Physiological rates (clearance and respiration rates) were converted to a standard body size (0.673 g) using the appropriate weight exponents (β) calculated based on the allometric relationship between dry tissue weight and physiological rate (Clearance rate: β = 0.891, n = 41; Respiration rate: β = 0.876, n = 40) as:

$$log Y_c = log\ Y_o - (\beta\ log X_o - \beta\ log\ X_c)$$

where Y_c is the corrected physiological rate for a standard dry tissue weight in grams (X_c), Y_o is the individual's measured physiological rate, and X_o is the individuals measured dry tissue weight in grams (J, 1985).

Calculation of Scope for Growth (SFG). All corrected physiological

rates were converted to energy equivalents (J g^{-1} h^{-1}) as follows:

Energy consumed/ ingestion rate (C).

$$C = CR\left(L\,g^{-1}\,h^{-1}\right) \text{ x POM of algae } \left(mg\,L^{-1}\right) \text{ x } 23\,J\,mg^{-1} \text{ ash free dry weight}$$

Energy absorbed (A).

$$A = (C) \text{ x absorption efficiency (AE)}$$

Energy respired (R).

$$R = Vo_2\ \left(\mu mol\ O_2\ g^{-1}\ h^{-1}\right) \text{ x } 0.456\ J\ \mu mol^{-1}\ O_2$$

Energy excreted (U).

$$U = VNH4\text{–}N\ \left(\mu mol\ NH_4 - N\ h^{-1}\right) \times 0.349\ J\ h^{-1}$$

SFG (J g^{-1} h^{-1}) was then calculated using the modified equation of Winberg (1960):

$$SFG = A - (R + U)$$

Ammonia excretion measured in the subset samples was found to be closely coupled to VO_2, forming only a negligible portion of the metabolic energy expenditure (<5 %; Supplementary Table 2). As a result, it was omitted from the calculation of SFG (Widdows, 1985).

2.4. Data analysis

Data were analysed using a non-parametric aligned-rank transform (ART) ANOVA (Wobbrock et al., 2011) using the "ARTool" package in R software (Kay and Wobbrock, 2016). ART ANOVA used "CO_2 treatment" (ambient or elevated) as the first fixed factor, "Temperature" (24 or 28 °C) as the second fixed factor and "Family line" as the third fixed factor. This was done to meet the assumptions of ANOVA because a non-normal distribution was determined by the Shapiro Wilk normality test and non-homogenous variances were determined by Cochran's test. Post-hoc pairwise comparisons of estimated marginal means were made using the "emmeans" package with Tukey-adjusted *P* values to determine significance among levels for factors or interactions of interest ($\alpha < 0.05$). Effect size (Cohen's d ± 95 % Confidence Interval) was calculated to determine the magnitude of effects of elevated pCO_2 on P_eCO_2.

3. Results

3.1. Extracellular acid-base balance variables

3.1.1. pH_e

Exposure to elevated pCO_2 led to a significant reduction in pH_e of *S. glomerata* ($F_{23,\ 480} = 3.81$, $P < 0.001$; Fig. 1), in 11 of the 24 family lines at both experimental temperatures, (family lines F, I, A, C, W, E, G, B, D, S, X). In the remaining 13 family lines (M, P, O, R, L, H, N, T, J, K, U, Q, V), however, there was no significant difference in pH_e at ambient and elevated pCO_2 and these were identified as having higher resilience. The effect of temperature also was significantly different among family, but pairwise tests found no significant differences ($F_{23,\ 480} = 3.01$, $P < 0.001$).

3.1.2. P_eCO_2

Elevated pCO_2 and temperature interacted to affect the P_eCO_2 of the families ($F_{23,\ 471} = 8.09$, $P < 0.001$; Fig. 2). P_eCO_2 of the oyster hemolymph was greater at elevated compared to ambient pCO_2 and between temperatures and among family lines. Analysis of effect size revealed that the extent of this effect was greater at 24 °C (effect size = 1.18 ± 0.5) compared to 28 °C (effect size = 0.80 ± 0.48). Effect size analysis also revealed that in the 13 families that had unchanged pH_e, increases in P_eCO_2 were smaller in magnitude compared to those that had changed pH_e (Cohen's d = 0.95 ± 0.66 and 1.5 ± 0.81 respectively).

