



Novel ecological interactions alter physiological responses of range-extending tropical and local temperate fishes under ocean warming

Minami Sasaki^a, Angus Mitchell^a, David J. Booth^b, Ivan Nagelkerken^{a,*}

^a Southern Seas Ecology Laboratories, School of Biological Sciences, The University of Adelaide, Adelaide, South Australia, Australia

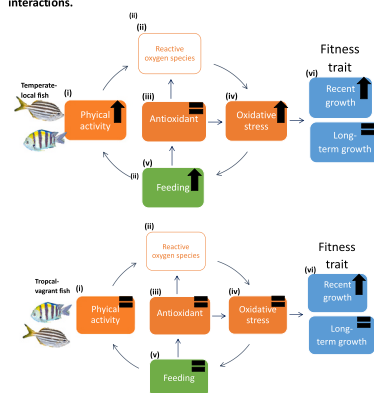
^b Fish Ecology Lab, Faculty of Science, University of Technology Sydney, Sydney, New South Wales, Australia

HIGHLIGHTS

- We tested the effects of ocean warming and novel interaction on temperate and tropical fish using cellular, behavioural and fitness responses.
- Both ocean warming and novel interaction altered the energy budget (energy uptake, cost, and growth) of temperate and tropical fish species.
- Changes in fitness response associated with novel interaction suggests that indirect factor was also a critical driver for the fish physiology.

GRAPHICAL ABSTRACT

Response of temperate (top) and tropical fish (bottom) to novel species interactions.



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ABSTRACT

Global warming facilitates species range-expansions, leading to novel biological interactions between local and range-expanding species. Little is still known of how such novel interactions modify the performance of interacting species or how these interactions might be altered under climate change. Here, we used an aquarium experiment to investigate the novel ecological interactions between a poleward range-extending coral reef damselfish ("tropical-vagrant") and a local temperate species ("temperate-local") collected from a climate warming hotspot in SE Australia. We measured the effect of novel interactions (isolated vs. paired fish species) on energy expenditure (activity levels, oxidative stress, and antioxidant responses), energy gain (feeding rates), and growth rates of both fish species under present-day (23 °C) and future ocean temperatures (26 °C). Short-term growth rates were faster in both species under novel interactions (paired species), regardless of elevated temperature. Compared to isolated species, activity level, feeding rate and oxidative stress level were also higher in the paired temperate fish but not in the paired tropical fish. The tropical fish showed an increased feeding rate and long-term growth under elevated temperature, irrespective of novel interactions. We conclude that novel ecological interactions under climate change can be an important driver of physiological traits in sympatric tropical and temperate fishes and can mediate critical physiological performance of fishes under ocean warming.

* Corresponding author.

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

1. Introduction

Anthropogenic climate change is facilitating species range-shifts, contractions, and extensions on a global scale (Pech et al., 2017). In marine ecosystems, concurrent ocean warming and intensifying boundary currents, have driven warm-affiliated species to extend their ranges to higher latitudes. These range-extensions into higher latitudes, have forced warm-affiliated and local species to interact for resources through novel species interactions (Montoya and Raffaelli, 2010; Vergés et al., 2014; Pinsky et al., 2020). Modification of water temperatures and biotic interactions alter energy demand (temperature: Neubauer and Andersen, 2019, biotic interactions: Garvey et al., 1994) and intake (temperature: Niimi and Beamish, 1974, biotic interactions: Nakano et al., 1998; Relyea, 2002) in animals. To survive under changing conditions, animals use plastic traits as an immediate behavioural response (e.g., moving to cooler temperatures, Biro, 1998; Hayes et al., 1998; Baird and Krueger, 2003, reduction in movement at higher temperatures, Goyer et al., 2014). Because the traits that allow animals to adjust to climate warming and altered biotic interactions (e.g., foraging and swimming) are directly linked to individual fitness, understanding both of these factors allows us to understand how animals interact with a changing environment (Lailvaux and Husak, 2014).

Species that overlap in their niches can affect each other's energy use through altered resource acquisition (e.g., energy and time) due to competition or avoidance (Gilad, 2008). For example, energy expenditure, measured by activity and swimming level, increased in native crayfish in the presence of invading crayfish (Garvey et al., 1994). Such increased physical activity can induce lipid peroxidation through the production of reactive oxygen species (ROS) (Banerjee et al., 2003; Kawamura and Muraoka, 2018), which is a response to oxidative damage to cellular and tissue component in organisms (Di giulio et al., 1989). To counteract this damage, organisms have developed a protective mechanism called antioxidants (Halliwell and Gutteridge, 1999), which catalyses ROS into less reactive molecules (Halliwell, 1994). The production of antioxidant defence against ROS is, however, costly and may restrict growth (Monaghan et al., 2009; Constantini, 2010; Smith et al., 2016; Anand et al., 2019). In this case, animals would benefit from

reducing physical activity. If this cannot be achieved, an animal may need to adjust its energy intake to reduce the higher ROS production. For example, Janssens and Stoks (2020) found that when damselfly larvae were fed ad libitum, the control group and group with artificially increased oxidative stress using benzoyl peroxide, which generates free radicals and has been shown to increase lipid peroxidation and reduce antioxidant defence in mice, both showed a similar level of ROS production. However, the latter showed higher levels of ROS than the former when both groups were exposed to starvation. As the interplay between energy cost and supply will be reflected in fitness traits, behavioural adjustment to reduce energy expenditure while increasing the energy supply will allow species to adjust to changing conditions such as climate change (Fig. 1).

