



Future shock: Ocean acidification and seasonal water temperatures alter the physiology of competing temperate and coral reef fishes

Angus Mitchell^a, Chloe Hayes^a, David J. Booth^b, Ivan Nagelkerken^{a,*}

^a Southern Seas Ecology Laboratories, School of Biological Sciences, The University of Adelaide, DX 650 418, Adelaide, SA 5005, Australia

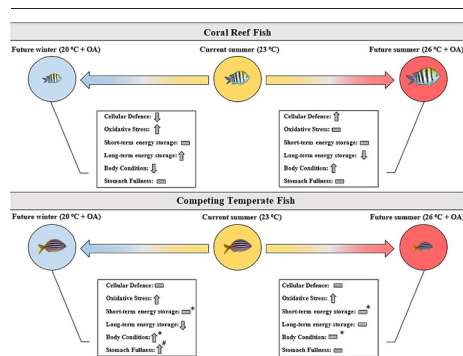
^b School of the Life Sciences, University of Technology Sydney, Ultimo, NSW 2007, Australia



HIGHLIGHTS

- Temperate and coral reef fishes were exposed to ocean acidification and ocean warming
- Coral reef fish decreased physiological performance in future winters (20 °C + OA)
- Coral reef fish increased lipid energy storage in future winter conditions
- Temperate fish increased oxidative damage in future summers (26 °C + OA)
- Future climate can modify the physiology of temperate and coral fishes seasonally

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change can directly (physiology) and indirectly (novel species interactions) modify species responses to novel environmental conditions during the initial stages of range shifts. Whilst the effects of climate warming on tropical species at their cold-water leading ranges are well-established, it remains unclear how future seasonal temperature changes, ocean acidification, and novel species interactions will alter the physiology of range-shifting tropical and competing temperate fish in recipient ecosystems. Here we used a laboratory experiment to examine how ocean acidification, future summer vs winter temperatures, and novel species interactions could affect the physiology of competing temperate and range-extending coral reef fish to determine potential range extension outcomes. In future winters (20 °C + elevated pCO₂) coral reef fish at their cold-water leading edges showed reduced physiological performance (lower body condition and cellular defence, and higher oxidative damage) compared to present-day summer (23 °C + control pCO₂) and future summer conditions (26 °C + elevated pCO₂). However, they showed a compensatory effect in future winters through increased long-term energy storage. Contrastingly, co-shoaling temperate fish showed higher oxidative damage, and reduced short-term energy storage and cellular defence in future summer than in future winter conditions at their warm-trailing edges. However, temperate fish benefitted from novel shoaling interactions and showed higher body condition and short-term energy storage when shoaling with coral reef fish compared to same-species shoaling. We conclude that whilst during future summers, ocean warming will likely benefit coral reef fishes extending their ranges, future winter conditions may still reduce coral reef fish physiological functioning, and may therefore slow their establishment at higher latitudes. In contrast, temperate fish species benefit from co-shoaling with smaller-sized tropical fishes, but this benefit may dissipate due to their reduced physiological functioning under future summer temperatures and increasing body sizes of co-shoaling tropical species.

* Corresponding author.

E-mail address: ivan.nagelkerken@adelaide.edu.au (I. Nagelkerken).

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1. Introduction

Biogeographic ranges of many species are shifting under climate change (Parmesan and Yohe, 2003; Chen et al., 2011; Pecl et al., 2017). Latitudinal and altitudinal species redistributions are altering ecosystem functionality (Doney et al., 2012), community assemblages (Soler et al., 2022) and the biodiversity of recipient communities (Lloyd et al., 2011; Soler et al., 2022). Biogeographic shifts have forced invaders and local species to interact for resources (Davis et al., 1998; Alexander et al., 2015). These novel interactions can either limit the invasion success of naïve species through competition (Coni et al., 2021a; Twiname et al., 2022) and predation (Beck et al., 2016) or promote establishment through positive novel species interactions (Smith et al., 2018; Pajmans et al., 2020). Therefore, understanding how local and invading species respond to novel biotic interactions, is important to make informed predictions upon range-shift outcomes within invaded ecosystems.

Global warming can modify physiological processes that underpin novel species interactions outcomes (Pörtner and Farrell, 2008; Alfonso et al., 2020). A small temperature increase can enhance the performance of range-extending species at their leading edge (Figueira and Booth, 2010), whilst the same increase can inhibit the physiological function of local species at their trailing range edge (Enzor and Place, 2014). Where range-shifting and resident species ranges overlap, small temperature increases can modify each species' fitness (Killen et al., 2013) and therefore alter biotic interactions that could determine range-shift outcomes (Figueira et al., 2019; Coni et al., 2021a). Thus, the concurrent effects of temperature and novel biotic interactions must be considered, to accurately predict the true pace of species range-extensions.

Marine species are often observed at the forefront of poleward range-extensions (Burrows et al., 2011). Anthropogenic-derived warming, strengthening poleward currents and species traits are the primary drivers of the rapid poleward redistribution of marine organisms (García Molinos et al., 2022). Marine taxa often move into higher latitudes or deeper waters to escape thermally unsuitable conditions at their trailing edges of distribution, or to expand into previously unsuitable ecosystems (Pecl et al., 2017). Physiologically sensitive ectotherms are commonly seen at the forefront of marine range shifts (Gervais et al., 2021). In Australia, over 150 coral reef fish species have been observed moving their distribution poleward into higher-latitude ecosystems (Booth et al., 2007; Feary et al., 2014; Fowler et al., 2018). Range-extending herbivores can reshuffle trophic pathways in recipient communities (Vergés et al., 2014; Pessarrodona et al., 2022), whilst gregarious coral reef fish species form shoals with local temperate reef species (Smith et al., 2018). These range-shifting species are commonly called 'vagrants' (Booth et al., 2011). Shoaling interactions with resident temperate species can provide fitness benefits to tropical vagrants (e.g. increased growth and reduced winter mortality; Smith et al., 2018; increased shoal size, prey access and reduced predation risk; Pajmans et al., 2020). However, little is known about how these novel interactions affect the fitness of resident species or how climate change (e.g. ocean warming and ocean acidification) might alter the outcomes of these novel shoaling interactions in the near future (Coni et al., 2021a; Mitchell et al., 2022).

