The effects of tropical fish range extensions on temperate communities

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Included publications

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Biographical sketch

Kelsey Kingsbury attended Cornell University in Ithaca, New York, from 2011 to 2015, graduating with a Bachelor of Science degree in Ocean Science and minoring in Climate Change. During her time at Cornell, she took part in the *Kumu pa'a i ka `aina* field program in Hawai'i, became an intern at the Hawai'i Marine Mammal Consortium, and was a Lynch Scholar at Friday Harbor Laboratories where she researched seagrass wasting disease. She then undertook a Master of Philosophy degree at The University of Adelaide in Adelaide, Australia as a member of the Southern Seas Ecology Laboratories from 2017 to 2019.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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Kelsey Kingsbury

Abstract

As anthropogenic stressors cause our planet to warm at unprecedented rates, species must either adapt or migrate, or else face local extinction. Were a species to migrate, its geographic distribution could shift towards a more favourable environment, or away from an undesirable environment, a phenomenon known as range shifting. Seventy five percent of current marine range shifts involve the expansion of ranges in a poleward direction, into cooler waters situated at higher latitudes. The equatorial tropics in particular are warming disproportionately to the rest of the planet, and as such, range-expanding species often originate from the tropics. Many range-extending tropical species, or vagrants, are now living in temperate communities, surrounded by temperate neighbours and new predator-prey interactions, potentially leading to competition for resources such as habitat and food. To understand how novel interactions between these newly-sympatric fish species affect their performance and behaviour, I assessed the partitioning of food sources, body condition, and performance of range-extending and local fish in these mixed communities. Food partitioning, or trophic niche use, was investigated using stable isotope analysis and stomach content analysis. Fish body condition and performance were evaluated using a combination of condition proxies (Fulton's condition index, protein content, and the ratio of carbon to nitrogen), and performance proxies (stomach fullness, bite rate, activity level, and growth rate). I discovered that tropical and temperate species largely occupy distinct trophic niches. Additionally, both groups fed on a wide variety of food items, indicating that they are trophic generalists. Tropical species exhibited a decrease in three performance proxies (bite rate, activity level, and growth rate) in cool waters as compared to their native region, yet showed no change in body condition. These tropical species likely faced a trade-off between growth and maintenance of body condition, favouring condition, due to the sub-optimal environmental conditions of the cooler south. Temperate species showed no change in body condition or performance between sub-tropical and temperate communities. As waters continue to warm and tropical species are once again in optimal thermal conditions, performance trade-offs may no longer be necessary, ultimately strengthening interactions between tropical and temperate species.

Chapter 1 – Introduction

Anthropogenic climate change has caused global sea surface temperatures to rise ~0.2 °C over the past three decades, with an increase of 3.0 °C expected by the end of the century (Hansen et al. 2006; Munday et al. 2009). As these ecosystems are altered, the balance between extinction and persistence is jeopardized (Sinervo et al. 2010; Cheung, Watson & Pauly 2013; Poloczanska et al. 2013). In order to persevere in such changing environments, species must either adapt or relocate (Maggini et al. 2011; Doney et al. 2012).

If species cannot adapt, they may shift their ranges in order to stay within their optimal temperature niches (Burrows et al. 2011; Doney et al. 2012), potentially impacting the structure and function of ecosystems (Dawson et al. 2011). During range shifts, edges are classified as 'leading', the edge that is expanding, and 'trailing', the edge that is contracting (Sorte, Williams & Carlton 2010). Range edges move in different directions and at different rates depending on factors such as latitude, with the spreading of species poleward often limited by cool temperatures (Parmesan & Yohe 2003). Under current climate conditions, marine species shift their range edges at an average rate of 19 km year^{-1} (Sorte, Williams & Carlton 2010), an order of magnitude faster than the average terrestrial rate of 0.6 km year^{-1} (Sorte, Williams & Carlton 2010; Maggini et al. 2011; Poloczanska et al. 2013), in part due to the oceans storing 80-90% of the heat associated with climate change (Church et al. 2011; IPCC 2013; Durack et al. 2014). Furthermore, tropical organisms are thought to be the most at-risk marine group under climate change (Comte & Olden 2017), because they have evolved in a thermally-stable environment (Tewksbury, Huey & Deutsch 2008) and often rely on coral, whose resident symbiotic algae are sensitive to temperature increases (Hoegh-Guldberg et al. 2007; Doney et al. 2012). Additionally, species that live along continental edges or at latitude maximums (i.e., equatorial and polar regions) are highly susceptible to environmental changes, as they have very few suitable environments to which to move (Hampe & Petit 2005). Presently, 75% of marine range shifts occur in a poleward direction, towards cooler water at higher latitudes (Sorte, Williams & Carlton 2010). These recipient communities are sub-tropical or temperate, and as such contain novel species assemblages.