While the importance of novel species interactions in the context of climate change is increasingly recognised (HilleRisLambers et al., 2013; Louthan et al., 2015), understanding the effects of these novel ecological interactions within a trophic level (e.g., competitive interactions) remains understudied compared to novel interactions across trophic levels (e.g., herbivory, meta-analysis in Vergés et al., 2014, but see Alexander et al., 2015; Mitchell et al., 2022). There is some evidence demonstrating that encounters with ecologically similar temperate local species can modify foraging behaviours (Coni et al., 2021) and growth (Smith et al., 2018) of tropical range-shifting species, while the behaviours of temperate local species remain unaffected by these novel interactions (Mitchell et al., 2023a). Various marine species including tropical herbivores (Hutchins, 1991; Booth et al., 2007; Fowler et al., 2017) and non-herbivorous tropical fish species (Pearce and Hutchins, 2009; Fowler et al., 2017) are observed annually entering temperate marine ecosystems (Booth et al., 2011; Vergés et al., 2014). Thus, it has become increasingly important to understand how local species respond to novel ecological interactions under current and future climate.

Novel species interactions during the initial stages of climate change may be modified under future warming conditions (e.g., Taniguchi and Nakano, 2000; Rodtka and Volpe, 2007; Carmona-Catot et al., 2013; Gracida-Juárez et al., 2022). Changing temperatures can modulate the state or the strength of species interactions (Tylianakis et al., 2008). The combined effects of temperature and novel species interactions can

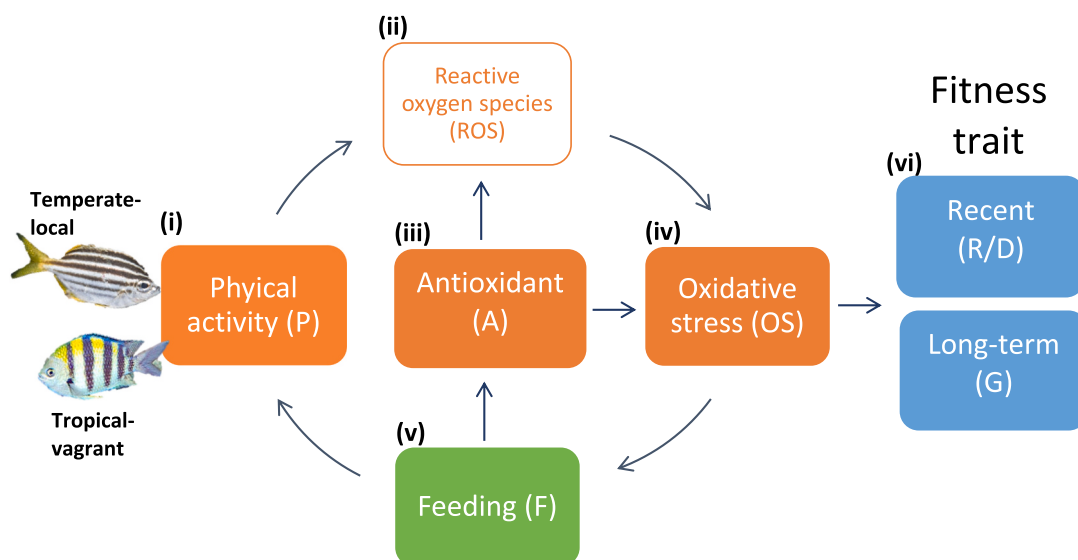


Fig. 1. Schematic overview of the link between responses relating to energy cost (orange), supply (green) and resultant fitness outcome (blue) that the current study used to understand the effect of the presence of novel species interactions (fish picture). The presence of novel interactions alters the level of physical activity (i). Higher activity can increase production of reactive oxygen species (ROS) (ii), and in order to alleviate the higher ROS production animal produce antioxidant defence (iii). The imbalance between antioxidant defence and ROS production causes the organism to experience oxidative stress (iv). Organisms increase their feeding rate to meet the energetic costs related to higher activity and oxidative damage (v), and feedback of energy supply and demand in a given condition results in altered growth rate indicated by recent and long-term growth (vi). Filled block represents the response that we measured in the current study while the unfilled block represents the response that we did not measure but is known to occur based on the literature.

modify habitat use (Milazzo et al., 2012), competitive outcomes (Carmona-Catot et al., 2013) and fitness (Mitchell et al., 2023b) of species experiencing novel species interactions. However, whether physiological responses to warming are altered by novel interactions are unknown, yet could provide insights into species persistence within ecosystems experiencing an increased magnitude of novel species interactions (e.g., global warming hotspots; Smith et al., 2018).

Southeastern Australian shallow marine ecosystems are considered a global warming hotspot (Hobday and Pecl, 2014), showing rates of temperature increases higher than the global average (Ridgway, 2007). Ocean warming in this region is largely driven by the intensified East Australian Current (EAC) (Ridgway, 2007). Along with warming, the EAC facilitates the long-distance transport of larvae from the tropics to temperate regions (Booth et al., 2007), altering biodiversity in the recipient ecosystems. Among vagrant species (i.e., species occurring outside their native range), *Abudefduf vaigiensis* ("tropical-vagrant") is one of the most frequently observed tropical vagrant species in temperate southeast Australia (Booth et al., 2007), where it spends the warmer months co-shoaling and interacting with temperate-local species such as *Atypichthys strigatus* (our focal "temperate-local"), *Trachinops taeniatus*, and *Microcanthus strigatus* (Smith et al., 2018; Coni et al., 2021) before their abundance drops in winter due to cold stress. Previous studies found that *A. vaigiensis* grew larger when shoaling with local temperate species than with conspecifics (Smith et al., 2018), although when provided with food they were often outcompeted by temperate species (Coni et al., 2021). However, we still know little about how behavioural changes due to novel interactions and warming interact to alter the fitness of invading and recipient species.