Ocean acidification is a concurrent environmental driver resulting from anthropogenic carbon dioxide emissions (Doney et al., 2009). Ocean acidification can alter the physiology of marine fishes (Heuer and Grosell, 2014; Heuer et al., 2019) and hence has the potential to also change the pace of species range shifts (Coni et al., 2021b). Past efforts assessing range shift outcomes often focus on ocean warming effects (Figueira and Booth, 2010; but see Coni et al., 2021b). Indeed, species responses to ocean warming could accelerate the pace of marine range-extensions (Figueira and Booth, 2010; Figueira et al., 2019). However, ocean acidification can modify species responses to ocean warming (Nagelkerken and Munday, 2016), and therefore, alter range-extension outcomes in marine ecosystems (Coni et al., 2021b). Ocean acidification can also modify a wide range of physiological parameters (Heuer and Grosell, 2014), and therefore also the fitness of both tropical vagrant and resident temperate fishes (Mitchell et al., 2022). In addition, the interactive effects of ocean

acidification and ocean warming could indirectly slow the pace of marine range extensions into high-latitude ecosystems through habitat regime shifts (Coni et al., 2021b). Therefore, the interaction between ocean acidification and ocean warming must be considered when assessing range shifts outcomes in marine environments.

Species range edges can shift in response to seasonal changes in local conditions (Figueira et al., 2009; Ljungström et al., 2021). Range-shifting species entering novel ecosystems during summer recruitment often fail to survive through winter (Booth et al., 2007), as seasonal shifts in temperature (Figueira et al., 2009), light (Langbehn et al., 2021), energetics (Ljungström et al., 2021) and resources (Figueira and Booth, 2010) can reduce species' fitness and preventing permanent establishment at cold-leading range edges. Species can also attempt to overwinter in novel ecosystems through behavioral modification, such as the expression of risk-averse behaviour (Coni et al., 2022) and physiological responses, such as lipid build-up (Fernandes and McMeans, 2019). Under increasing ocean warming, winter limitations on range-extension success are predicted to dissipate in the near future (Figueira et al., 2009; Figueira and Booth, 2010), which may allow tropical fish to establish in temperate ecosystems permanently. However, it remains unknown how future winter temperatures could modify tropical fish physiology and therefore, their influence their capacity to establish in temperate ecosystems. In contrast, future summer temperatures could be thermally stressful for resident temperate species at their trailing edges, compromising proper physiological function (Birnie-Gauvin et al., 2017), anti-predator behaviour (Figueira et al., 2019) and reducing their ability to compete against invading tropical species (Birnie-Gauvin et al., 2017). Hence, seasonal temperature-driven shifts in the fitness of interacting vagrants and local temperate species may alter competitive interaction outcomes on a seasonal basis.

Here we used a controlled laboratory experiment to assess the multi-stressor effects of future projected summer versus winter ocean temperatures, ocean acidification, and novel species interactions on the physiology of a range-extending coral reef fish and a co-shoaling temperate fish species across a ~40-day exposure period. Our proxies for short-term (hepatosomatic index) and long-term (total lipid content) energetic storage, energetic intake (stomach fullness), oxidative damage (Malondialdehyde concentration), cellular defence (total antioxidant capacity), and body condition (Fulton's condition index) were measured at the end of the experimental exposure. This enabled us to test how climate change stressors and novel interactions might alter the physiological performance of co-shoaling coral reef and temperate fish species to infer how future conditions might modify the pace of range-extension by coral reef fish and contractions by temperate fish.

2. Materials & methods

2.1. Experimental setup

Flow-through 20-litre transparent tanks (IKEA product number: 898.914.70; dimensions: 39 × 28 × 28 cm, height × length × width; $n = 120$) were installed across two adjacent flowthrough temperature/pH control rooms at the Sydney Institute of Marine Science in New South Wales, Australia. Two 0.5-cm (diameter) holes were inserted 4-cm from the top of each tank (lengthways; Fig. S1.) to allow water to flow bilaterally out of each tank. Each tank was allocated a tank identifier and an experimental treatment (Fig. S1). We provided PVC piping (10 × 10 cm, length × external diameter) to each tank to act as shelter (Fig. S2). Tanks were randomly assigned one of the two CO₂ × three temperature treatments ($N = 6$ treatments; Table S1). The ocean warming and ocean acidification treatments reflected projected future summer (26 °C and pH 7.7), and winter conditions (20 °C and pH 7.7) for the respective leading range edge of coral reef fish and the trailing edge of co-shoaling temperate fish (latitude: 34° S, IPCC, 2021) by 2100 (Table 1). Current summer temperatures (23 °C and pH 8.1) were selected as the experimental control and are also reflective of

Table 1

Selected experimental temperatures relative to range location average seasonal temperatures within their Great Barrier Reef core range and the leading-edge extents of coral reef fish and the respective trailing edge of temperate fish (coral reef fish: *Abudefduf vaigiensis*, temperate fish: *Atypichthys strigatus*; Froese and Pauly, 2016; Kaschner et al., 2016).

Range locations	Water Temperatures		
	20 °C	23 °C	26 °C
Coral reef fish core range (20° S)	N/A	Current winter	Future winter
Coral reef fish leading edge/ Temperate fish trailing edge (34° S)	Future winter	Current summer	Future summer

current winter temperatures experienced in coral reef fish core breeding population range (Table 1).

The experimental temperature and pH levels of fish tanks were monitored daily (Table S1) using an Ohaus Starter 300 Portable pH Meter with probe (IC-ST320) - IC-ST300-G. Fish tanks were provided with flow-through seawater supplied by a thermocouple solenoid feedback system with constant monitoring and controlled by computer software. Ocean acidification treatments were reached by bubbling pure CO₂ into 100-litre header tanks (one header tank for every four fish tanks) to reflect future values. Header tank water flowed into fish tanks at ~150 ml.min⁻¹.

