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**Kelsey M Kingsbury¹, Bronwyn M Gillanders¹, David J Booth², Ericka OC Coni¹,
Ivan Nagelkerken^{1,*}**

¹Southern Seas Ecology Laboratories, School of Biological Sciences, and The Environment
Institute, The University of Adelaide, Adelaide SA 5005, Australia

²Fish Ecology Lab, School of Life Sciences, University of Technology Sydney, Ultimo NSW
2007, Australia

*Corresponding author. Email: ivan.nagelkerken@adelaide.edu.au

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**Kelsey M Kingsbury^a, Bronwyn M Gillanders^a, David J Booth^b, Ericka OC Coni^a, Ivan
Nagelkerken^{a,*}**

^aSouthern Seas Ecology Laboratories, School of Biological Sciences, and The Environment
Institute, The University of Adelaide, Adelaide SA 5005, Australia

^bFish Ecology Lab, School of Life Sciences, University of Technology Sydney, Ultimo NSW
2007, Australia

*Corresponding author. Email: ivan.nagelkerken@adelaide.edu.au

ABSTRACT

As ocean waters warm due to climate change, tropical species are shifting their ranges poleward to remain within their preferred thermal niches. As a result, novel communities are emerging in which tropical species interact with local temperate species, competing for similar resources, such as food and habitat. To understand how range-extending coral reef fish species perform along their leading edges when invading temperate ecosystems, we studied proxies of their fitness, including somatic growth (length increase), feeding rates, and body condition, along a 730-km latitudinal gradient situated in one of the global warming hotspots. We also studied co-occurring temperate species to assess how their fitness is affected along their trailing edges under ocean warming. We predicted that tropical fishes would experience reduced performance as they enter novel communities with suboptimal environmental conditions. Our study shows that although tropical fish maintain their body condition (based on three proxies) and stomach fullness across all invaded temperate latitudes, they exhibit decreased *in situ* growth rates, activity levels, and feeding rates in their novel temperate environment, likely a result of lower metabolic rates in cooler waters. We posit that tropical fishes face a growth–maintenance trade-off under the initial phases of ocean warming (i.e. at their leading edges), allowing them to maintain their body condition in cooler temperate waters but at the cost of slower growth. Temperate fish exhibited no distinct patterns in body condition and performance along the natural temperature gradient studied. However, in the face of future climate change when metabolism is no longer stymied by low water temperatures, tropical range-extending species are likely to approach their native-range growth rates along their leading edges, ultimately leading to increased competitive interactions with local species in temperate ecosystems.

Keywords: ocean warming, range shifts, growth, feeding performance, trade-offs, reef fishes

1. Introduction

Anthropogenic climate change is forcing species to either locally adapt or relocate to more suitable habitats. This relocation can be a change in altitude (Dirnböck et al., 2011), a change in water depth (Perry et al., 2005), or a change in latitude (Booth et al., 2011; Feary et al., 2014). In the case of marine species, water temperature increases due to ocean warming may exceed their optimal thermal ranges (Burrows et al., 2011; Doney et al., 2012), forcing them to move to environments with more appropriate water temperatures. Range shifts involve a ‘leading’, or expanding edge, which is usually the coolest area of a species’ range, and/or a ‘trailing’, or contracting edge, which is generally the warmest area (Donelson et al., 2019). Currently, 75% of marine range expansions occur in a poleward direction, towards cooler waters at higher latitudes (Sorte et al., 2010). Often these range extensions are facilitated by the strengthening of ocean currents such as the East Australian Current (Booth et al., 2007) and can be altered by changes in freshwater flow related to rainfall and droughts (Booth et al., 2011; Johnson et al., 2011). The range extension of tropical fish into temperate communities is known as tropicalization, a phenomenon being observed increasingly around the world, including in Japan (Nakamura et al., 2013), Mexico (Heck et al., 2015), and Australia (Vergés et al., 2014).