Here, we examined how the presence of novel species interactions and ocean warming alter the behaviour and physiology of a tropical range-extending and co-shoaling local temperate fish species. We measured energy cost (activity levels, oxidative stress, and antioxidant responses) and energy gain (feeding rates) in both species, and how feedback between these responses could result in altered fitness – measured through recent and long-term growth. Using an aquarium experiment, we exposed our focal fish species to summer ocean temperature representing current and year 2100 values, respectively, as forecast by the RCP 8.5 scenario (+3 °C) at temperate latitudes. Fish were exposed to experimental temperatures with and without novel interactions. As behavioural adjustments in response to environmental change are critical for species persistence, we hypothesised that species with the capacity to maximise their net energy gain under changing conditions (i.e., novel interactions and warming) will exhibit increased fitness and hence likely be a 'winner' species under future climate change.

2. Materials and methods

2.1. Experimental design

To test the presence of novel species interactions and the effect of elevated temperature and their interaction on fish performance, an aquarium experiment was conducted at the Sydney Institute of Marine Science (SIMS) between March and April 2019. Juvenile tropical *A. vaigiensis* (wet weight range = 0.38–1.40 g) and co-shoaling temperate *A. strigatus* (wet weight range = 1.14–5.14 g) were collected using hand-nets with anaesthetics and a barrier net from Little Manly (33°48'23.85"S, 151°17'8.76"E) and Freshwater beach (33°46'50.69"S, 151°17'34.14"E) in New South Wales, Australia, during February and March 2019. Due to later recruitment of the tropical species, the tropical-vagrant species were smaller than their paired temperate-local species, with an average ($\pm$ SD) of difference of 1.30 ± 0.44 cm and 1.23 ± 0.43 cm for 23 and 26 °C, respectively. However, as the size difference in the field between co-shoaling *A. vaigiensis* and *A. strigatus* is approximately 2 cm (Smith et al., 2018), the size difference in our study reflects the body size differences as observed in the wild.

Both collection sites are located within 5 km from each other and are positioned near the leading-edge for the tropical species, while representing the trailing-to-core range for the temperate species (Fig. S1). Live fish were transported in 8 L buckets with seawater and battery-operated aeration to SIMS where all fish were placed in either 10 or 20 L tanks in temperature-controlled rooms. The aquaria received flow-through seawater (approx. 10 L/hour) at ambient temperature of the collection site (i.e., 23 °C) until the beginning of the experiment. Ten centimeter lengths of PVC pipe (10 cm diameter) were provided as shelter in each aquarium. Fish were fed ad libitum with adult frozen *Artemia*, three times a day. We created a light regime with 12 h of daytime and 12 h of night-time. We did not include the interactions between two local or two range-shifting species because the aim of the current study was to investigate the effects of novel interactions, and inclusion of more interactions was not logistically feasible.

Tropical and temperate fish were randomly assigned to either a 10 L or a 20 L tank. Single fish (i.e., either a tropical or a temperate fish) were housed in 10 L tanks while paired fished (i.e., one tropical-vagrant species and one temperate-local species) were kept in 20 L tanks, to account for density-dependent effects. In total, 10 replicates were tested at each temperature treatment (i.e., 23 °C and 26 °C) for each species with no novel interactions, and 10 replicates each were performed at 23 °C and 26 °C with the two species combined to test for the effect of novel interactions. After the fish had been added to the aquaria, the water temperature was increased from ambient temperature ($\sim$ 23 °C) to 26 °C in half of the tanks at a rate of 0.5 °C per day before the experiments started. Water temperatures were controlled in a separate mixing chamber where cold and hot seawater were mixed to achieve the target temperature before the water flowed into the aquaria. All fish were exposed to either ambient or elevated temperature with <0.5 °C fluctuation for 3 weeks. For consistency, we refer to the elevated temperature (ocean warming) treatment as 'temperature', with all responses at 26 °C being compared to the control of 23 °C. Similarly, we refer to the presence of novel species interactions as 'novel interactions', comparing all the responses of the combined species (n: 2 fish/tank) to that of the control of no-interactions (individual tanks) (n: 1 fish/tank).

Wet weight and standard length of each fish were recorded at the beginning and the end of the experiment. At the end of the experiment, fish were euthanized using *Ike jime* and immediately placed in an ice slurry. Muscle tissue from the caudal peduncle was dissected and stored in *RNAlater* for quantification of RNA:DNA ratios, while the remainder of the fish was stored in liquid nitrogen for consecutive measurement of biomarkers (oxidative stress and total antioxidant capacity).

2.2. Behaviour: activity levels and foraging rates

On day 19 of treatment exposure, between 0900 and 1700 h, behaviour of fishes was filmed in 9-min video recordings. We placed GoPro Hero 4 Silver cameras at the right side of each tank (lengthways) and commenced recording. Video recordings lasted for 6 min, excluding 3 min of acclimation time to the cameras, and were split into two 3-min periods (period 1: general activity, period 2: feeding behaviour) (recording duration of >3 min used previously, Biro et al., 2010; Coni et al., 2021). Observers were blinded to temperature treatments of each video recording during video analysis until data collection was completed.