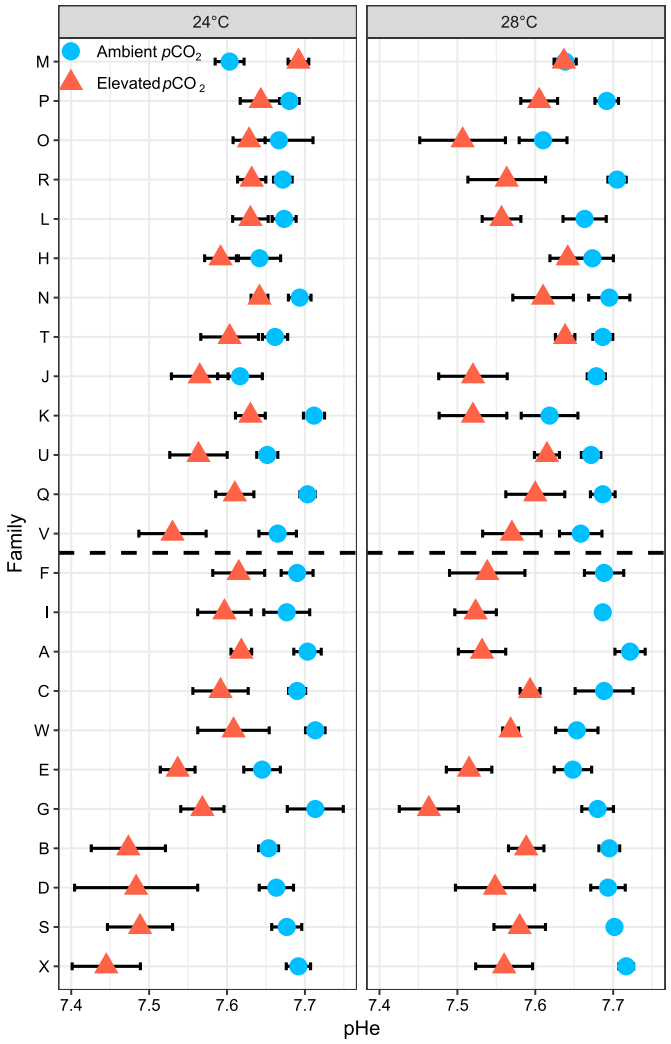

Fig. 1. Mean ± SE ($n = 6$) pHe values measured in each of 24 distinct families of the Sydney rock oyster *Saccostrea glomerata* (named A-X) following exposure to ambient and elevated pCO_2, at 24 and 28 °C for 4 weeks. Familes are ordered based on the difference between pHe at elevated and ambient pCO_2, averaged across the two temperature treatments. The lefthand panel is measurements taken at 24 °C, right handpanel is measurements taken at 28 °C. Red triangles are mean ± SE values at Elevated pCO_2 and blue circles are mean ± SE values at ambient pCO_2 values. The pHe of families above the dashed line were found not to be significantly affected by elevated pCO_2 and therefore identified as resilient, those below the line were significantly affected ($F_{23,\ 480} = 3.81$, $P < 0.001$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Scope for growth variables

3.2.1. Clearance rate (CR)

Clearance rate of *S. glomerata* was significantly different between pCO_2, temperature, and family line (CO_2: $F_{1,\ 247} = 4.75$, $P < 0.05$; Temperature: $F_{1,\ 247} = 13.12$, $P < 0.001$; Family line: $F_{12,\ 247} = 2.09$, $P < 0.05$; Fig. 3) and ranged from 2.35 ± 0.91 to 19.57 ± 5.94 L g^{-1} h^{-1}. In general, the clearance rate was greater at ambient compared to elevated CO_2 and at elevated 28 °C compared to ambient temperature 24 °C. Family line H had significantly lower clearance rate than family line K, with all other family lines being similar to each other.