Transition areas, or the regions where the leading edge of tropical range-extending species overlaps with existing temperate communities, are often more biodiverse as they are composed of complex species assemblages from different origins that are adapted to a variety of habitats (Horta e Costa et al., 2014). Within these temperate transition zones, species

distributions are mainly determined by water temperature. Presently, more warm-water species are advancing into cool waters as opposed to cold-water species retreating from warm waters (Hawkins et al., 2009). As tropical fish extend their ranges into temperate ecosystems, novel species assemblages and changes in trophic food webs may arise in these transition zones (Perry et al., 2005). Consequences of such range extensions include food scarcity (Ramos et al., 2014), interactions with novel predators (Siepielski & Beaulieu, 2017), effects on extant species (Vergés et al., 2016) and competition for resources (Comte et al., 2017). Consequences could also be physiological in nature, such as changes in feeding performance and growth (Amara et al., 2007; Bolger & Connolly, 1989). Several *in-situ* proxies exist to test how range-extending species adjust to suboptimal conditions in their new ranges. For example, bite rate is indicative of food intake. Similarly, activity levels are indicative of energy expenditure. Somatic growth rate gives a quantitative value of how much of any excess energy (i.e. not needed for basic maintenance) has been allocated to growth. Body condition (i.e. energy reserves) can be correlated to individual fitness (Irons et al., 2007) and survival of an organism (Bolger & Connolly, 1989; Lambert & Dutil, 1997; Schulte-Hostedde et al., 2001). Survival, growth, and reproduction are usually higher in fish with better condition (Brosset et al., 2016; Lloret et al., 2014; Millar & Hickling, 1990), linking body condition with future population success (Jakob et al., 1996; Van Beveren et al., 2014).

Temperature plays a crucial role in the physiology and therefore ecological success of range-extending species (Angilletta et al., 2002; Pörtner & Farrell, 2008). At the trailing edges of temperate species ranges, increasing water temperatures have been shown to increase the growth rate of marine ectotherms, until maximum thermal tolerances are reached (Pörtner, 2002). In contrast, at the leading edges of range extensions, low temperatures have been shown to decrease the growth rate of tropical fishes by decreasing metabolism (Enders et al., 2006; Green & Fisher, 2004; Pörtner et al., 2001) which can lead to decreased swimming ability and

activity levels due to energy redistribution to other, more critical physiological processes (Batty & Blaxter, 1992; Lyon et al., 2008). Energy allocation theories, such as the Dynamic Energy Budget (DEB), state that energy is stored in reserves and then divided among physiological processes, such as basic maintenance (body condition), development, reproduction, and growth (Lika & Kooijman, 2003; Monaco et al., 2014), with maintenance taking precedence (Heino & Kaitala, 1999; Jokela & Mutikainen, 1995; Kooijman, 2001). In situations where organisms are unable to maximise all of their life-history traits simultaneously, trade-offs may occur among physiological processes (Brosset et al., 2016; Stearns, 1992), especially in environments with limited resources (Stearns, 1989).

Here we test how invading tropical and native temperate fish species perform physiologically in co-inhabited shallow-water assemblages along their Australian leading and trailing edges, respectively. The southeast coast of Australia is a ‘hotspot’ for ocean warming, with water temperatures increasing at a rate more than triple the global average (Hobday & Pecl, 2014; Ridgway, 2007). Our study was performed along 730 km or 6° latitude of coastline, providing a natural temperature gradient for testing the performance of tropical and temperate species. We hypothesize that tropical species may trade-off growth rate for maintenance and exhibit decreased growth rate along their leading edge in cool, higher-latitude communities while temperate species increase growth rate along their trailing edge in warm, lower-latitude communities. We show that tropical fishes make this growth–maintenance trade-off in favour of body condition maintenance in cool waters, resulting in decreased growth rates in temperate ecosystems.

2. Materials & Methods

2.1 Fish collection

To assess how latitude-associated temperature differences affect fish performance, three distinct regions were studied, with both tropical and temperate fishes sampled from two sub-tropical (North and Middle) and one temperate (South) region. Regions were grouped according to mean sea surface winter temperatures (Table S1) and flow regime of the East Australian Current, both of which affect local recruitment of tropical fishes (NOAA). Fishes were collected along the southeast coast of Australia in the summer of 2018. Sample locations included South West Rocks (two sites) and Port Stephens (two sites) (“North”); Sydney (two sites) (“Middle”); Bass Point (one site), Narooma (one site), and Merimbula (two sites) (“South”) (Fig. 1, Table S1). These locations were chosen based on their geographical location and spacing, as well as *a priori* knowledge that our species of interest reside there (Booth et al., 2007). Bass Point was considered a southern location – even though it was located closer to the Middle location (i.e. Sydney) than the other two South locations (i.e. Narooma and Merimbula) – because its mean winter temperature (18.3 °C) was a degree lower than that in the Middle location (19.3 °C). This sharp decrease in seawater temperature along such a short latitudinal gradient among these two locations is caused by the warm East Australian Current diverging offshore around Sydney (Middle location), creating unstable eddies further south (Oke et al., 2013). Indeed, condition and performance measures were very different at Bass Point compared to Sydney (Figs. S1, S2). At each location, replicate sites (if any) were pooled (rather than tested as a random factor) due to low number of fishes found at some sites.