In these novel communities, species may compete for trophic resources. If species occupy overlapping trophic niches, competition for food is likely. If species are segregated, however, co-existence is possible. Niche divergence, or character displacement, is a common evolutionary response to inter-specific competition (Grant 1972; Dayan & Simberloff 2005;

Svanbäck & Bolnick 2007). Were inter-specific trophic competition to increase, growth rates and biomass of fish species may decrease in response (van de Wolfshaar et al. 2012). However, if tropical range-extending vagrants and temperate residents are able to successfully partition trophic niches, with both species groups occupying distinct niches, cohabitation may be possible. By investigating how these fish groups partition their niches, we gain a better understanding of trophic competition, allowing for better and more accurate environmental decision-making, including the protection of key food sources. Until now, studies have neglected to explore the direct trophic interactions of vagrant tropical and temperate species in these novel marine communities.

The goal of this thesis was to understand how newly-sympatric tropical range-extending vagrants and temperate fish species may co-exist under climate change in temperate communities, by focusing on two major objectives:

Objective 1: How are the trophic niches of tropical range-extending fish and local temperate species being partitioned in mixed temperate communities?

Objective 2: How is fish body condition and performance of range-extending species affected by inhabiting these novel mixed-assemblage temperate communities?

I begin by providing a summary of related literature to act as a framework for the research presented in this thesis. Two manuscripts are then presented, each addressing one of the aforementioned objectives. Chapter 2 highlights the trophic niche usage of tropical and temperate species in novel mixed temperate communities, while Chapter 3 builds upon these findings by investigating how fish performance is in turn affected. I conclude with a general discussion of my findings, including potential future research directions.

Range shifts

The southeast coast of Australia is a climate ‘hotspot’, with tropical fish species moving from warm tropical waters into temperate communities at a rate well above the global average (Ridgway 2007; Booth, Bond & Macreadie 2011; Vergés et al. 2014a). As tropical range-extending fish enter temperate communities, they encounter temperate species with whom they do not normally interact. In these novel communities, competition for resources and unfavourable predator-prey interactions may arise (Pörtner & Farrell 2008b; Gilman et al.

2010; Wernberg et al. 2011). Non-native consumers (vagrant tropical fish species in the present study) have the potential to outcompete native populations of prey due to their high rates of predation, and communities could suffer if these native consumers are replaced by non-native species (McKnight et al. 2017). This replacement could intensify the local extinction rates of native species by increasing their susceptibility to anthropogenic stressors, having both ecological and commercial repercussions (McKnight et al. 2017). This can be seen along the southeast coast of Australia, where range-shifting tropical rabbitfish are drastically reducing the biomass of algae and invertebrates, as well as the overall biodiversity of temperate reefs (Vergés et al. 2014b). Other negative effects include the alteration of ecosystem functions, the spreading of tropical infectious diseases that can harm native species and humans, declines in the nutritional value of tissue, stunted growth rates, and fish biomass declines due to trophic competition (Schlaepfer, Sax & Olden 2011; Gallardo et al. 2016). Species that remain along the trailing edge of a range shift may be particularly vulnerable as their food sources may instead track the advanced leading edge (Peers et al. 2014). Not all consequences of these tropical range-extensions are negative, however. Vagrant species may provide food and habitat for common and rare species, serve as functional substitutes for extinct species, and offer desirable ecosystem functions, such as erosion control (Schlaepfer, Sax & Olden 2011). Due to their high adaptability, vagrant species may also be helpful in achieving future conservation goals by providing vital ecosystem services, such as biofiltration by bivalves and pollination by insects, in areas where climate is rapidly changing, potentially leading to the evolution of new local taxa (Schlaepfer, Sax & Olden 2011).