2.2. Fish acclimation and husbandry

A. vaigiensis is omnivorous, exhibits a dispersive larval stage, has high site fidelity in the adult stage, and reaches up to 20 cm in length. The resident temperate species *A. strigatus* grows up to 25 cm in length, is also omnivorous and is observed shoaling with *A. vaigiensis* in southeastern Australia (Smith et al., 2018).

Sixty *A. vaigiensis* and 180 *A. strigatus* were collected during 7–24 March 2020, using barrier and handnets at Little Manly Cove (−33.806771° S, 151.285644° E) and Freshwater Beach (−33.781688° S, 151.294088° E) at depths of 0.1–2 m. Following collection, fish were transported in aerated 50-litre buckets filled with fresh seawater (~23 °C and pH 8.1) to 23 °C and pH 8.1 holding tanks (volume: 100 l) at the Sydney Institute of Marine Science.

Range-extending coral reef fish obtain fitness benefits by shoaling with temperate residents, growing faster and surviving longer into winter than conspecific tropical shoals in temperate ecosystems (Smith et al., 2018; Pajmans et al., 2020). Hence, we selected temperate + temperate and tropical + temperate fish pairs, respectively, to understand how novel co-shoaling species in temperate ecosystems (i.e. range-extending tropical) might alter temperate fish physiology in mixed-species shoals (i.e. future conditions) compared to conspecific temperate fish pairs (i.e. present-day conditions), and how the project future temperature and ocean acidification effects modify physiology. Comparison of mixed-species and single-species interactions can inform us about potential impacts on temperate fish communities. As a result, and because of space limitations, we did not include pairs of tropical species.

In addition, shoal size and composition can modify novel shoaling interactions and physiological responses of shoal members (Nadler et al., 2016; Pajmans et al., 2020). However, because of space limitations, we did not include shoal size as a treatment in our study.

Fish were randomly assigned to pairing tanks (coral reef fish, $N = 60$, mixed with temperate fish, $N = 60$; temperate-only paired fish, $N = 120$) across environmental-controlled rooms. Temperate-only selected fishes were paired with individuals of similar body sizes to minimise the competitive advantages that larger fish could develop in obtaining food and shelter. However, mixed-species shoaling fish displayed different body sizes, which reflected the current field situation of coral reef fish being smaller than their co-shoaling temperate species (Smith et al., 2018; Table S2). Initial wet weight (mean ± SE) was: coral reef fish 0.31 ± 0.04 g; mixed-species temperate fish 1.24 ± 0.15 g; temperate-

only fish 4.04 ± 0.20 g. The initial standard length was: coral reef fish 18.6 ± 0.7 mm; mixed-species temperate fish 29.3 ± 1.5 mm; temperate-only fish 53.2 ± 0.8 mm. Fish in the environmental treatments were acclimated from 23 °C and pH 8.1 by decreasing pH at a rate of 0.06 units/day (through gradually increasing the pCO₂ concentration in header tanks) and by raising or decreasing temperatures by 0.5 °C per day to minimise rapid thermal and pH stress responses. Fish introduction and acclimation to experimental tanks were staggered to prevent fish in control treatments (23 °C, pH 8.1) from gaining an acclimation advantage over fish in treatments that required more acclimation steps (e.g. 20 °C and pH 7.7). The maximum acclimation period for fish was 6 days.

API™ Stress Coat solution was added to each tank daily during acclimation and experimental periods. No fish mortality was recorded during the acclimation period. All fish were fed in pairing tanks under a restricted feeding regime of 2.86 g of Ocean Nutrition™ frozen Artemia mixed into 60 ml fresh seawater twice daily. Fish were exposed to experimental conditions for a maximum length of 40 days.

After 35–40 days of treatment exposure, fish were euthanised using the *iki jime* technique (Diggle, 2016). We added 2.86 g of Ocean Nutrition™ frozen Artemia to each tank ~8 h before euthanasia protocol commenced to standardise stomach fullness measures. Whole bodies were flash-frozen in liquid nitrogen and stored at −80 °C. Fish samples were transported on dry ice to The University of Adelaide and stored at −80 °C until further processing.

2.3. Water chemistry

Total alkalinity values were estimated by Gran titration (Metrohm 888 Titrando™) from 60 ml water samples from every tank on exposure days 24 and 25. Mean pCO₂ values were calculated using CO2SYS (Pierrot et al., 2006) for Excel with constants from Mehrbach et al. (1973), refitted by Dickson and Millero (1987) (Table S1).

2.4. Physiological proxies

Each fish's cellular, energetic and condition responses were evaluated by assessing different indicators (Table 2).

2.5. TAC and MDA

Muscle tissue (~50 mg) was used to prepare a 10 % tissue homogenate in an ice bath, which was used to assess total protein content (TP), total antioxidant capacity (TAC) and malondialdehyde concentration (MDA, indicative of oxidative damage). The Colorimetric method (per manufacturer's instructions, Elabscience®, catalogue number: E-BC-K168-S) used to measure the protein concentration in the homogenate, and the absorbance (optical density, OD) was measured with a Jenway 6405 spectrophotometer (Cole-Parmer, Staffordshire). Elabscience® assay kits were used to calculate total protein concentration (catalogue number: E-BC-K168-S, measured at 595 nm), TAC (catalogue number: E-BC-K136-S, measured at 520 nm) and MDA (catalogue number: E-BC-K025-S, measured at 532 nm) following the manufacturer's manuals. TAC kits measured the total concentration of

Table 2

List of physiological proxies analysed following the experimental exposure period.