2.2.1. Period 1: general activity

We measured the (1) swimming activity and the (2) basal bite rate of each fish during the first 3-min period of the video recording:

- (1) Activity levels: We quantified activity levels, by overlaying 6 cm² grids on a screen monitor (screen size: length: 30 cm $\times$ length: 45 cm) and quantified the total grid crosses made by each fish across a transverse plane during Period 1 of recordings. Total grid

crosses were converted into an activity rate (grid crosses·min⁻¹) using the following formula;

$$\text{Activity rate} = \frac{\text{Total grid crosses}}{\text{Recording time (min)}}$$

- (2) Basal bite rate: We quantified the total number of bites each fish performed over the first 3 min of video recordings and calculated the bite rate as number of bites·min⁻¹. Bites were defined as “fish elicits a rapid opening and closing of mouth towards potential prey items in water column.”

2.2.2. Period 2: feeding

Approx. 1.43 g of Ocean Nutrition™ frozen *Artemia* mixed into 60 mL fresh seawater was administered after the 3 min of general activity recording via a syringe into each 20 L tank and approx. 0.715 g (in 30 mL of fresh seawater) of frozen adult *Artemia* into 10 L tanks. Tanks were left undisturbed while filming for 3 min following the addition of food to tanks.

- (3) Bite rate: We quantified the feeding bite rate during video analysis by counting the total number of bites taken during the 3 min of allocated feeding subtracted by the basal bite rate quantified during the first 3-min period before food was added, to isolate the effect of feeding from random, non-feeding bites (Booth and Beretta, 2004). The total bite rate was then converted into bites·min⁻¹.

2.3. Biomarkers

2.3.1. Malondialdehyde (MDA) – oxidative stress proxy

Lipids provide energetic and cellular functions important for survival (Booth and Hixon, 1999; Booth and Beretta, 2004), yet are one of the major targets of oxidative stress (Monaghan et al., 2009), and polyunsaturated fatty acids are particularly sensitive to oxidative damage (Lushchak and Bagnyukova, 2006). Lipid peroxidation (i.e., oxidation of lipids) leads to several highly damaging products (Davies, 2000; Monaghan et al., 2009). MDA is one of the most widely used biomarkers of lipid peroxidation (Lushchak and Bagnyukova, 2006; Monaghan et al., 2009). We measured the level of MDA as a proxy for oxidative stress in white muscle tissue of both fish species. MDA assay kits (TBA method) (Cat: E-BC-K025-S, Elabscience) were used for MDA analysis, following the manufacturer's protocol for microscale operation. Aliquots of homogenates from protein extraction were used in this assay. Absorbance was measured at 532 nm and the level of MDA in each sample was calculated as follows:

$$\text{Tissue MDA content (nmol/mg protein)} = \frac{\text{ODsample} - \text{ODcontrast}}{\text{ODstandard} - \text{ODblank}} \times \frac{\text{Standard concentration (10nmol/mL)}}{\text{Protein concentration (mgprot/mL)}}$$

Protein concentration of each sample was quantified using Coomassie brilliant blue dye (Total protein assay) (Cat: E-BC-K168-S, Elabscience) with the absorbance (OD) measured at 595 nm with a Jenway 6405 spectrophotometer.

2.3.2. Total antioxidant capacity (TAC) – antioxidant defence system

TAC is non-enzymatic, often comprising both hydrophilic and hydrophobic low-molecular-weight substances including but not limited to glutathione, ascorbic acid and uric acid (Bartosz, 2003). The roles of these types of antioxidants include converting reactive free radicals into less reactive radicals, reacting with oxidizing substances that cause damage to important molecule, or repairing damaged target such as lipid membrane (Davies, 2000; Bartosz, 2003). We measured the level of TAC in both species using total antioxidant capacity (TAC) assay kits

(Cat: E-BC-K136-S, ElabScience). Aliquots of homogenates from protein extraction were used in this assay. Absorbance was measured at 520 nm and the level of TAC in each sample was calculated as follows:

$$\text{TAC (U/mg protein)} = \frac{\text{ODsample} - \text{ODcontrast}}{0.01} \div 30 \times \frac{\text{volume of homogenate}}{\text{Protein concentration (mgprot/mL)}}$$

2.3.3. RNA/DNA ratio

RNA/DNA ratios in animal tissues have been used to measure physiological responses of animals (e.g., nutritional condition, Wagner et al., 1998; protein synthesis, Foster et al., 1992; growth, Ciotti et al., 2010; Reef et al., 2010), based on the assumption that the amount of RNA varies in relation to protein synthesis (Chícharo and Chícharo, 2008) while that of DNA remains relatively constant in response to changing environmental conditions (Bulow, 1987). Given that RNA/DNA ratio estimates growth rate over periods as short as one day and up to about one week (Bulow, 1987), we use the ratio as proxy for recent growth rate. Higher growth rate tends to lead to a higher ratio than slower growth rate. RNA and DNA from white muscle were co-extracted using ZR-Duet DNA/RNA MiniPrep Plus (Zymo Research) by following the manufacturer's instructions. Each nucleic acid was quantified using Quantus Fluorometer (Promega).