There are many studies that discuss the mechanisms and implications of species invasion within terrestrial systems (Schlaepfer, Sax & Olden 2011; Peers et al. 2014; Estrada et al. 2016), but different traits and processes facilitate invasion in marine ecosystems, and therefore the same principles and practices may not be applicable to both environments (Dawson et al. 2011; McKnight et al. 2017). Isotherms on the ocean surface have migrated faster than isotherms over land over the past 50 years, contributing to the exceptional speed of marine range shifts (Burrows et al. 2011). Additionally, marine species often have larger geographic ranges, fill their thermal niches more fully, and are less adapted to thermal variability than terrestrial species, meaning that changes to temperature may have a greater effect (Donelson et al. 2011b; Donelson et al. 2019). Even within marine ecosystems, changes cannot be generalized due to the irregularity of range edges and the indiscriminate nature of waterway movement (Bates et al. 2014; McKnight et al. 2017). Irregularities occur when range edge changes transpire near islands and continental edges, where habitat is limited by land boundaries (Cahill et al. 2012; Wernberg et al. 2016). The main drivers of climate change-related marine range shifts are 1) increasing water temperatures, 2) reduction in freshwater flow due to drought and changes in rainfall, and 3) changes in ocean currents (Booth, Bond & Macreadie 2011). Range shifts may be facilitated by strong boundary currents, such as the East Australian Current (EAC) along the east coast of Australia, and the subsequent transport of the pelagic eggs of benthic tropical fish into temperate communities (Figueira & Booth 2010). Additionally, the strengthening of the EAC has caused the surrounding waters to warm at a rate of 0.023 °C year^{-1}, quadruple the average global ocean warning rate (Ridgway 2007; Wernberg et al. 2011). Tropical vagrant species most commonly originate from communities situated at higher equatorial latitudes, and individuals with a large body size and strong swimming abilities are more successful in their colonization of temperate habitats (Feary et al. 2014).

It is necessary to distinguish between true range shifts, species introductions, and natural temporal vagrancy. Range shifts refer to the movement of a species from its native habitat to an *adjacent* habitat (Chapman & Carlton 1991). Introductions occur when a species enters a community that is geographically *separate* from its habitat of origin through human activities (Chapman & Carlton 1991), and is defined by the process of 1) inoculation, 2) establishment, and 3) colonisation or secondary spread (Sorte, Williams & Carlton 2010). Natural temporal vagrancy is defined as the occurrence of fish species outside of their usual ranges due to natural environmental variations (Davis & Shaw 2001; Ralston et al. 2017). Temporal vagrancy can result from the El Niño-associated northward movement of tropical species in the northern Pacific, and is not necessarily indicative of range shifts (Fogarty et al. 2017). True range expansions can be characterised as 1) arrival, 2) population increase, and 3) persistence. Conversely, range contractions are characterised as 1) performance decline, 2) population decrease, and 3) local extinction (Bates et al. 2014). Range edges may move at different speeds, depending on the rate at which a species tracks climate change (Ralston et al. 2017; Donelson et al. 2019). Declining species may be unable to track their historical niches beyond current range peripheries, leading to decreased niche filling, or niche contraction (Ralston et al. 2017). Early detection of range shifts is crucial in identifying a true range shift versus natural temporal variation, allowing us to better forecast the ecological impacts and accompanying costs to fisheries (Fogarty et al. 2017).

While range-shifting vagrant species are distinct from introduced species, some of the same principles may apply to both. The enemy-release hypothesis (ERH) states that introduced species leave their co-evolved natural enemies behind as they enter into a recipient community and can greatly increase in abundance as a consequence (Keane & Crawley 2002; Sorte, Williams & Carlton 2010). The Darwin Naturalisation Hypothesis states that species that enter into communities of phenotypically-similar genera tend to be more vulnerable to parasites and predation, and experience competitive exclusion (Daehler 2001; Strauss, Webb & Salamin 2006; McKnight et al. 2017). According to Darwin, species that exist in abiotically 'stressful' environments, such as high elevation and high latitude, have their population growth and range limits set by abiotic factors, whereas species in less stressful environments have their growth and range limits set by species interactions (Louthan, Doak & Angert 2015; Louthan et al. 2018). Depending on which of these theories holds true for the range-extending species used in this study, tropical fish may experience competitive exclusion from resources, or experience growth limits due to environmental stress. By investigating how trophic resources are partitioned and how fish condition and performance (including growth) are altered, the effects of these novel mixed communities can begin to be seen.