Tropical species studied were the Indo-Pacific damselfish (*Abudefduf vaigiensis*) and the scissortail sergeant damselfish (*A. sexfasciatus*), both in the family Pomacentridae, as well as the threadfin butterflyfish (*Chaetodon auriga*, family Chaetodontidae). Temperate species include stripey (*Microcanthus strigatus*) and mado (*Atypichthys strigatus*), both in the family

Kyphosidae, as well as the white-ear damselfish (*Parma microlepis*, family Pomacentridae). Table S2 shows the seasonal presence of tropical species at our study sites, confirming that the latter represent the species' range edges. Due to small sample sizes, *C. auriga* was not used in measures of bite rate or activity levels, and neither *C. auriga* nor *P. microlepis* were used in otolith growth analysis. Fishes were sprayed with a solution of ethanol and clove oil, and caught with a hand net while snorkelling. Fishes were then euthanized using the *iki jime* method and immediately put on ice to be frozen within a few hours. In this study, we limited our analyses to juvenile fish of 3-7 centimetres in standard length, to ensure that all fishes were of the same life stage and that analyses were reflective of their time in the regions of interest, and not an artefact of their pelagic life pre-settlement (Bolger & Connolly, 1989; Rätz & Lloret, 2003).

2.2 Sample preparation

In the laboratory, scales and skin were removed from the frozen fish, and stomachs were removed for later use in stomach fullness analysis. A small piece of clean white muscle tissue was obtained for nutritional analysis. This tissue was then freeze-dried for a minimum of 36 hrs, and ground to a fine powder using a ball mill, to ensure homogeneity. Samples were then weighed into tin capsules and analysed for percent protein (based on percent nitrogen) and the atomic mass ratio of carbon to nitrogen (C:N(a), hereafter referred to as C:N), using a Nu Instruments Horizon Continuous Flow IRMS (CF-IRMA).

2.3 Condition indicators

The condition or body maintenance of each fish was determined using 3 approaches: including Fulton's condition index, % protein, and C:N ratio. Fulton's condition index determines the length to weight ratio, essentially a body mass index (BMI; Kloppmann et al., 2002). This weight:length ratio relates to the energy content of muscle and liver (Lambert & Dutil, 1997), and can be an indicator of fecundity in mature adults (Lambert & Dutil, 2000) and of survival success under increased temperatures (Robinson et al., 2008). Fulton's condition index is calculated as follows:

$$K = \frac{W}{L^3}$$

Where K = Fulton's condition factor, W = wet weight of fish, and L = length of fish (we used standard length).

Percent nitrogen (%N) acts as a proxy for tissue protein content (Manthey-Karl et al., 2016), which was determined by multiplying the %N value by 6.25 (AOAC Method #968.06, 2005). The ratio of atomic mass carbon to nitrogen, or C:N ratio, reflects the lipid content of the fish's tissue, and can be used to assess nutritional quality, with high values of C:N indicative of high nutritional quality (Fagan et al., 2011; Perkins et al., 2018; Sullivan et al., 2014). A C:N value of 4, for example, indicates that there are four carbon atoms for every one nitrogen atom. As lipids are composed mostly of carbon and very little nitrogen, high values of C:N are indicative of high nutritional quality (Fagan et al., 2011).

2.4 Performance indicators

Fish performance was evaluated using stomach fullness, activity level, and bite rate. Frozen fish stomachs were thawed and observed under a stereo microscope. The fullness of each stomach was visually estimated to be one of 5 values (0, 25, 50, 75, or 100% full, by volume (Hynes, 1950)).

To determine activity level and bite rate in mixed tropical/temperate fish communities *in situ*, underwater videos of tropical and temperate fishes were recorded in the summer of 2018 using GoPro® cameras. Individual fish were tracked throughout the duration of each video, ranging in length from 20 seconds to 120 seconds, and activity level and bite rate were obtained for each fish. For activity level measurements, cameras were consistently situated 50 cm away from the fishes, and only fishes swimming in the same plane as the recording (i.e. not swimming away or towards the camera under an angle) were included, to decrease bias caused by two-dimensional recordings of three-dimensional movement. This method was repeated in all regions, with the assumption that any bias occurred equally across sites. Video recordings were then divided into intervals of 10 seconds, and fish were noted to be either ‘active’ or ‘inactive’ between each interval. ‘Activity’ was defined as the movement of the fish, and individuals were considered active when they moved more than five times their body length in comparison to their position in the previous interval. The activity level was then calculated as the proportion of intervals that the fish was active over the course of the entire video. For bite rates, a fish nipping at a piece of food, whether successful or not, was considered a ‘bite’. Bite rate was continuously recorded (i.e. no intervals) and calculated as the number of bites taken in the entire video divided by the video length (seconds), resulting in an average bite rate of bites/second. Due to small sample sizes, *C. auriga* was not used in measures of bite rate or activity levels.