Physiological Proxy	Description
Total antioxidant capacity (TAC)	Indicator of cellular defence (Birnig-Gauvin et al., 2017)
Malondialdehyde (MDA)	Indicator of oxidative damage (Rodriguez-Dominguez et al., 2019)
Fulton's condition index	Indicator of body condition (Izzo et al., 2015)
Hepatosomatic index (HSI)	Indicator of short-term energy storage (Chellappa et al., 1995)
Stomach fullness	Indicator of relative energy acquisition (Booth, 1990)
Total lipid content	Indicator of long-term energy storage (Post and Parkinson, 2001)

antioxidant macromolecules, antioxidant molecules and enzymes in the white muscle tissue of studied fishes. TP, TAC and MDA were calculated as follows:

$$TP \text{ (g/L)} = \frac{OD_{\text{sample}} - OD_{\text{blank}}}{OD_{\text{standard}} - OD_{\text{blank}}} \times \text{standard conc. (0.563 g/L)}$$

$$TAC \text{ (u/mg protein)} = \frac{OD_{\text{sample}} - OD_{\text{contrast}}}{0.01} \div 30 \times \frac{\text{volume of homogenate}}{\text{protein conc. (mg protein/ml)}}$$

$$MDA \text{ (nmol/mg protein)} = \frac{OD_{\text{sample}} - OD_{\text{contrast}}}{OD_{\text{standard}} - OD_{\text{blank}}} \times \frac{\text{standard conc. (10 nmol/ml)}}{\text{protein conc. (mg protein/ml)}}$$

2.6. Fulton's condition index

Before experimental commencement, all individual fish had their initial wet weight (WW \pm 0.01 g) and standard length (SL \pm 0.01 mm) measured. Final WW and SL were measured after the fish were euthanised. Fulton's condition index was calculated to assess the body condition of each fish. The initial and final Fulton's condition index was calculated as follows:

$$\text{Fulton's condition index} = \frac{WW \text{ (g)}}{SL \text{ (mm)}^3} \times 100$$

The final Fulton's condition index was subtracted by the initial Fulton's condition index to calculate a treatment's effect (e.g., increase or decrease in body condition under ocean warming) on body condition.

2.7. Hepatosomatic index

Livers were dissected from the frozen fishes, fixed in 100 % ethanol (~24 h), and then weighed to the nearest 0.0001 g. The hepatosomatic index for each fish was calculated as liver weight relative to total fish wet weight and expressed as a percentage (Chellappa et al., 1995).

$$\text{Hepatosomatic index} = \frac{\text{weight of liver (g)}}{\text{wet weight of fish (g)}} \times 100$$

2.8. Stomach fullness

We added 2.86 g of Ocean Nutrition™ frozen Artemia to each tank ~8 h before euthanasia protocol commenced to standardise stomach fullness measures. Fish were then euthanised using the *iki jime* technique (Diggles, 2016) and stomachs were dissected from each fish. Stomach contents were dried in a drying oven at 60 °C for 24 h. Dried stomach contents were weighed to the nearest 0.0001 g. Stomach fullness was calculated as follows:

$$\text{Fullness index} = \frac{\text{dry weight of stomach contents (g)}}{\text{wet weight of fish (g)}} \times 100$$

2.9. Total lipid content

Muscle tissue (0.05 g for *A. vaigiensis* and 0.40 g for *A. strigatus*) was used to determine lipid content using Bligh and Dyer lipid extraction (Bligh and Dyer, 1959). Extracted lipids were dried, weighed and expressed as a percentage of muscle tissue weight.

$$\text{Total lipid percent} = \frac{\text{weight of dried lipid (g)}}{\text{weight of muscle tissue (g)}} \times 100$$

2.10. Statistical analysis

We first investigated individual temperate fish physiological proxies using linear regression models. We used R (R Core Team, 2021) and the 'lme4' package (Bates et al., 2015) for linear regression model analysis (LM). To disentangle potential body-size difference effects between mixed-species and single-species shoaling temperate fish, initial wet weight (WW) was included as a variable for temperate fish analyses. Dependent variables were square root transformed to achieve normality.

Linear regression analyses, including covariate initial 'wet weight', did not show significant relationships ($p < 0.05$) between factors (independent) and physiological proxies (dependent); hence, we chose not to include starting WW as an explanatory variable in our statistical analysis.

The effect of pair type (temperate-only vs. mixed-species) and temperature (23 °C vs. 26 °C), ocean acidification (control vs ocean acidification), and their interactions on cellular defence (TAC), oxidative damage (MDA), Fulton's body condition (k), short-term (HSI) and long-term energy storage (total lipid content) were analysed using a permutational ANOVA with 9999 permutation in statistical software package Primer v.7 (Clarke and Gorley, 2015). ANOVAs were performed on Euclidian resemblance matrices. Where significance ($p < 0.05$) of the main effect (explanatory variables) were found pairwise tests were used to compare the respective means (Anderson, 2008).

3. Results

Physiological responses of coral reef fish to temperature and ocean acidification.

Oxidative damage (MDA) and cellular defence (TAC) significantly increased, whilst body condition (Fulton's condition index) significantly decreased at future winter (20 °C) compared to current summer temperatures (26 °C) (Figs. 1A, D, 2D; $p < 0.039$; Tables 3, S3–5). Cellular defence (TAC) and body condition significantly increased, whilst long-term energy storage (total lipid content) significantly decreased at future summer (26 °C) compared to future winter temperatures (20 °C) (Figs. 1A, 2A, D; $p < 0.041$; Tables S4–S6).

Under ocean acidification, oxidative damage (MDA) significantly increased, whilst cellular defence (TAC) significantly decreased for future winter temperatures (20 °C) compared to current (23 °C) and future summer temperatures (26 °C) (Fig. 1A, B; $p < 0.048$; Tables S3–4). At future winter temperatures (20 °C), oxidative damage (MDA) significantly increased, whilst cellular defence (TAC) significantly decreased under ocean acidification compared to control $p\text{CO}_2$ (Fig. 1A, B; $p < 0.001$; Tables 3, S3–4). Long-term energy storage and body condition remain unaffected by ocean acidification (Fig. 2A, D; $p > 0.05$; Tables 3, S5–6). Stomach fullness and short-term energy storage (HSI) remained unaffected by experimental treatments (Figs. 1G; S3A; $p > 0.05$; Tables 3, S7–8).