As the nutritional value of marine organisms declines, there may be negative consequences for higher trophic levels, such as decreased nutrient uptake and the need for increased feeding rates (Garzke et al. 2016). Due to temperature-driven lipid depletion, copepods are declining in growth and abundance, potentially having negative implications for the many species that consume them, and ultimately affect humans (Garzke et al. 2016). Fish provides 3.1 billion people with 20% of their animal protein intake, and accounts for nearly 17% of the world population's protein (United Nations 2016). As temperatures rise, the mean temperature of catch (MTC) of fisheries, defined as the average temperature preference of exploited species weighted by their annual catch, has increased 0.19 °C per decade globally (0.23 °C per decade in temperate regions), resulting in an observable change in fishery catch (Cheung, Watson & Pauly 2013). In West Africa, climate change is affecting fish production and protein supply, with annual landed values estimated to drop 21% by 2050 (Lam et al. 2012). Other regions, such as Japan, Iceland, the Republic of Korea, Norway, and various island states, have either developed a preference for fish or have no readily-available protein alternatives, and would feel the effects of fish biomass decline very strongly (United Nations 2016). Additionally, as temperatures continue to rise, fish may experience increased metabolic costs (Nagelkerken & Connell 2015), leading to further reductions in growth rate and biomass.

Trophic niche

When entering a novel ecosystem, species possessing traits that enhance survival, such as high feeding success and thermal tolerance, have a greater chance of establishing and spreading

(Poff et al. 2010). Another such trait is that of trophic generalism. Trophic generalism refers to the consumption of a wide range of food items, as opposed to trophic specialists, which feed on a limited variety of sources (Gerking 1994). Generalist feeding strategies are important in minimising trophic competition and thereby facilitating co-existence through spatial partitioning (Eurich et al. 2019). Generalists are thought to have an advantage over specialists, as they feed on a larger spectrum of food sources and are therefore less susceptible to food shortages (Wilson et al. 2008; Clavel, Julliard & Devictor 2011). Due to high trophic niche plasticity, generalists may be less vulnerable to climate change as they are able to adapt to resource depletion by consuming other, unaffected food items (Travis 2003; Slatyer, Hirst & Sexton 2013; Afonso Silva et al. 2017). Although generalism is thought to be the appropriate feeding strategy in the face of climate change, generalists may decrease in abundance as climate change continues to take its toll (Albouy et al. 2014). In a study of the Mediterranean Sea, species richness, the number of feeding links, and predator generality (i.e. the mean number of prey species per predator species), are predicted to decrease by the end of the century, with predator generality expected to decrease from 30.0 to 25.4 (Albouy et al. 2014). The overall food web connectance (i.e., the number of actual links divided by the fraction of all possible links) is projected to increase from 0.26 to 0.29, due to the loss of feeding links (Albouy et al. 2014).

As tropical vagrant species shift poleward and enter these temperate communities, predator-prey relationships and trophic competition may arise (Pörtner & Farrell 2008a; Wernberg et al. 2011; Alexander et al. 2016). Such novel interactions between species brought together by climate change are thought to be the greatest contributor to climate change extinctions (Cahill et al. 2012), yet previous studies have largely neglected to explore trophic interactions in temperate communities containing tropical vagrants (Johnson et al. 2011). In order to assess the contributions of these novel trophic interactions to species persistence, it is necessary to disentangle the interactions themselves. One way to do this is through the examination of trophic niche use and partitioning (Strayer 2012). To avoid trophic competition, niches that are occupied in part or in full by temperate species must be partitioned (Schulze et al. 2012), and the use of stable isotope analysis allows us to see in what way the trophic niches are being partitioned. Possible trophic niche arrangements include segregation, overlap, displacement, or expansion and/or contraction. Were the trophic niches of vagrant tropical species to overlap significantly with that of local temperate species, the likelihood of trophic competition is high.