Growth rate was calculated using fish ear bones (otoliths). Otoliths are bone-like accretions containing concentric growth increments. These increments provide valuable information about the fish’s environment, age, and growth. Lapilli otoliths, the mid-sized of three pairs of otoliths, were used for this study, as they show growth increments that have been validated as occurring on a daily basis in many coral reef species (Fowler, 1989; Lou & Moltschaniwskyj, 1992; Morioka & Machinandiarena, 2001). Although there has yet to be

official validation of daily growth increments for the species used in this study, this is not always necessary, particularly when used for ecological, non-fishery purposes (Choat et al., 2009). We measured the distances between the outer 15 increments only, along a standardised axis, allowing us to determine the relative growth rate for the final two weeks of each fish's life. Four species, *Abudefduf vaigiensis*, *A. sexfasciatus*, *Microcanthus strigatus*, and *Atypichthys strigatus*, were used in growth analyses.

Lapilli otoliths were extracted from each fish and connective tissue was removed. Otoliths were then mounted onto glass slides using super glue, being sure to cover the top of the otolith entirely. To expose the growth increments, otoliths were polished using incremental grades of lapping film (30 μm , 9 μm , 3 μm). Polishing continued until all increments were visible, with great care taken to avoid over-polishing past the core and planar axis. For a more detailed explanation of otolith preparation see Schultz and Taylor (1987).

2.5 Statistical analyses

Statistical analyses were performed using Primer-e (Anderson et al., 2008) and SPSS (IBM, 2016). Permutational (i.e. non-parametric) univariate analysis of variance (ANOVA – type III error) was used to test the effects of region (“Re”; North, Middle, South) and species (“Sp”) on body condition (6 species), tissue C:N ratios (6 species), tissue protein content (6 species), stomach fullness (6 species), activity level (5 species) and bite rate (5 species), and growth (4 species). A permutational ANOVA was used as these are more appropriate to analyse unbalanced designs (i.e. different number of locations for each region) (Anderson et al., 2008; Mazzaro et al., 2001). All residuals were permuted under a reduced model. Where significant differences were found, *post-hoc* pairwise tests were used to determine which treatments differed significantly ($p < 0.05$). In some cases, the $\text{Re} \times \text{Sp}$ interaction was pooled when its p -

value was > 0.25 , with the df and SS being combined with the next hierarchically-occurring term to enable a more powerful test of the main effects (Underwood, 1996; Winer et al., 1991).

3. Results

3.1 Body condition

Temperate species showed no difference in the three proxies of their body condition as a function of latitude (i.e. water temperature) (two-way ANOVAs: Fulton's condition index $p = 0.504$; tissue protein content $p = 0.057$), with the exception of tissue C:N ratio in one species (region \times species interaction $p = 0.004$), which was higher in the Middle compared to the South for *A. strigatus* (Figs 2, S1, Tables S3a, S4a). Likewise, tropical species showed no differences in any condition proxy as a function of latitude (Fulton's condition index $p = 0.601$; protein content $p = 0.339$; C:N ratio $p = 0.656$; Figs 2, S1, Table S3b).

3.2 Performance

For temperate species, performance did not differ with latitude (two-way ANOVAs, stomach fullness $p = 0.223$; activity levels $p = 0.319$; bite rate $p = 0.101$; Figs 3, S2, Tables S3a, S4a), although one species differed in growth rate: *M. strigatus* exhibited a higher growth rate in the South than in the Middle region (Table S4). For tropical species, however, all three proxies of performance were lower in cooler than warmer waters irrespective of species identity

(activity levels $p = 0.019$; bite rate $p = 0.015$; growth rate $p = 0.027$; Figs 3, S2, Tables S3b, S4b), in contrast to stomach fullness which remained similar across all latitudes ($p = 0.599$).