3.1. Physiological responses of temperate fish to temperature, ocean acidification, and novel shoaling

Oxidative damage (MDA) and long-term energy storage (total lipid content) significantly increase, whilst cellular defence (TAC) and short-term energy storage (HSI) significantly decreased at future summer (26 °C) compared to future winter temperatures (20 °C) (Figs. 1B, C, E, F, H, I, 2A; $p < 0.042$; Tables 4, S9–10, S12, S14). Body condition (Fulton's condition index) significantly increased at future winter (20 °C) than current summer temperature (23 °C) (Fig. 2E, F; $p = 0.011$; Tables 4, S13).

Oxidative damage (MDA) significantly increased for ocean acidification than control $p\text{CO}_2$, but only at future winter temperatures (20 °C) (Fig. 1E, F; $p < 0.001$; Tables 4, S10).

Short-term energy storage (HSI) and body condition significantly increased in mixed-species pairs than in single-species pairs (Fig. 1H, I; $p < 0.001$; Table S12; Fig. 2E, F; $p < 0.001$; Tables 4, S13). Long-term energy storage significantly increased in mixed-species pairs compared to single-species pairs, but only under control $p\text{CO}_2$ levels (Fig. 2B, C; $p < 0.001$;

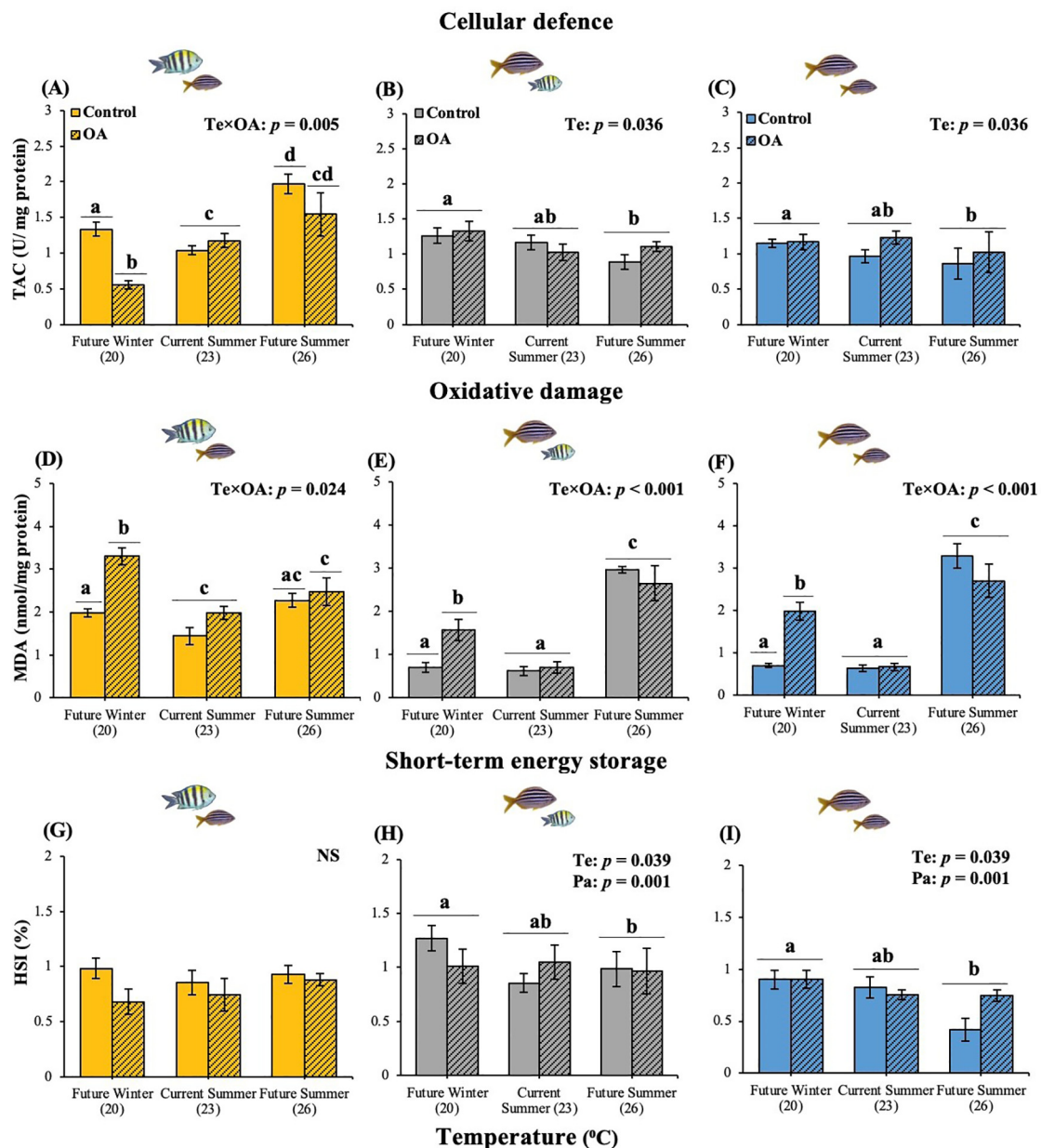


Fig. 1. Mean differences (\pm SE) of muscle tissue Total Antioxidant Capacity (Cellular defence; A, B, C), Malondialdehyde concentration (MDA, oxidative damage; D, E, F), and hepatosomatic index (HSI, short-term energy storage; G, H, I) for coral reef fish (yellow), temperate fish paired with a tropical fish (grey), and temperate fish in temperate-only pairs (blue). Different letters above bars indicate significant differences between experimental treatments ($p < 0.05$; Table S). NS = not significant ($p > 0.05$).

Tables 4, S14). Stomach fullness significantly increased in mixed-species pairs than in single-species pairs, but only at current summer temperatures (23 °C) (Fig. S3B, C; $p = 0.014$; Tables 4, S11).