2.3.4. Long-term growth

To measure the fish weight, we used a small container filled with seawater. The container with seawater was placed on the scale. We then tared the container weight on the scale and introduced an individual fish to the container. We calculated instantaneous growth rate of each fish using the equation:

$$G_{INST} = \frac{\ln\left(\frac{WW_{final}}{WW_{initial}}\right)}{\Delta t}$$

where WW_{final} and $WW_{initial}$ are wet weight of same individual at the end and the beginning of the experiment, respectively, and Δt is the duration of the experiment. As the growth period measured by the somatic growth is longer than that by RNA/DNA ratio, we use somatic growth rate as long-term growth in the current study.

2.4. Statistical analyses

The effect of novel interactions (isolated vs. paired species) and warming (23 °C vs. 26 °C) and their effect on bite rate, activity levels, oxidative stress (MDA), antioxidant defence (TAC), recent growth (RNA/DNA ratio), and long-term growth rate (instantaneous somatic growth rate) were analysed using a permutational ANOVA with 9999 permutation using *vegan* in R (R Core Team, 2020). Where significance of the main effect (explanatory variables) were found, we performed *post-hoc* comparisons using *pairwiseAdonis* in R (Martínez Arbizu, 2020). We tested each species separately.

3. Results

3.1. The effect of temperature on fish performance

For the tropical vagrant fish, feeding rates ($p < 0.001$, Table 1, Fig. 2d) and longer-term somatic growth ($p < 0.001$, Table 1, Fig. 2f) were higher at the warmer treatment, regardless of novel interactions. Temperature change had no effect on the activity levels, antioxidant defence levels, oxidative stress levels, or recent growth.

For the temperate local fish, warming increased activity levels ($p < 0.001$, Fig. 3a) and feeding rates ($p = 0.001$, Fig. 3d) but had no effect on the other physiological traits (Table 1, Fig. 3).

3.2. The effect of novel interactions on fish performance

When paired with a temperate species, the tropical fish showed a higher level of RNA:DNA ratio compared to the isolated tropical fish ($p < 0.001$, Table 1, Fig. 2e), with no effect of elevated seawater temperature. The altered RNA:DNA ratio was not associated with any differences in activity levels, antioxidant levels, oxidative stress levels, bite rate, or long-term growth rate, respectively, in the tropical fish (Fig. 2, Table 1).

In the presence of the tropical fish, the temperate fish became more active (but only significantly at 23 °C, $p = 0.001$, Fig. 3a), showed higher levels of oxidative stress ($p = 0.011$, Fig. 3c), fed at higher rates ($p = 0.001$, Fig. 3d), and displayed faster recent growth as measured by RNA:DNA ratios ($p = 0.001$, Fig. 3e, Table 1) in comparison to isolated temperate fish, but with no changes observed in antioxidant levels (Fig. 3b) or long-term growth (Fig. 3f).

3.3. The effect of temperature on novel interactions

Temperature altered the effect of novel interaction in activity level of the temperate species. Paired temperate fish was more active than isolated temperate fish at 23 °C but this differences in the activity level between isolated and paired temperate fish disappeared at 26 °C (Fig. 3a). In contrast to the temperate fish, temperature change did not alter any of the performance for the tropical species (Table 1).

Table 1

Summary of analysis using ANOVA testing the effect of the presence of novel species interactions (“Novel interaction”), elevated temperature (“Warming”), and their interaction (“Novel × Warming”) on responses that are associated with energetic cost (“Activity level”, “Antioxidant” and “Oxidative stress”), supply (“Feeding”) and fitness outcome (“Recent growth” – RNA:DNA ratio, “Long-term growth” – somatic growth rate) of tropical *A. vaigiensis* (top row) and temperate *A. strigatus* (bottom row). Statistically significance (p -value < 0.05) is indicated with (*).

Response	<i>Abudefduf vaigiensis</i>				<i>Atypichthys strigatus</i>			
	df	Sum of square	F	P	df	Sum of square	F	P
Activity level								
Novel interaction	1	1.80×10^{-7}	0.040	0.850	1	0.044	9.111	0.001*
Warming	1	1.05×10^{-5}	2.440	0.138	1	0.115	23.671	<0.001*
Novel × warming	1	8.98×10^{-7}	0.200	0.664	1	0.034	7.037	0.005*
Residual	35	1.57×10^{-4}			30	0.145		
Antioxidant								
Novel interaction	1	2.06×10^{-3}	0.233	0.655	1	0.012	0.985	0.329
Warming	1	3.90×10^{-4}	0.044	0.888	1	8.24×10^{-3}	0.687	0.419
Novel × warming	1	5.83×10^{-4}	0.066	0.850	1	6.61×10^{-3}	0.501	0.464
Residual	33	0.292			32	0.384		
Oxidative stress								
Novel interaction	1	1.15×10^{-3}	0.084	0.934	1	0.080	7.176	0.011*
Warming	1	0.010	0.924	0.351	1	8.39×10^{-3}	0.754	0.405
Novel × warming	1	0.020	1.677	0.204	1	2.60×10^{-3}	0.233	0.677
Residual	33	0.454			32	0.356		
Feeding								
Novel interaction	1	2.30×10^{-3}	0.491	0.484	1	0.092	11.887	0.001*
Warming	1	0.440	177.693	<0.001*	1	0.093	11.935	0.001*
Novel × warming	1	3.48×10^{-3}	1.406	0.240	1	8.20×10^{-4}	0.105	0.794
Residual	34	0.084			30	0.233		
Recent growth								
Novel interaction	1	0.060	8.957	0.002*	1	0.182	11.051	0.001*
Warming	1	9.58×10^{-3}	1.375	0.240	1	0.021	1.283	0.265
Novel × warming	1	4.29×10^{-3}	0.615	0.476	1	4.65×10^{-3}	0.282	0.641
Residual	36	0.25077			35	0.577		
Long-term growth								
Novel interaction	1	1.61×10^{-3}	0.711	0.417	1	2.60×10^{-7}	0.058	0.820
Warming	1	0.040	17.876	<0.001*	1	1.04×10^{-5}	2.309	0.139
Novel × warming	1	1.40×10^{-3}	0.622	0.451	1	8.89×10^{-7}	0.200	0.664
Residual	36	0.08			35	1.57×10^{-4}		