3.2.2. Absorption efficiency (AE)

Absorption efficiency of *S. glomerata* was significantly different between pCO_2 levels ($F_{1,\ 247} = 4.00$, $P < 0.05$) and temperature x family

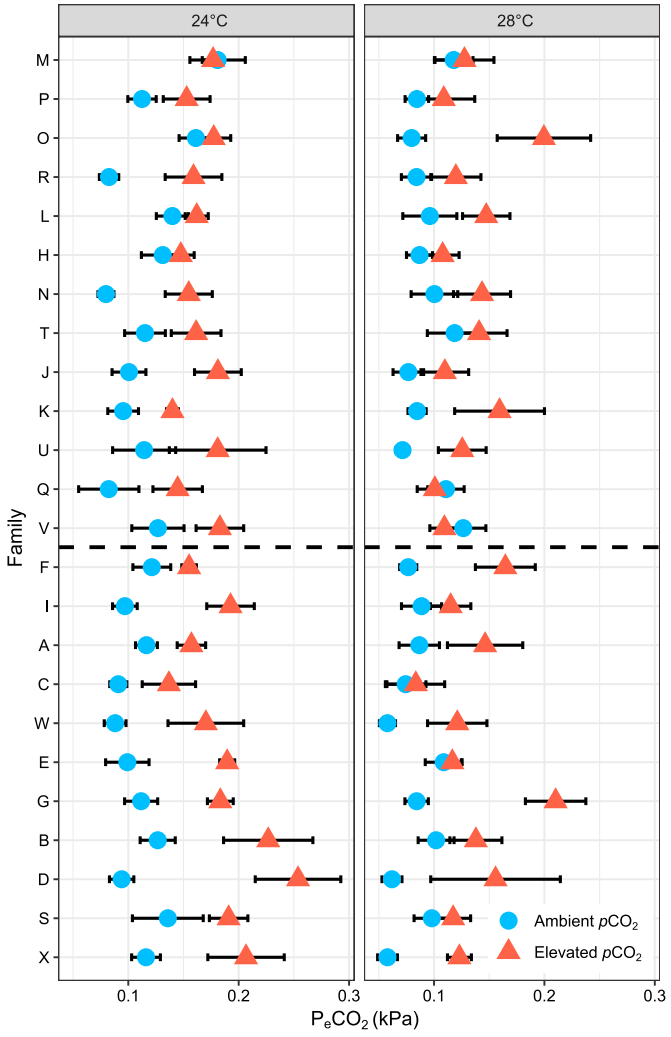

Fig. 2. Mean ± SE (n = 6) P_eCO_2 values measured in each of 24 distinct families of the Sydney rock oyster *Saccostrea glomerata* (named A-X) following exposure to ambient and elevated pCO_2, at 24 and 28 °C for 4 weeks. Familes are ordered based on the difference between pHe at elevated and ambient pCO_2, averaged across the two temperature treatments. The lefthand panel is measurements taken at 24 °C, right handpanel is measurements taken at 28 °C. Red triangles are mean ± SE values at Elevated pCO_2 and blue circles are mean ± SE values at ambient pCO_2 values. The pHe of families above the dashed line were found not to be significantly affected by elevated pCO_2 and therefore identified as resilient, those below the line were significantly affected ($F_{23,\ 480} = 3.81$, $P < 0.001$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