4. Discussion

Here we show that ocean acidification and future winter temperatures projected for temperate ecosystems could negatively modify the physiological function of range-extending coral reef fishes. Reduced cellular defence and body condition, and increased oxidative damage during future winters compared to current summer temperatures (at which coral reef fish currently establish in higher latitude ecosystems, [Figueira and Booth, 2010](#)) may seasonally limit coral reef fish persistence in temperate ecosystems. This effect appears to be exacerbated by ocean acidification. Increased oxidative damage during future winters could degrade cellular integrity and negatively modify cellular processes and physiological traits (e.g., growth and digestion: [Costantini, 2019](#)) which underpin successful range-

extensions into temperate ecosystems. Indeed, the overall effect of ocean warming will likely benefit range-extending coral reef fishes (compared to current-day seasonal temperatures; [Figueira et al., 2009](#); [Figueira and Booth, 2010](#)). However, whilst previous models suggest future summer temperatures will accelerate coral reef fish establishment at temperate latitudes ([Figueira and Booth, 2010](#)), our findings emphasise that future winter conditions (ocean acidification and cold waters at 20 °C) are likely to reduce coral reef fish physiological function (Fig. 3) and will continue to seasonally modify their performance at temperate latitudes. We conclude that whilst ongoing ocean warming will increasingly relax temperature stress during summers, future winter conditions will still limit the physiological performance of coral reef fishes, and therefore slow down their permanent establishment or performance in temperate ecosystems.

Future winter conditions may negatively impact coral reef fish physiological functions, but their overwintering capacity in temperate ecosystems appears to be increased through physiological trade-offs. Increased long-term energy storage, maintenance of stomach fullness and short-term

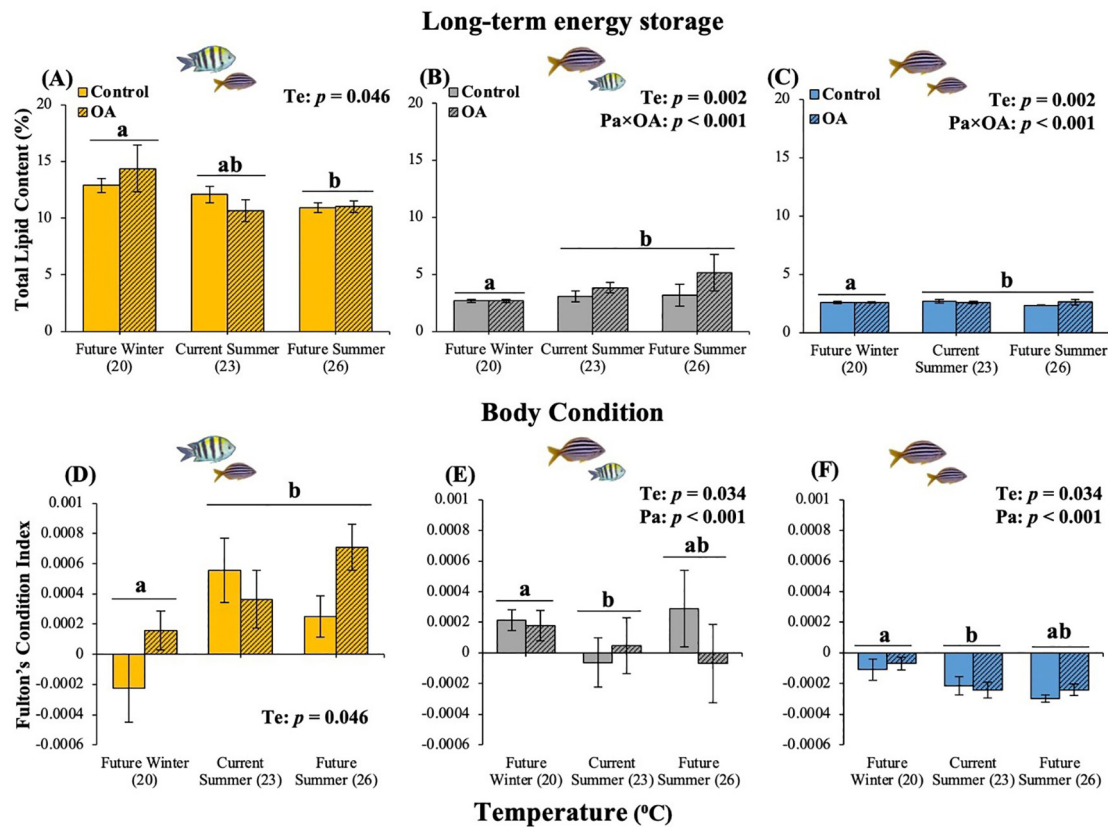


Fig. 2. Mean differences (\pm SE) of muscle tissue total lipid content (long term energy storage; A, B, C), Fulton's condition index (body condition; D, E, F) for coral reef fish (yellow), temperate fish paired with a tropical fish (grey), and temperate fish in temperate-only pairs (blue). Different letters above bars indicate significant differences between experimental treatments ($p < 0.05$; Table S). NS = not significant ($p > 0.05$).

energy reserves, but reductions in body condition, suggests that coral reef fish prioritise long-term energy storage over body condition, under future winter conditions. Seasonal energy partitioning through the accumulation of long-term energy reserves in future winters may also aid future summer growth (Booth and Keast, 1986), resulting in increased summer body condition and overwinter survival (Fernandes and McMeans, 2019) of coral reef fishes in temperate ecosystems. Maintenance of stomach fullness by tropical fishes across temperature treatments, could occur through reduced metabolic rate that coral reef fish experience at cooler temperatures (Djurichkovic et al., 2019), and may therefore slow digestion, causing the stomach to stay full for longer (Booth, 1990). We suggest that under future winter conditions, coral reef fish show physiological plasticity by trading-off body condition in favour of long-term energy storage, which could increase their capacity to overwinter in temperate ecosystems.