4. Discussion

4.1 Growth–maintenance trade-off in tropical species

We show that tropical fishes that are invading temperate ecosystems face a trade-off between maintenance of body condition and growth (Table S5). As these fishes extend their ranges into higher latitudes, the cooler waters typically decrease their metabolism (Enders et al., 2006). We found that this was associated with lower activity levels, including reduced bite rates, which would lead to decreased food intake and consequently reduced energy allocation to hierarchically less-important processes such as somatic growth. Previous studies have shown that range-extending species exhibit growth rate declines, increased predation, and increased mortality at higher latitudes (Batty & Blaxter, 1992; Lyon et al., 2008). For example, the tropical fish *A. vaigiensis* exhibits decreased growth rate, burst swimming ability, survival, and feeding rate during winter months in cool temperate habitats (Figueira et al., 2009). The optimal temperature for *A. vaigiensis* lies around 22–26 °C, below which feeding ceases and above which growth rates decline (Nakano et al., 2004; Eme and Bennett, 2008; Djurichkovic et al., in press). Some species may adjust to suboptimal environmental conditions by exhibiting seasonal energy partitioning through the build-up of energy reserves in winter for summer growth, resulting in increased summer growth and overwinter survival (Booth & Keast, 1986). Even though the stomach fullness of tropical fishes did not appear to differ between warmer

and cooler waters, the decreased metabolic rate that tropical fishes are experiencing at high latitudes is likely causing the stomach contents to be digested more slowly, therefore causing the stomach to stay full for longer (Booth, 1990; Pang et al., 2011). Another possible explanation is that bite rate may have been an inaccurate proxy of food intake, perhaps due to variability in bite size (Bruggemann et al., 1994), in which case the regional consistency in stomach fullness may be an accurate reflection of feeding conditions, with tropical species maintaining food intake across latitudes. Basal maintenance, tested here using three body condition proxies, did not differ between warmer and cooler waters for the three tropical species despite decreases in feeding rates in cooler waters. As maintenance (i.e. physiological homeostasis) is higher up the hierarchy of physiological processes than somatic growth (Heino & Kaitala, 1999; Jokela & Mutikainen, 1995; Kooijman, 2001), more energy appears to be allocated towards maintenance of body condition. By linking behaviour and physiology, we show that the observed declines in feeding performance and activity levels, and consequently reduced energy intake of tropical fishes in temperate waters results in a trade-off between maintenance and growth in favour of maintenance.

4.2 Thermal niche and temperate species performance

As opposed to tropical species, temperate fishes did not appear to make maintenance-growth trade-offs while experiencing warmer temperatures along their northern trailing edge. Their stomach fullness, activity levels, bite rates, tissue protein content, and Fulton's condition index were similar across all latitudes studied, while some species experienced changes in tissue C:N ratio or growth rates along their trailing edge (*A. strigatus* and *M. strigatus*, respectively). We predicted that the growth rate of our temperate species would be higher at their warm trailing edge, because warmer water temperatures would facilitate growth up until

a thermal threshold is crossed (Pörtner, 2002), but this was not observed. Rather than exhibiting higher growth rates in the North along their warm trailing edge, the temperate *M. strigatus* showed the highest growth in the purely temperate conditions in the South. This is likely due to the species already living in their optimal thermal niche in their native range. A study looking at three seagrass-associated temperate fishes from different latitude ranges along the east coast of Australia showed that while northern-ranging temperate species exhibited increased growth under increased temperatures, south-ranging species (less than 32° latitude) experienced a decrease in growth rate at temperatures above 18°C (Booth et al., 2014). One explanation for this is that fish populations of the same species that are separated by latitude may adapt to local temperature gradients, and respond differently to changes in water temperature (Gardiner et al., 2010). Likewise, growth rate of a temperate fish species (*Cheilodactylus spectabilis*) increased with warming waters in the middle of the species' range, but along the equatorial range edge, growth rate declined as the metabolic costs were too high (Neuheimer et al., 2011). Because growth rates did not increase with warming waters, the temperate fishes investigated in the present study are likely living on the edge of their fundamental thermal niche and do not benefit from increases in water temperatures (Edsall et al., 1993; Sax et al., 2013), potentially increasing their vulnerability to further ocean warming.

4.3 Future climate conditions

Under present climate conditions, most tropical fishes cannot yet survive the minimum winter temperatures at higher-latitude ranges (Figueira & Booth, 2010), making low temperatures the limiting factor preventing tropical fishes from permanently establishing in temperate communities (Eme & Bennett, 2008). As winter water temperatures continue to rise, tropical fishes are expected to rapidly increase survival rates throughout winters as far south as

Sydney (our Middle region) by 2080 (Figueira & Booth, 2010), and continue to advance their ranges poleward while temperate species slowly retreat (Hawkins et al., 2009; Horta e Costa et al., 2014). Tropical species living in temperate communities are predicted to once again exist in optimal temperature conditions in the near future, and it is likely that they will then no longer need to make the observed performance trade-offs. With an increasing performance of tropical species in temperate ecosystems, stronger interactions with local temperate species may accelerate the retreat of the latter at their trailing edges.