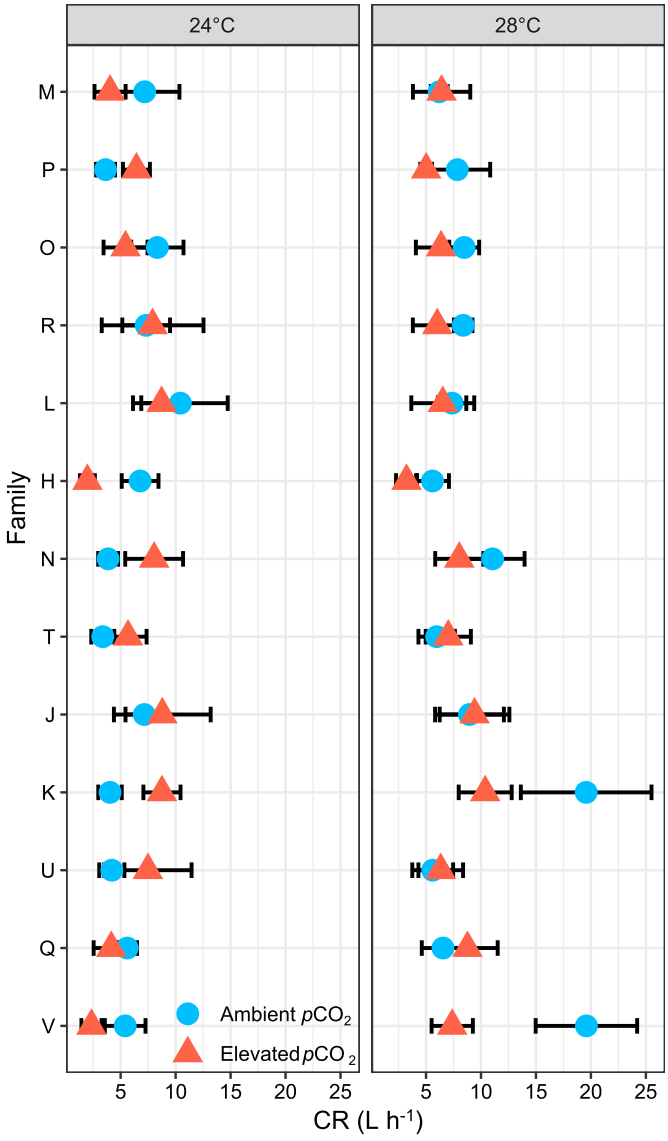

Fig. 3. Mean ± SE (n = 6) Clearance Rate (L h^{-1}) values for each of the 13 families identified as resilient based on their pHe. The lefthand panel is measurements taken at 24 °C, right handpanel is measurements taken at 28 °C. Red triangles are mean ± SE values at Elevated pCO_2 and blue circles are mean ± SE values at ambient pCO_2 values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

line interaction ($F_{12,\ 247} = 2.89$, $P < 0.0001$) and ranged from 0.56 ± 0.06 to 0.90 ± 0.19 (Fig. 4). In general, absorption efficiency was found to be greater at elevated compared to ambient pCO_2. At 24 °C, AE was greater in family lines M, R and V compared to families J, K, L, N and P. At 28 °C, absorption efficiency was greater in family U compared to family lines L, N and P.

3.2.3. Oxygen consumption (Vo_2)

Oxygen consumption of *S. glomerata* was significantly different between temperatures and ranged from 25.72 ± 1.56 to 55.60 ± 5.17 μmol O_2 g^{-1} h^{-1} a (Fig. 5). Oysters had greater oxygen consumption at elevated 28 °C compared to ambient temperature = 24 °C ($F_{1,\ 246} = 21.50$, $P < 0.001$). Oxygen consumption was greatest in families J, K, L, N, O and R and lowest in families P, T, U and V ($F_{12,\ 246} = 8.68$. $P < 0.001$).

3.2.4. Scope for growth (SFG)

The Scope for Growth of *S. glomerata* was significantly different dependent on a CO_2 × Temperature × Family line interaction ($F_{12,\ 241} = 3.12$, $P < 0.001$) and ranged from −9.18 ± 3.67 to 608.80 ± 192.09 J g^{-1} h^{-1} (Fig. 6). At ambient conditions (ambient pCO_2; 24 °C) there were no significant differences in SFG among families. In all other treatment combinations, however, SFG was significantly lower in families H, M, O, R and V (12.41 ± 5.16 J g^{-1} h^{-1}) compared to in families with higher SFG (185.96 ± 20.67 J g^{-1} h^{-1}). Low clearance rate and/or high oxygen consumption appeared to be the driving force of low SFG in families H, M, O, R and V, with absorption efficiency found to be high in each of these families.

Interestingly, exposure to elevated CO_2 and temperature did not negatively impact the overall net energy budget of the families, and SFG was similar across the treatment combinations. For example, elevated CO_2, negatively impacted the clearance rate of oyster families, but this was compensated for by an increase in absorption efficiency. Similarly,