4. Discussion

Here we show that range-shifting tropical and co-occurring native temperate fishes in a climate warming hotspot in temperate Australia responded differently to increasing water temperature and novel species interactions that are predicted to increase in occurrence as tropical fishes expand their ranges poleward under climate change. In response to simulated ocean warming, the tropical species experienced accelerated longer-term somatic growth while that of the temperate species remained unaffected. Meanwhile, both species increased their feeding rate under increase temperatures. The presence of novel interactions further led to faster short-term growth in both species, and this growth acceleration was associated with increased feeding rates and higher oxidative stress levels in the temperate species when paired with the tropical species.

4.1. The role of ocean warming on individual performance

Elevated temperature in the laboratory increased the energy expenditure of the temperate species only and increased the growth for the tropical species. We showed that while both species increased energy intake (i.e., feeding rate) with warming, this was only associated with a faster growth rate for the tropical species. This contrast between the two species is likely associated with resource availability for growth. In order to have surplus energy for growth, animals have to feed more than is

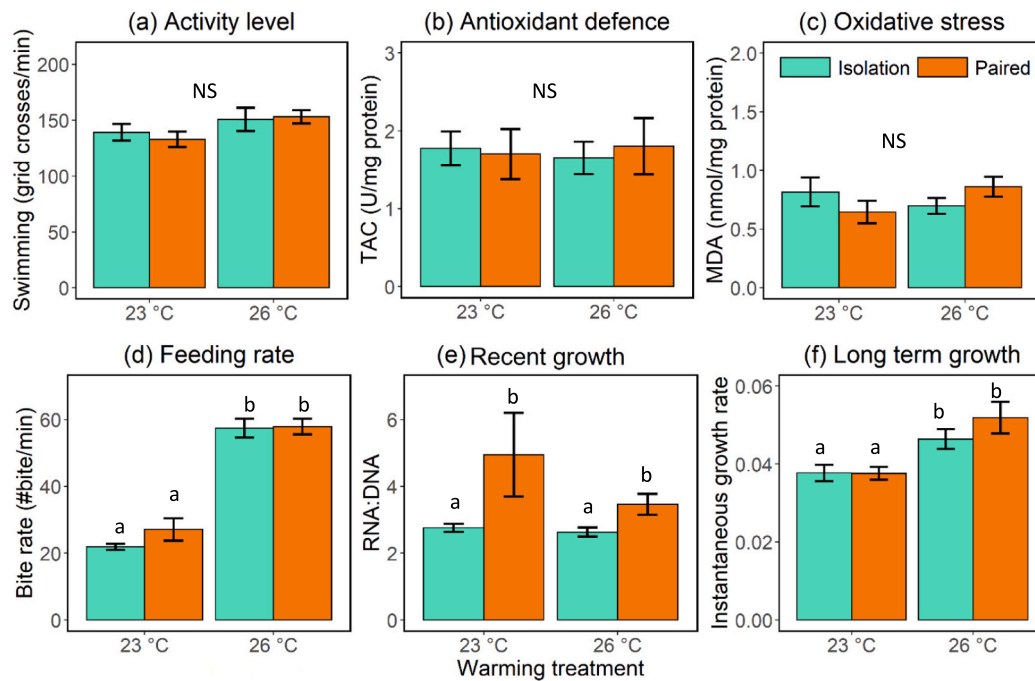
Abudefduf vaigiensis

Fig. 2. Effect of the presence of novel species (Isolation vs. Paired) and warming (23 °C vs. 26 °C) on the tropical-vagrant for: energy cost responses including (a) Activity, (b) Antioxidant defence system, (c) Oxidative stress, and energy intake via (d) Feeding rate and fitness response including (e) recent growth and (f) long term growth. Each value is presented with standard error (error bar). Different letters indicate statistically significant differences at $p < 0.05$ and NS for non-significant results.