The southeast coast of Australia provides a unique natural laboratory to understand the ecological interactions between range-extending and local species under climate change, due to the presence of a strong latitudinal temperature gradient and the fact that tropical vagrant species have yet to establish breeding populations at higher latitudes (Donelson et al., 2019). Nevertheless, field observation studies also have their caveats, including the fact that environmental factors are not manipulatable. Biogeographical differences in subspecies, or behavioural factors such as competition for habitat (Matis et al., 2018) or lack of conspecifics with which to school (Griffiths, 2003) may also have played a role.

5. Conclusions

In summary, tropical fishes maintained their body condition in temperate environments despite declines in activity and feeding performance due to cooler waters. These fishes appear to face a trade-off between growth rate and body condition, favouring condition due to its hierarchical importance for fitness. Temperate fishes predominantly did not exhibit differences in body condition and showed similar performance across latitudes. With seawater temperatures set to further increase under climate change, trade-offs between key physiological

functions are expected to decrease in tropical range-extending species, resulting in a strengthening role of species interactions in terms of population dynamics and persistence of local temperate species.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at xxxx

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Figure Legends

Fig. 1: Sample locations in a natural warming hotspot along 730 km (6° latitude) of the southeast coast of Australia. Locations include South West Rocks (two sites) and Port Stephens (two sites) (included in region “North”, **red** marker); Sydney (two sites; included in region “Middle”, **purple** marker); Bass Point (one site), Narooma (one site), and Merimbula (two sites) (included in region “South”, **blue** marker). See Table S1 for location and site coordinates and their respective mean winter seawater temperatures.

Fig. 2: Mean (\pm SE) measures of condition of tropical (solid lines) and temperate (dashed lines) fish species. Condition proxies are based on Fulton’s condition index (**a**), muscle tissue protein content (**b**), and the atomic ratio of carbon to nitrogen in muscle tissue (C:N) (**c**). **ab** letters indicate significant regional differences within species. See Fig. S1 for location-specific data.

Fig. 3: Mean (\pm SE) measures of performance of tropical (solid lines) and temperate (dashed lines) fish species. Performance was measured as: stomach fullness (**a**), percent time active *in situ* (**b**), *in situ* bite rate (**c**), and growth rate (daily otolith growth increments) (**d**). Stomach fullness was examined for all species, while activity level and bite rate analyses did not include *C. auriga*. Neither *C. auriga* nor *P. microlepis* were included in growth analysis. **ab** letters indicate significant regional differences within species. Species without letters showed no significant differences. See Fig. S2 for location-specific data.