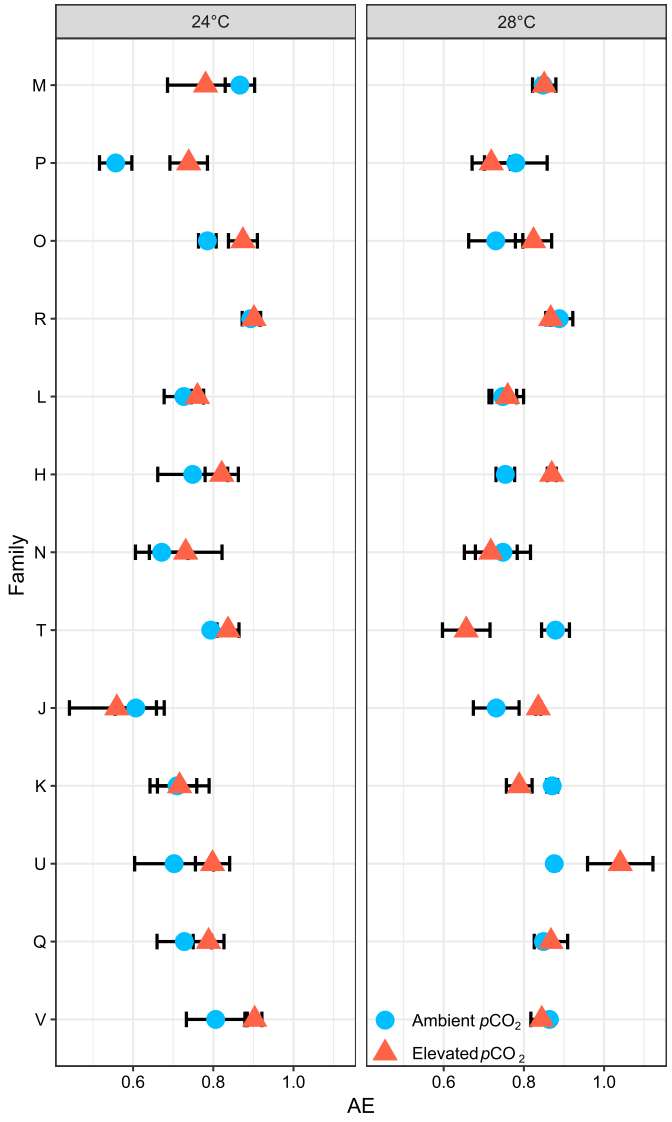

Fig. 4. Mean ± SE (n = 6) Absorption Effiency values for each of the 13 families identified as resilient based on their pHe. The lefthand panel are measurements taken at 24 °C, right-hand panel are measurements taken at 28 °C. Red triangles are mean ± SE values at Elevated pCO_2 and blue circles are mean ± SE values at ambient pCO_2 values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

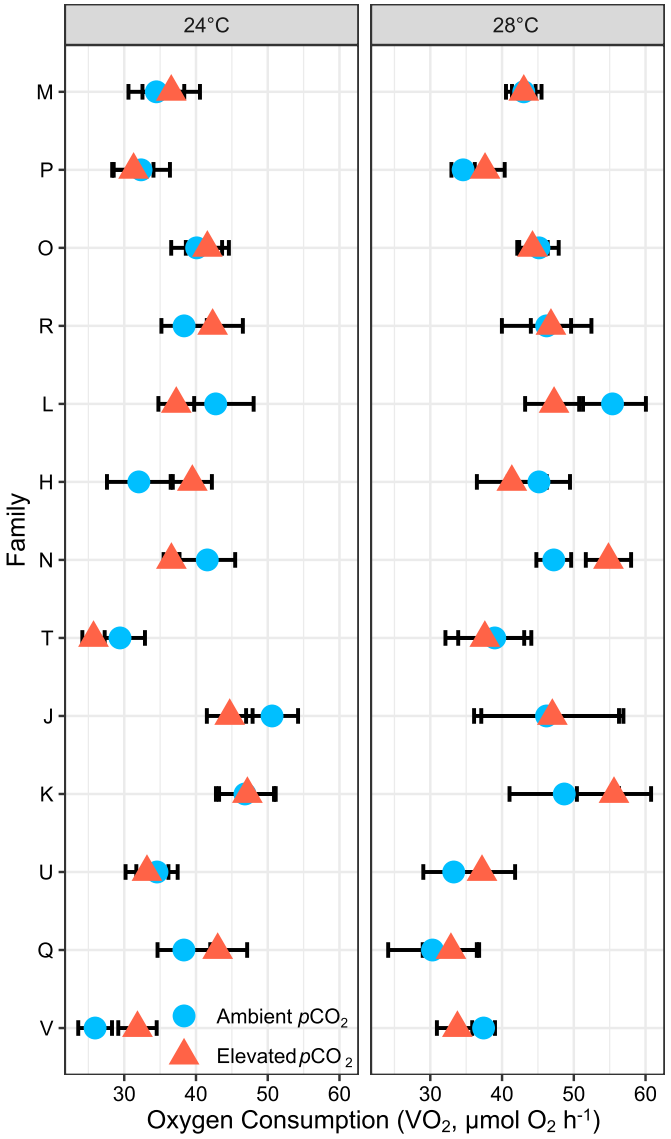

Fig. 5. Mean ± SE (n = 6) Oxygen Consumption (VO_2) values for each of the 13 families identified as resilient based on their pHe. The lefthand panel are measurements taken at 24 °C, right handpanel are measurements taken at 28 °C. Red triangles are mean ± SE values at Elevated pCO_2 and blue circles are mean ± SE values at ambient pCO_2 values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

elevated temperature increased the energy expenditure of oyster families as indicated by an increase in VO_2 but this was compensated by an increase in CR/ energy intake. There was, significant variability in the energy budget of each of the families; some families had a low or even negative SFG, while others had high SFG.