Temperate fish physiology was degraded by future summer temperatures (compared to future winter temperatures), irrespective of ocean acidification. Decreases in cellular defence, body condition and short-term energy storage, and increased cellular stress under future summer conditions may reduce temperate fish physiological function and reduce their abundances and performance at their warm-range trailing edge (Fig. 3). Declines in temperate fish physiological function coincides with increased coral reef fish physiological function (this study), fitness (Djurichkovic et al., 2019; Mitchell et al., 2022) and reduced performance (Figueira et al., 2019) under future summer temperatures, which could seasonally improve coral reef fish performance in temperate ecosystems. However, future winter conditions will be advantageous to temperate and detrimental to coral reef species at higher latitudes, leading to a reversal in the physiological performance of competing range-extending and local species as a function future seasonal conditions. We suggest that the opposing physiological performance of the temperate and coral reef species during future

summers vs future winters are likely to seasonally modify the abundance of both species at their overlapping leading (tropical) and trailing (temperate) range edges in temperate ecosystems.

Novel species interactions may temper negative ocean warming effects on temperate fish physiological performance under current ocean warming. Increases in body condition and short-term energy storage of the temperate fish paired with a tropical fish (compared to single-species temperate pairs) could enhance their current performance at their warm-range trailing edges. In mixed-species pairs, body size differences between temperate and coral reef fish (i.e., current temperate summers, with temperate fish generally being larger than coral reef vagrants; Coni et al., 2021a) may explain physiological differences between mixed- and single-species paired temperate fish (Ward et al., 2006). Larger temperate fish often outcompete smaller-bodied coral reef fish in present-day temperate ecosystems (Coni et al., 2021a). Therefore, superior foraging competency by larger-bodied temperate fish may explain why temperate fish in mixed-species pairs show higher body conditions, short-term energy storage and stomach fullness (but only in present-day summer conditions) compared to single-species paired temperate fish. We suggest that mixed-species shoaling could enhance temperate fish physiology by reducing intra-shoal competition and lessen ocean warming impacts on temperate species residing at their warm-range edges.

5. Conclusion

We conclude that whilst ocean warming will likely benefit coral reef fishes extending their ranges into temperate ecosystems, future winter conditions may still reduce coral reef fish physiological function, and may therefore, slow their establishment at higher latitudes. In

Table 3

Summary of analysis using ANOVA testing the effects of seasonal water temperatures ("temperature"), ocean acidification and their interaction ("Te × OA") on physiological responses of coral reef fish (*A. vaigiensis*). Note: **bold** denotes significant differences ($p < 0.05$).

Coral reef fish				
Physiological response	df	SS	F-value	p-value
Cellular defence				
Temperature (Te)	2	6.295	17.764	<0.001
Ocean acidification (OA)	1	1.667	9.410	0.003
Te × OA	2	1.979	5.585	0.005
Residuals	48	5.179		
Oxidative damage				
Temperature (Te)	2	8.467	11.684	<0.001
Ocean acidification (OA)	1	6.348	17.521	<0.001
Te × OA	2	2.797	3.860	0.024
Residuals	48	17.392		
Short-term Energy Storage				
Temperature (Te)	2	0.102	0.452	0.639
Ocean acidification (OA)	1	0.300	2.666	0.114
Te × OA	2	0.141	0.626	0.531
Residuals	46	5.179		
Long-term energy storage				
Temperature (Te)	2	72.009	3.154	0.046
Ocean acidification (OA)	1	2.892	0.253	0.624
Te × OA	2	8.464	0.371	0.695
Residuals	48	547.88		
Body condition				
Temperature (Te)	2	<0.001	4.517	0.015
Ocean acidification (OA)	1	<0.001	1.892	0.177
Te × OA	2	<0.001	1.743	0.185
Residuals	48	<0.001		
Stomach fullness				
Temperature (Te)	2	0.102	4.517	0.015
Ocean acidification (OA)	1	0.300	1.892	0.177
Te × OA	2	0.141	1.743	0.185
Residuals	46	5.179		

comparison, competing temperate fish species gain benefits from co-shoaling with smaller-sized coral reef fish, but this benefit may dissipate due to increased coral reef fish body size and decreased physiological function under future summer temperatures.

CRedit authorship contribution statement

AM, DB, IN conceived the study. AM and CH were responsible for experimental set-up, fish husbandry and physiological analysis. AM performed data analysis. AM wrote the manuscript with help from all authors. All authors read and approved the final manuscript.

Ethics statement

This experiment was conducted according to The University of Adelaide Animal Ethics and University of Technology guidelines and permits: S-2020-13 and 2017-1117, and under New South Wales DPI Scientific Collection Permit: F94/696(A)-9.0.

Data availability

The data that support the findings of this study are publicly available in Figshare at <https://doi.org/10.25909/22144460>.

Declaration of competing interest

The authors declare no competing interest.

Table 4

Summary of analysis using ANOVA testing the effects of seasonal water temperatures ("temperature"), ocean acidification, pair type, and their interactions on physiological responses of coral reef fish (*A. strigatus*). Note: **bold** denotes significant differences ($p < 0.05$).

Temperate fish				
Physiological response	df	SS	F-value	p-value
Cellular defence				
Temperature (Te)	2	0.215	3.475	0.036
Ocean acidification (OA)	1	0.030	0.968	0.322
Pair type (Pa)	1	0.035	1.125	0.293
Te × OA	2	0.015	0.243	0.778
Te × Pa	2	0.018	0.284	0.748
OA × Pa	1	0.049	0.157	0.687
Te × OA × Pa	2	0.071	1.141	0.324
Residual	91	2.816		
Oxidative damage				
Temperature (Te)	2	50.638	78.341	<0.001
Ocean acidification (OA)	1	0.934	2.890	0.095
Pair type (Pa)	1	0.312	0.966	0.326
Te × OA	2	8.576	13.267	<0.001
Te × Pa	2	0.228	0.353	0.704
OA × Pa	1	0.003	0.010	0.917
Te × OA × Pa	2	0.442	0.684	0.502
Residual	91	29.411		
Short-term energy storage				
Temperature (Te)	2	0.764	3.358	0.042
Ocean acidification (OA)	1	0.015	0.134	0.710
Pair type (Pa)	1	1.260	11.075	<0.001
Te × OA	2	0.279	1.226	0.296
Te × Pa	2	0.131	0.577	0.562
OA × Pa	1	0.058	0.510	0.477
Te × OA × Pa	2	0.392	1.725	0.187
Residuals	84	9.558		
Long-term energy storage				
Temperature (Te)	2	10.588	6.947	0.002
Ocean acidification (OA)	1	2.015	2.645	0.112
Pair type (Pa)	1	9.36	12.282	0.002
Te × OA	2	0.663	0.435	0.637
Te × Pa	2	3.353	2.2	0.128
OA × Pa	1	5.584	7.327	0.011
Te × OA × Pa	2	4.852	3.183	0.051
Residuals	91	69.351		
Body condition				
Temperature (Te)	2	<0.001	3.458	0.034
Ocean acidification (OA)	1	<0.001	0.270	0.601
Pair type (Pa)	1	<0.001	18.167	<0.001
Te × OA	2	<0.001	0.537	0.588
Te × Pa	2	<0.001	0.3677	0.698
OA × Pa	1	<0.001	0.736	0.39
Te × OA × Pa	2	<0.001	1.088	0.346
Residuals	91	<0.001	3.458	0.034
Stomach fullness				
Temperature (Te)	2	0.038	0.389	0.683
Ocean acidification (OA)	1	0.149	1.531	0.221
Pair type (Pa)	1	0.009	0.092	0.767
Te × OA	2	0.473	2.434	0.091
Te × Pa	2	0.742	3.820	0.023
OA × Pa	1	0.035	0.355	0.552
Te × OA × Pa	2	0.041	0.212	0.805
Residuals	91	8.841		