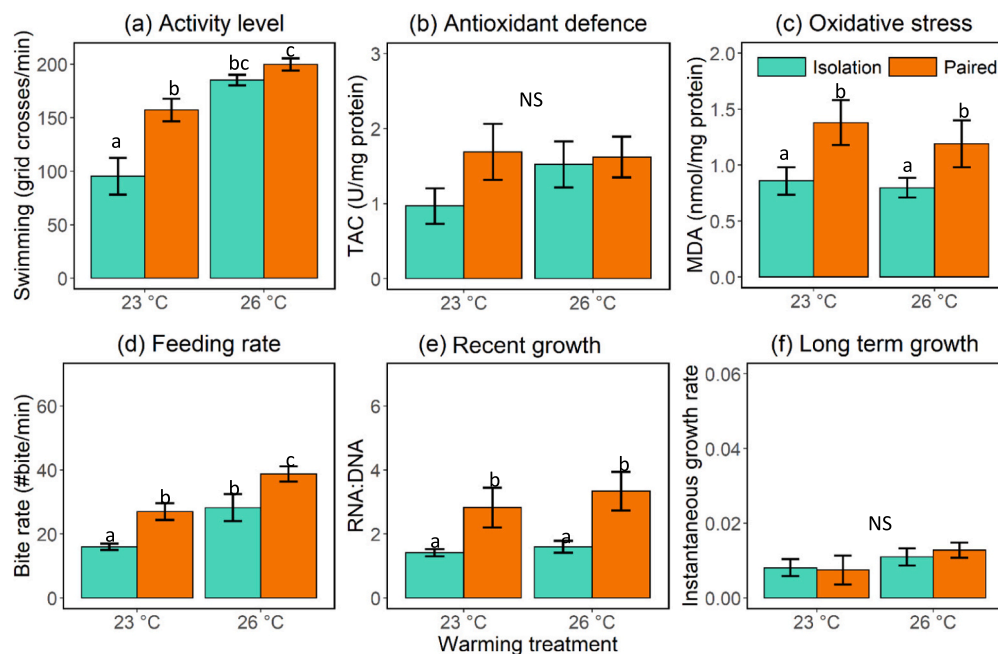
Atypichthys strigatus

Fig. 3. Effect of the presence of social interaction (Isolation vs. Paired) and warming (23 °C vs. 26 °C) on the temperate-local species for: energy cost responses including (a) Activity, (b) Antioxidant defence system, (c) Oxidative stress, and energy intake via (d) Feeding rate, and fitness response including (e) recent growth and (f) long term growth. Each value is presented with standard error (error bar). Different letters indicate statistically significant differences at $p < 0.05$ and NS for non-significant results.

needed for the cost of maintaining basic activities (e.g., respiration, digestion, and locomotion) (Costa and Williams, 1999; Weidner et al., 2020). As water temperatures increase, ectothermic organisms often increase the rate of food intake as a result of increased obligatory energy expenditure (Volkoff and Rønnestad, 2020). This leads to growth acceleration until when temperatures reach to optimal temperature for growth (Jobling, 1997). However, when temperatures exceed the optimal, the cost of basic maintenance (i.e., basal metabolic rate) increases with temperature faster than the rate of energy intake (Jobling, 1997), resulting in a decelerating growth rate. Thus, a lack of energy transfer from enhanced feeding to faster growth in the temperate species can be explained by the higher energy requirements for maintenance under future warming (26 °C), as well as higher energy expenditure through activity levels. As a temperate origin, the aerobic capacity of *A. strigatus* declines at higher temperatures. For example, Figueira et al. (2019) found that *A. strigatus* was able to perform multiple tests (i.e., burst swimming and predation trial) at 17 °C and 21 °C but not at 25 °C, supporting our finding that 26 °C is suboptimal for this temperate species. This would not be the case for the tropical species because 26 °C would overlap with present-day seawater temperatures in their core range (Nakano et al., 2004). The resultant difference in performance between temperate and tropical species also agrees with the observation that warm-adapted species displayed higher optimal temperatures than cool-adapted species (Payne et al., 2015).

4.2. The impact of novel interactions on the temperate local fish

In contrast to the longer-term growth, enhanced feeding rate in combination with novel interactions led to faster short-term growth (RNA:DNA ratio) in the temperate species. Consumption rates play a vital role in fish growth (e.g., Cadarin et al., 2022), and social interactions can alter feeding rate of an animal through social facilitation or inhibition. For example, juvenile chum salmon (*Oncorhynchus keta*) increased food consumption in the presence of feeding companion (Ryer and Olla, 1991). In the field, Coni et al. (2021) observed our temperate species to be more competitive than our tropical species upon artificial release of food, with the temperate species displacing the tropical from the released food. This may explain why feeding rate of the temperate species was higher when paired than when isolated, with the enhanced energy intake subsequently leading to faster short-term growth in the temperate species.

Novel species interactions might be associated with accumulation of malondialdehyde (MDA), and consequently higher oxidative damage in the local temperate species. Contrary to our expectations, increased metabolic rates from higher physical activity were unlikely (solely) responsible for the observed oxidative stress status because higher MDA levels were also observed in the absence of higher activity levels at 26 °C between paired and isolated species. Feeding and growth are known to alter metabolism and have been suggested to affect oxidative stress in fishes (feeding: Pascual et al., 2003; Zengin, 2021, growth: Alonso-Alvarez et al., 2007; Monaghan et al., 2009). Feeding was unlikely responsible for the accumulation of MDA in the current study because temperate fish experienced increased feeding rates under warming but maintained MDA levels (compared to present-day temperatures). Likewise, starvation rather than satiation has been more often associated with oxidative stress status (Pascual et al., 2003; Morales et al., 2004; Bayir et al., 2011). Hence, it is possible that the increased short-term growth might be responsible for the increased oxidative stress in the temperate species paired with a tropical species at both temperatures. Alternatively, the novel interaction with the paired tropical species might have increased oxidative stress levels, as previously shown by social species. For example, the oxidative stress status in dominant yellow cichlid males was thought to be caused by displaying agonistic behaviours towards community members (Border et al., 2019), and that in subordinate Burtoni cichlids was associated with high levels of cortisol (Culbert et al., 2023). During our experiment, the presence of

tropical species increased the activity level in the temperate species at 23 °C (and slightly at 26 °C). As higher locomotor activity is known to be one of the proactive stress coping behaviours associated with increasing cortisol levels (e.g., Øverli et al., 2002), it is also possible that psychological stress induced by social interaction caused cellular oxidation in the temperate species.