4. Discussion

The aim of this study was to determine whether it is possible for *S. glomerata* to have resilience to climate change without the negative effects previously observed in their energy budget and thus secure the persistence of this ecologically and economically significant habitat forming species. Families which had resilience were defined as those that were able to 1). Defend acid-base balance and 2). Maintain a high SFG in response to climate change stress. We found, that out of the 24 families 13 were able to partially defend their extracellular acid-base balance, with no significant difference in pH_e when exposed to elevated CO_2 and temperature. SFG in these 13 families, varied considerably. Five families had low SFG suggesting that these families have limited energy available for other fitness sustaining processes and low resilience. In the eight remaining families, there was a high SFG suggesting high energy available for other fitness sustaining processes and greater resilience. This study has found for the first time, resilience to climate change (i.e. elevated CO_2 and temperature) for *S. glomerata* without negative effects on their energy budget.

The energy budget of marine organisms is pivotal to their fitness and success (Sokolova, 2013). Typically, the energy budget can be divided into five sectors: the proportion of total energy that is required to maintain essential life processes – known as maintenance (measured by SMR), and the remaining proportion that is devoted to other fitness sustaining processes including growth, reproduction, activity, and storage (Sokolova, 2013; Pörtner, 2008). While resilience to climate change has previously been observed in marine organisms, this has often

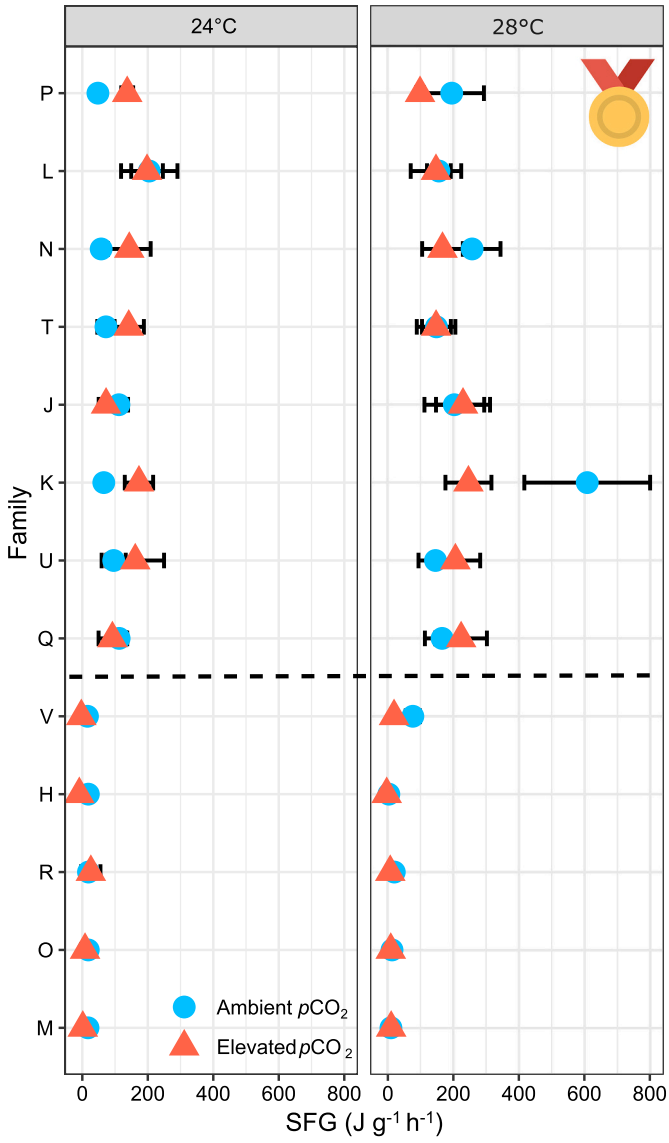

Fig. 6. Mean ± SE (n = 6) Scope for Growth (SFG, J g^{-1} h^{-1}) values for each of the 13 families identified as resilient based on their pHe. The lefthand panel are measurements taken at 24 °C, right handpanel are measurements taken at 28 °C. Red triangles are mean ± SE values at Elevated pCO_2 and blue circles are mean ± SE values at ambient pCO_2 values. Families above the dashed line are identified as retaining relativly higer SFG at Elevaed or Ambient pCO_2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