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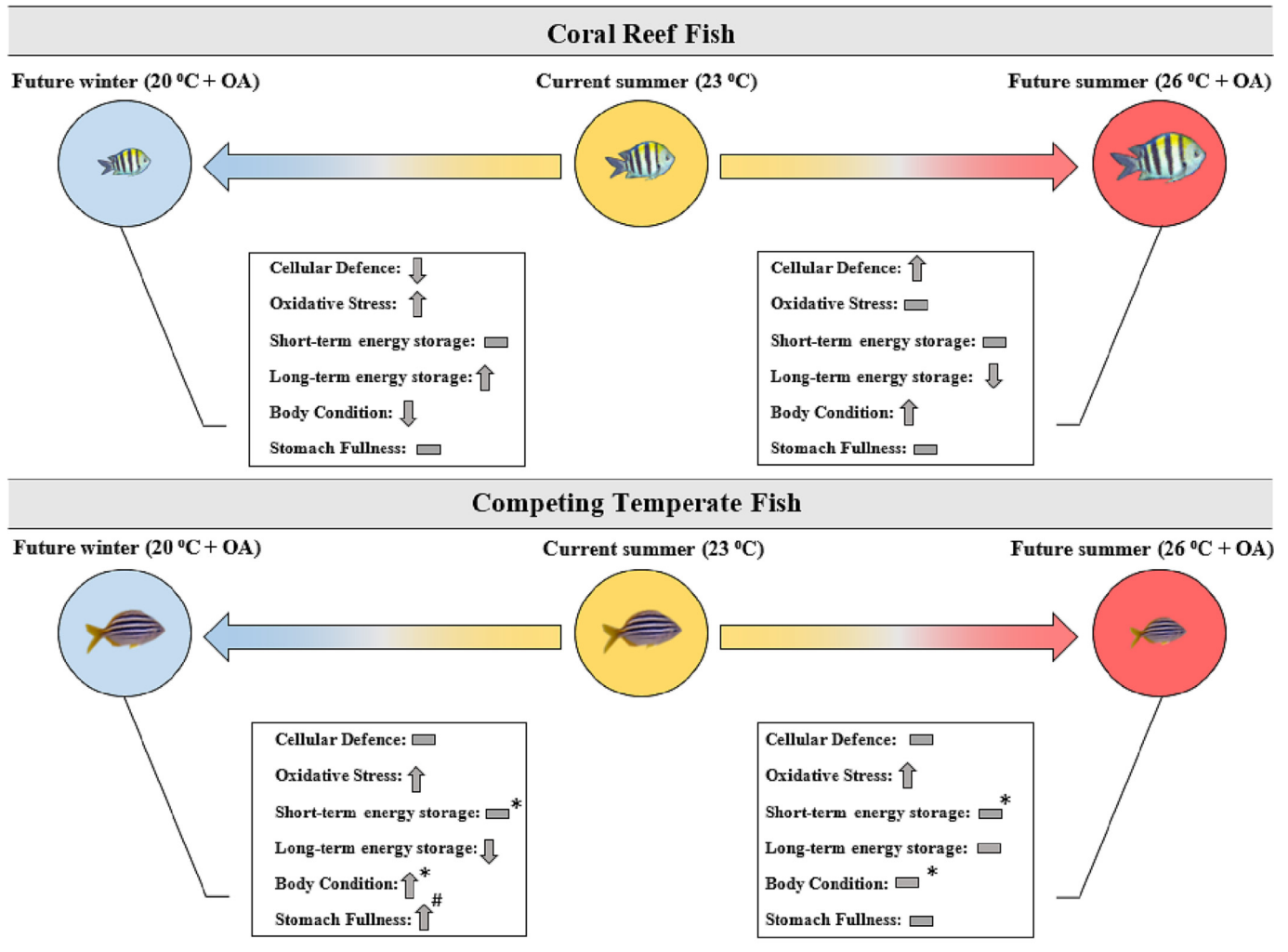


Fig. 3. Schematic diagram showing how projected future winter and summer water temperatures and ocean acidification modify the physiological function of interacting coral reef fish (top panel) and competing temperate fish (bottom panel) compared to current summer conditions (23 °C and pH 8.1) at 34° S, where the distributions of co-shoaling coral reef and temperate fishes overlap. Arrows indicate significant change (comparisons between future summer and future winter vs current summer conditions; $p < 0.05$) in a proxy. '□' indicates proxy remained unaffected ($p > 0.05$). * indicates significantly higher response in mixed-spp. paired temperate fish compared to single-spp. pairs ($p < 0.05$). # denotes significant increase in stomach fullness in temperate fish, but only in single-species pairs ($p < 0.05$).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.163684>.

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