Figure 1

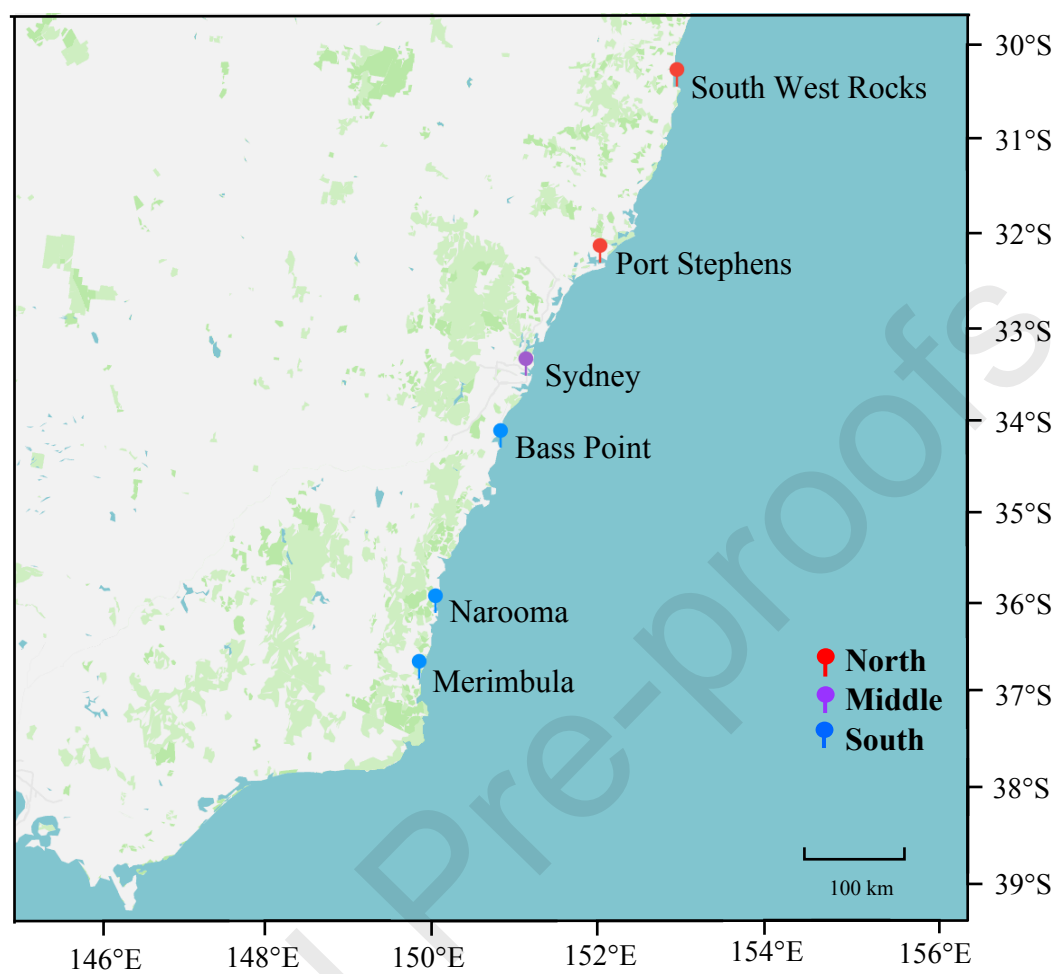


Figure 2

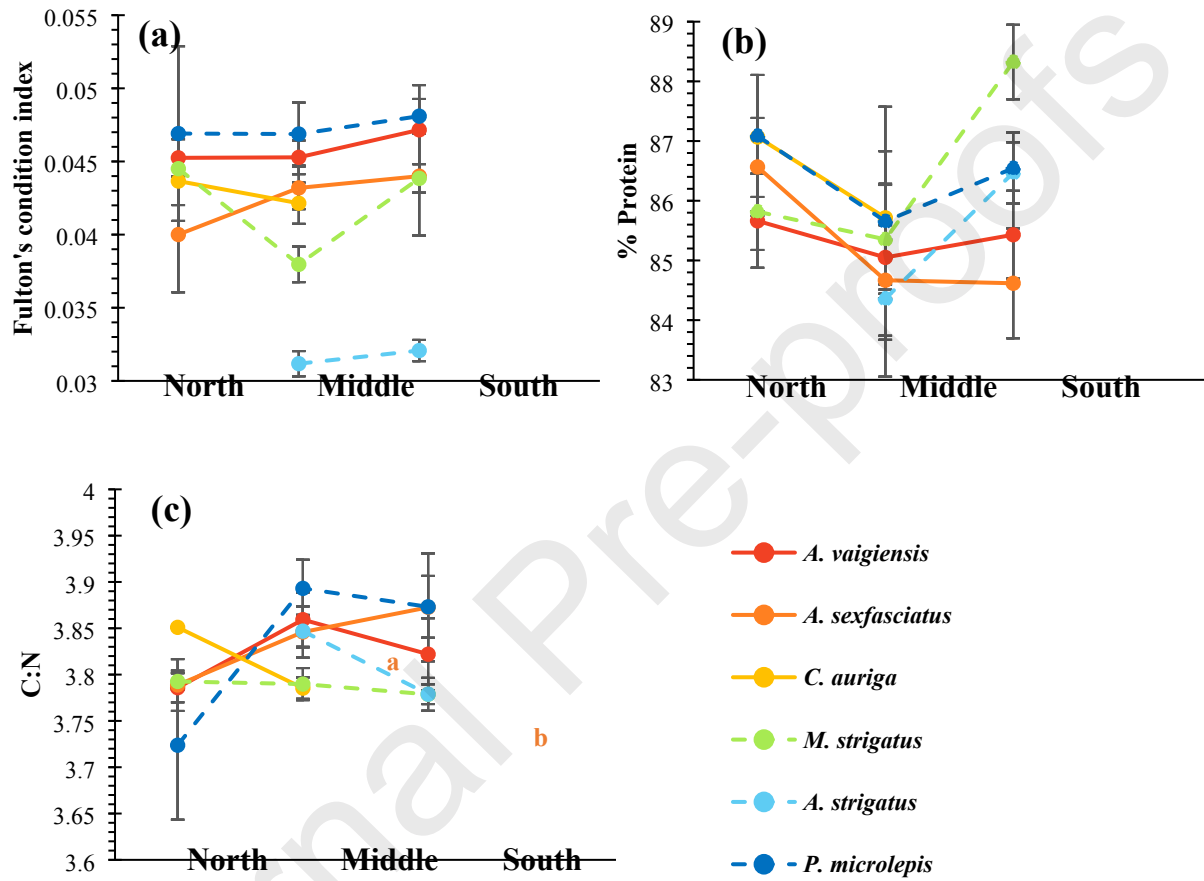
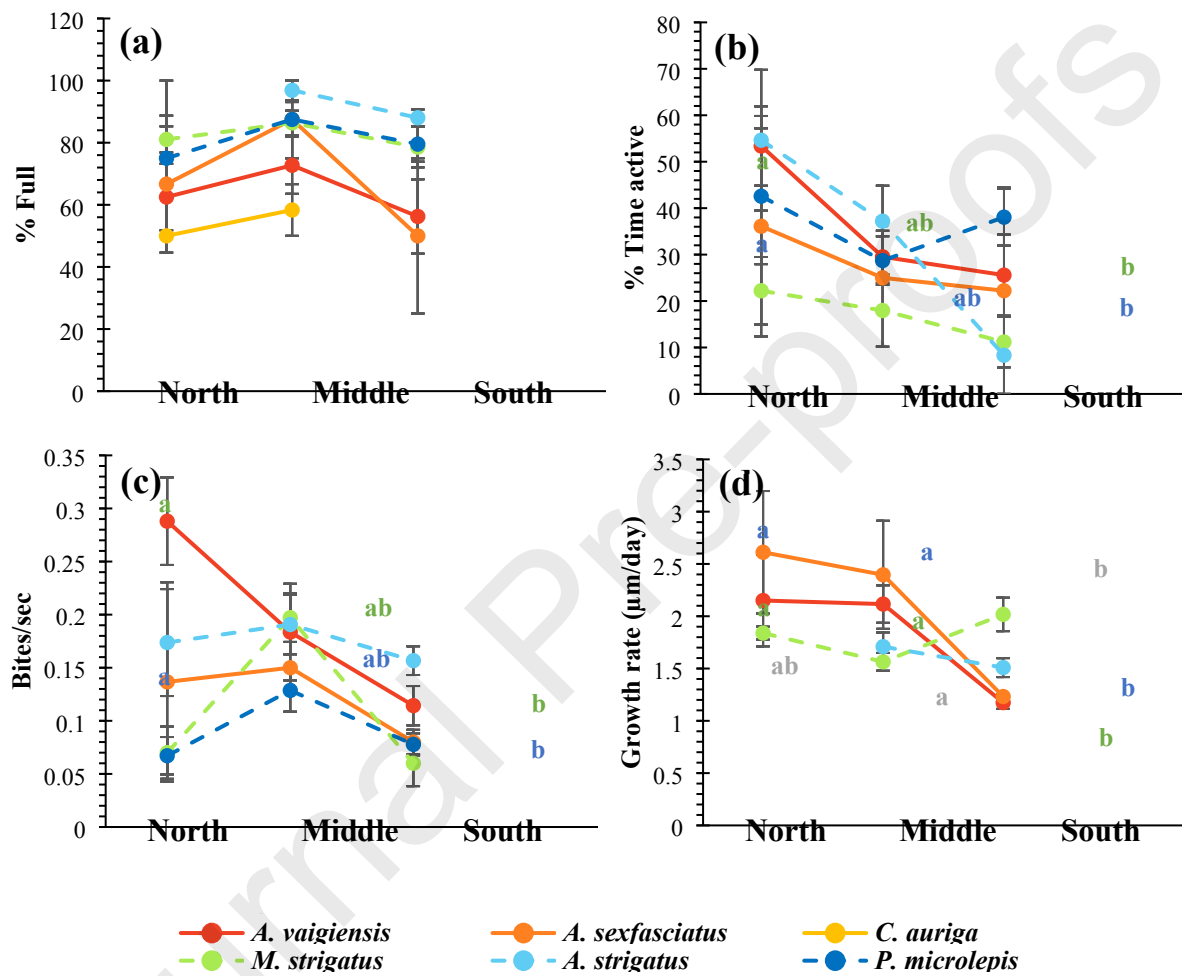


Figure 3



- Climate change is driving poleward range extensions in tropical fishes
- This did not affect proxies of body condition in tropical or temperate fishes
- Reduced temperatures decreased performance in tropical fishes

- Increased temperatures did not alter performance in temperate fishes
- Tropical fishes trade-off growth for body maintenance in their novel climate range