coincided with an increase in maintenance costs (Parker et al., 2017a; Parker et al., 2015; Thomsen et al., 2017). Previous studies on larvae and juveniles of selectively bred *S. glomerata*, have also found increased resilience to a sole stressor i.e. ocean acidification but reduced tolerance to multiple co-occurring stressors i.e. elevated temperature, reduced food concentration, intertidal air exposure (Parker et al., 2017a; McAfee et al., 2017). This study has identified resilience to climate change i.e. warming and acidification varies among genotypes of *S. glomerata*, with some genotypes experiencing little to no negative effects on their energy budget. This will have long-term downstream benefits for these oyster genotypes with more energy available for fitness sustaining processes.

Of importance to note, we found that the elevated temperature of +4 °C used in this study had very little impact on the energy budget of the *S. glomerata* families exposed to elevated CO_2. In fact, for most family lines, the respiration rate of adults increased at the elevated temperature of 28 °C, which suggested that adults of *S. glomerata* were still within their optimal thermal tolerance range (Pörtner et al., 2017). This thermal tolerance may be because selectively bred families of *S. glomerata* used in this study are in the middle of their thermal distribution range at Port Stephens rather than the and upper limit of their thermal distribution range. Studies of marine ectotherms suggest, however, that populations at the upper limits of their thermal distribution range may be more vulnerable to warming (Tomanek, 2010; Stillman, 2002; Somero, 2010; Gleason and Burton, 2013).

Also important to note in this study were the small amounts of pseudofeces that were observed during the clearance rate measurements i.e. algal material cleared from the water column but not ingested. The presence of pseudofeces may have led to energy consumption/ ingestion rates slightly higher than actual values. As energy consumed/ ingestion rate is the calculation of clearance rate x food concentration when pseudofeces are not produced (Bayne, 1999), While the overall effect of this on the SFG values is expected to be minimal, it may have led to higher SFG. It is not unusual for SFG to exceed >100 J/g/h in oysters considering values of up to 500 j/g/h by Guzmán-Agüero et al. (2013) in the oyster *C. corteziensis,* especially at elevated temperatures. In addition, *C. gigas* selected for fast growth have reported a mean SFG of 300 j/g/h (Zhang et al., 2018). Considering that oyster family lines used in this study were selected for fast growth, our SFG values appear to be consistent with those previously reported.

In this study, there were 11 families which did not defend their extracellular acid-base balance, with a decrease in pH_e measured when oysters were exposed to elevated CO_2 and temperature. While these families may go on to demonstrate positive SFG, they were not considered to have levels of resilience similar to those eight families which could both defend pH_e and have positive SFG. Without the capacity to defend acid-base balance even with positive SFG, there would likely be trade-offs. That is there may be increased energetic costs for acid-base and ion-regulatory processes (Melzner et al., 2009; Stapp et al., 2018), metabolic depression (Melzner et al., 2009; Michaelidis et al., 2005; Reipschlager and Portner, 1996) and acidification at the site of calcification (Ramesh et al., 2017). Evidence for impacts of resilience to climate change on the energy budget have been found in a wide range of marine organisms, presumably as they try to balance energy allocation between different physiological traits (Cunning et al., 2015; Jones and Berkelmans, 2010; Kelly et al., 2016; Chakravarti et al., 2016; Suckling et al., 2015; Cardoso et al., 2018). For example, in the corals, *Pocillopora damicornis* and *Acropora millepora,* increased resilience to warming has been associated with a reduction in growth (Jones and Berkelmans, 2010; Cunning et al., 2015). Experiments on the impacts of ocean acidification following transgenerational exposure in the Atlantic cod *Gadus morhua*, have also found increased survival at high food concentrations, but lower survival and organ damage at low food concentrations (Stiasny et al., 2018). Further, in the sea urchin *Sterechinus neumayeri*, an increase in larval resilience to climate change came at the cost of an increased proportion of larvae being abnormal (Suckling et al., 2015). A loss of available energy can have profound downstream effects on the fitness and success of marine populations. As a marine organism responds to the stress of climate change, a trade-off in physiological variables such as growth or reproduction may be inevitable, but not all individuals in a population will respond similarly. Our results suggest resilience of marine organisms to climate change can occur while maintaining a positive energy budget which reduces the likelihood of negative trade-offs. Whether this persists when oysters are transplanted into the real multiple stressor environment in the field is an area for further research.