Water temperature

In addition to potential trophic interactions, cool water temperatures may present a challenge to range-extending tropical fish species, with several studies suggesting a need for further research (Shoo, Williams & Hero 2006; Booth et al. 2018). Cool water may lead to declines in body condition and performance (Pörtner 2010). Poor body condition can be caused by low food availability, poor feeding conditions, competition for food, infection, and sub-optimal environmental conditions, such as temperature extremes (Lambert & Dutil 1997; Donelson et al. 2011a; Poulos & McCormick 2015). Body condition is very sensitive to environmental and trophic changes, with significantly different condition levels observed for fish inhabiting the same reef (Beruman, Pratchett & McCormick 2005). Maintenance of homeostasis and storage of energy reserves are crucial for survival and reproduction, with female herrings trading off increased growth rates for reproductive success by allocating growth resources to reproduction (Rajasilta et al. 2015). Reduced condition can lead to decreased health and increased susceptibility to diseases (Anderson & Neumann 1996), reduced growth rates, and declines in reproductive potential and fecundity (Murphy & Willis 1996; Rätz & Lloret 2003), in turn negatively affecting population densities and replenishment (Forrester 1990; Booth 2002). This is especially true for juveniles, such as those used in the present study, as they have fewer fat reserves and metabolise food more quickly compared to older life stages (Donelson, Munday & McCormick 2009) and further investigations have been called for (Thresher et al. 2007). Similarly, fish performance may be affected in these mixed temperate communities. Performance, including metabolic rate, swimming performance, feeding performance, activity level, and growth (Yuen et al. 2019), may be altered by temperature due to its effect on biochemical reaction rates (Fry 1971; Laubenstein et al. 2019). While range-extending tropical species are living in water temperatures at their thermal minima, they may be subject to changes in performance. Assessing the body condition and performance is important when evaluating a species' ability to survive and breed, allowing us to make more accurate predictions about the successful establishment of these range-extending tropical fish in temperate ecosystems.

While there is ample literature that addresses range shifts and trophic niche partitioning, there are very few studies that have looked specifically at the effect of range-extension on trophic niche partitioning and the associated effects on fish performance. The East Australian Current flows along the southeast coast of Australia, connecting northern tropical communities with sub-tropical and temperate communities, and provides an ideal natural laboratory to study such effects. This thesis is composed of two data chapters, followed by a discussion of both chapters in the context of the broader thesis. Chapters 2 and 3 are manuscripts submitted to journals. Chapter 2 explores trophic niche partitioning and diet overlap between tropical and temperate fish, but additional factors must be considered when assessing the overall effect of tropical vagrants in temperate communities, such as the fish's condition. Chapter 3 builds upon the findings of Chapter 2 by delving further into the investigation of tropical range-extending fish species in temperate communities, but this time by looking at the body condition and performance of the fish itself. These two chapters are related in that they both assess the consequences of tropical range-extension into temperate communities. The combined use of trophic niche space assessment and physiological performance indicators paints a picture of how fish are coping in these mixed communities, and provides estimates of what we can expect as we go forward into future warming scenarios.

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Chapter 2 – Trophic niche segregation allows range-extending coral reef fishes to co-exist with temperate species under climate change

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i. the candidate's stated contribution to the publication is accurate (as detailed above);

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Abstract

Changing climate is forcing many terrestrial and marine species to extend their ranges poleward to stay within the bounds of their thermal tolerances. However, when such species enter higher-latitude ecosystems, they engage in novel interactions with local species, such as altered predator-prey dynamics and competition for food. Here we evaluate the trophic overlap between range-extending and local fish species along the east coast of temperate Australia, a hotspot for ocean warming and species range extensions. Stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of muscle tissue and stomach content analysis were used to quantify overlap of trophic niche space between vagrant tropical and local temperate fish communities along a 730 km (6˚) latitudinal gradient. Our study shows that in recipient temperate ecosystems, sympatric tropical and temperate species do not overlap significantly in their diet – even though they forage on broadly similar prey groups – and are therefore unlikely to compete for trophic niche space. The tropical and temperate species we studied, which are commonly found in shallow-water coastal environments, exhibited moderately-broad niche breadths and local-scale dietary plasticity, indicating trophic generalism. We posit that because these species are generalists, they can co-exist under current climate change, facilitating the existence of novel community structures.