Projected ocean warming (+3 °C by year 2100) altered the effect of novel interactions on activity levels of the temperate local fish species. The paired temperate species was more active than the isolated temperate fish at 23 °C, but the difference in activity level between the paired and isolated fish disappeared at 26 °C. Aerobic metabolic performance declines with increasing temperatures due to decreasing capacity of the ventilatory and circulatory systems to supply demanded oxygen (oxygen- and capacity-limited thermal tolerance, Pörtner and Knust, 2007). Therefore, it is possible that the temperate fish reached its peak performance level at 26 °C and thus there was no further scope for increased activity level in the presence of a novel (tropical) species. Elevated temperature has been found to reduce the maximum burst swimming speed in the temperate *A. strigatus* (Figueira et al., 2019). Although sustained and burst swimming involve different muscle fibres (red vs. white) and pathways (aerobic vs. anaerobic) (Webb, 1994), this previous result (Figueira et al., 2019) supports our finding that increased summer seawater temperatures limit activity levels in temperate fish species.

4.3. The impact of novel interactions on the tropical vagrant fish

Comparable to the temperate species, the tropical species also showed faster short-term growth rate when paired vs. isolated with a novel species, as measured by RNA:DNA ratios. A shift in energy allocation (i.e., reducing the territory area for vigilance) via social interactions has been suggested as a main driver for positive growth in *A. vaigiensis* in the field (Smith et al., 2018). By contrast, *A. vaigiensis* did not reduce the level of physical activity in the presence of the temperate species in our experiment. Similar to our temperate species, feeding conditions may have attributed to faster short-term growth in the tropical species. While we did not observe an effect of novel interactions on the feeding rate of the tropical species during the 9 min of recording, it is possible that under our experimental ad libitum feeding conditions tropical fishes foraged for longer time periods (at similar bite rates) throughout the day, leading to higher RNA:DNA ratios in the paired species experiment.

No interaction effects between temperature and novel interactions on activity levels were detected in the tropical species (as was the case for the temperate species). We showed that the activity level between isolated and paired tropical-vagrant species did not differ at 23 °C and remained the same at 26 °C. In a previous study where the authors found the interaction between temperature and species interaction on fish behaviour, fish abundance appeared to play an important role in the interaction. For example, Milazzo et al. (2012) found that the time spent by cool-water wrasse did not differ between preferred and less preferred habitats under present and warming conditions when the abundance of counterpart warm-water wrasse was equal to that of the former; however, the former spent more time at less preferred habitat under the warming condition when the abundance of the latter tripled. Indeed, other fish species also displayed density-dependent changes in behaviour (e.g., pumpkinseeds and blugills, Mittelbach, 1988; damselfishes, Holbrook and Schmitt, 2002). The previous field study also demonstrated that *A. vaigiensis* increased the retreat rate from prey sources as the abundance of temperate fish increased and formed a large barrier to food (Coni et al., 2021). In the current study, one temperate species was unlikely sufficient to pose physical barriers to food and alter the behaviour of tropical species. Therefore, our laboratory conditions likely hindered the novel interaction from influencing *A. vaigiensis* behaviour under current and future warming conditions.

In the previous study, larger body of temperate fish was suggested as

one of the potential factors compromising the feeding activity of smaller-sized *A. vaigiensis* in the field (Coni et al., 2021). In the current study, the paired tropical species was on average 23 % smaller than paired temperate species, but feeding rate of the paired tropical species at 26 °C was greater than that of the paired temperate, suggesting that being smaller did not affect their response to larger novel competitor under laboratory conditions. The currently observed body size differences between sympatric tropical and temperate species in the field will dissipate under further ocean warming, as growth rates of competing tropical and temperate fishes are modified under ocean warming (Mitchell et al., 2023a). Such conversion in body size difference between the two has been shown to increase competition for resource (e.g., Woodward and Hildrew, 2002). The observed lack of body size disadvantage in the tropical species suggests that potential competition associated with reducing body size difference differences between tropical and temperate fishes in the future will likely affect the temperate species much more than the tropical species in temperate ecosystems.

5. Conclusions

Our study highlights the role of novel ecological interactions in altering the behavioural, cellular, and growth responses of interacting tropical and temperate fish species in a climate change hotspot where both species co-occur. The novel interactions promoted faster short-term growth (RNA:DNA ratio) in both tropical and temperate fish under both current and future ocean warming scenarios and were also associated with oxidative stress status in the latter. As growth rate (Pörtner and Peck, 2010) and oxidative stress (Carney Almroth et al., 2012) can affect life-history strategies in fish species, assessing whether and how these novel interactions can modify growth and cellular oxidation in a changing environment will improve our understanding of the impact of warming-induced environmental change on fish performance. Given our relatively short experimental duration, additional work is still required to assess the long-term effects on fitness. Nonetheless, our work still demonstrated the mediating effect of novel species interactions and global warming on fish responses that are relevant to growth and survival.

CRedit authorship contribution statement

Minami Sasaki: Conceptualization, Data curation, Formal analysis, Writing – original draft. **Angus Mitchell:** Data curation, Writing – review & editing. **David J. Booth:** Conceptualization, Writing – review & editing, Funding acquisition, Supervision. **Ivan Nagelkerken:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.169413>.

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