The building of reslience in marine species has, however, not come without concerns for potential negative impacts on marine ecosystems (Van Oppen et al., 2015; Hoffmann et al., 2021). For example, more resilient individuals may cause outbreeding depression (Filbee-Dexter and Smajdor, 2019; Hoffmann et al., 2021), displace current populations (Van Oppen et al., 2015; Filbee-Dexter and Smajdor, 2019), provide a

competitive advantage over non-target species (Van Oppen et al., 2015), carry a risk of disease (Van Oppen et al., 2015) and/or lower the genetic potential for a marine organism to respond to yet unknown threats. To date, there has been no evidence that resilient oysters have these impacts. For example, there has been no evidence of genetic introgression between selectively bred and wild populations of *S. glomerata* (Thompson et al., 2017). This is significant when one considers that commercial farming of *S. glomerata* commenced in 1870 in this area (O'Hare et al., 2021) and introduction of selectively bred populations has been present since the early 1990's (Thompson et al., 2017; Dove et al., 2020). While these concerns require thoughtful consideration, the benefits of building resilience to climate change for aquaculture species such as oysters, may outweigh the risks compared to non-aquaculture species such as corals.

Diverse responses to ocean acidification and warming are well documented both within and across populations of molluscs. This diversity has been identified as a potential avenue for adaptation via natural selection (DeWitt, 1998; Gleason and Burton, 2013; Somero, 2010; Stapp et al., 2017; Ross et al., 2023). In the mussel, *M. edulis*, for example, genetically distinct family lines created from dam-sire crosses of a mussel population collected from Kiel Fjord in the Baltic Sea, varied considerably in their level of resilience to ocean acidification, with larvae of some families undergoing successful settlement under elevated CO_2 (2400 μatm), and others experiencing close to 100 % mortality (Stapp et al., 2017). Further, in the intertidal snail, *Chlorostoma funebralis*, adults from a Northern California population were found to be more resilient to a + 4 °C warming than those from a Southern California population (Gleason and Burton, 2013). How widespread and abundant resilient genotypes, such as those identified in this study, are within wild populations of *S. glomerata* is currently unknown and requires further investigation to determine the capacity for wild populations to positively adapt to ocean acidification and warming via natural selection.

Much like corals (Anthony et al., 2017) and other habitat forming species across the globe, oyster reefs have experienced severe declines in abundance (Beck et al., 2011). More research is needed to determine whether oysters with resilience as found in this study can assist in the sustainability of oyster reef restoration (La Peyre et al., 2014; Grabowski and Peterson, 2007; McAfee and Connell, 2020; McAfee et al., 2016). The future of oyster reef restoration may carry a risk of failure as the current cumulative pressures increasingly combine with ocean acidification and warming.

It is likely without interventions to build the resilience of marine species that in the coming decades some marine species and ecosystems, will reach their tipping point and may face irreversible collapse (Rilov et al., 2020). The focus on building the resilience of marine organisms to climate change has, to date, has been largely focused on coral reefs. Here, we show that resilience is possible for a critical mollusc which provides ecological services and is also at the basis of a significant ecological aquaculture industry in Australia. We advocate that understanding the trade-offs of resilience is essential as a climate change mitigation strategy for other marine species.

CRediT authorship contribution statement

L.P., P.R., W.O., A.E. and H—O. P. designed the study, M.D. and W.O. supplied the experimental animals, L.P. and E.S. ran the experiment, E.S. and L.P. analysed the data. L.P., P.R. and E.S. wrote and revised the manuscript with feedback from all other co-authors.

Declaration of competing interest

We have no declarations of interest to declare.

Data availability

The data used for analysis are available on the DRYAD repository.

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We have no Conflict of Interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.115788.

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