Keywords: ocean warming, niche use, range shifts, stable isotopes, diet

Introduction

To persevere in a changing environment, species must acclimate (Stillman 2003; Donelson et al. 2011), adapt, or relocate (Perry et al. 2005; Booth, Bond & Macreadie 2011; Pecl et al. 2017). The balance between persistence and extinction is jeopardized by climate change, causing shifts in range edges (Sinervo et al. 2010; Cheung et al. 2012; Poloczanska et al. 2013), greatly impacting the structure and function of ecosystems (Dawson et al. 2011). Marine species shift their range edges under global warming at an average rate of 19 km year^{-1} (Sorte, Williams & Carlton 2010), an order of magnitude faster than the average terrestrial rate of 0.6 km year^{-1} (Sorte, Williams & Carlton 2010; Maggini et al. 2011; Poloczanska et al. 2013). Range shifts may be facilitated by the strengthening of boundary currents, such as Australia's East Australian Current (EAC), as well as a drought-related reduction in freshwater flow (Booth, Bond & Macreadie 2011; Johnson et al. 2011; Last et al. 2011). To date, 75% of marine range shifts occur in a poleward direction (Sorte, Williams & Carlton 2010).

Whilst there are ample insights into the mechanisms and implications of species invasions within terrestrial systems (Chen et al. 2011; Peers et al. 2014; Estrada et al. 2016), different traits and processes (e.g. ocean currents) can regulate invasions in marine ecosystems, and therefore the same principles may not be relevant to both biomes (Burrows et al. 2011; Dawson et al. 2011; McKnight et al. 2017). Even among marine ecosystems, range edge movement cannot always be generalized, in part due to the largely indiscriminate nature of water movement, e.g. non-linear eddies (Bates et al. 2014; McKnight et al. 2017). When range shifts occur near islands and continent edges, where habitat is limited (Cahill et al. 2012; Wernberg et al. 2016), or where water movement is caused by non-linear currents and eddies (Garciá Molinos, Burrows & Poloczanska 2017), range shifts become even more difficult to predict, and sometimes recede rather than extend.

Many studies have focused on range-extensions of warm-affiliated species to higher latitudes, but we still lack a detailed understanding of how recipient ecosystems and communities are affected by these native invasions (Bates et al. 2014; Feary et al. 2014). Several scenarios exist in which range-extending species might exert positive effects or ecosystem services on recipient communities. For example, range-extending species can serve as functional substitutes for extinct local species and provide food and habitat to rare local species, which may be vital in achieving future conservation goals (Dudgeon & Smith 2006; Gozlan 2008; Schlaepfer, Sax & Olden 2011). Research on the range extensions of boreal arctic generalist fish showed an increase in connectivity between pelagic and benthic communities and a subsequent reduction in modularity (Kortsch et al. 2015). Additionally, range-extending species may be more adaptable than native species, and as the climates continue to change, outlast local species and ultimately evolve into new endemic species (Schlaepfer, Sax & Olden 2011).

Negative effects of range-extensions include novel predators causing local extinction of native species (Bampfylde & Lewis 2007; Wiens 2016), hybridization altering the integrity of local species (Gozlan 2008), threating ecosystem functions, such as the overgrazing of macrophytes (Gallardo et al. 2016) and the creation of urchin barrens (Ling et al. 2015), and carrying infectious diseases that can harm native species (Schlaepfer, Sax & Olden 2011). If a non-native species has high rates of consumption and growth, they have the potential to damage local communities by outcompeting, and potentially replacing, native consumer populations (Schlaepfer, Sax & Olden 2011; McKnight et al. 2017). This replacement could intensify the local extinction rates of native species by increasing their susceptibility to anthropogenic stressors, having both ecological and commercial repercussions (McKnight et al. 2017). On the other hand, tropical species in temperate environments may experience greater predation by local predators, as they are a novel species within the community (Almany & Webster 2004). The exact effect of range-extending species on recipient ecosystems, however, depends on a variety of factors including a species' geographic range, abundance, and per capita effects. Species are thought to have a high per capita effect if they are functionally distinctive in their food web position, their response to environmental factors, their acquisition of resources, or their effects on disturbance regimes (Vitousek 1990; Chapin et al. 1997; Wardle et al. 2011). In general, it is difficult to estimate the per capita impact that a species will have until the invasion begins to happen (Strayer 2012).

Here we test how range-extending tropical reef fish, thought to be the most at-risk group under future climate change (Comte & Olden 2017), create novel trophic niches in temperate coastal ecosystems. Novel interactions such as changes in predator-prey relationships and trophic competition are likely to arise between newly sympatric groups (Pörtner & Farrell 2008; Wernberg et al. 2011; Alexander et al. 2016). Using stable isotopes and stomach contents, we determine how trophic niche partitioning might facilitate co-existence among coastal vagrant tropical and local temperate species by exploring several scenarios of niche modification: segregation, overlap, displacement, and expansion or contraction (Fig. 1). Our study focuses on the temperate east coast of Australia, where coastal waters are warming at a rate 3-4 times the global average (Holbrook & Bindoff 1997; Ridgway 2007; Johnson et al. 2011).

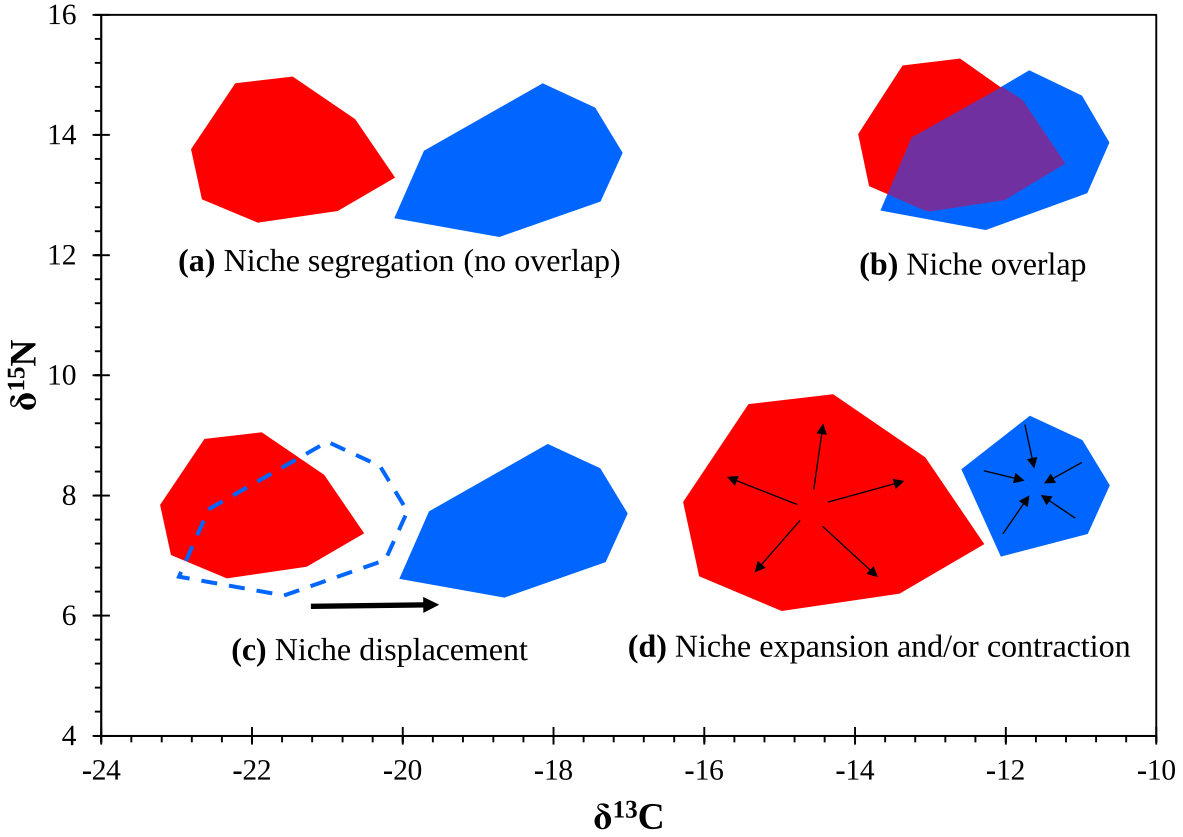

Fig. 1: Conceptual diagram of trophic niche space of co-existing species based on existing theory. Niches are displayed as convex hull polygons in isotope ($\delta^{15}N$ and $\delta^{13}C$) space. Possible arrangements include niche segregation (no overlap) (**a**), niche overlap (**b**), niche displacement (**c**), and niche expansion and/or contraction (**d**). The different coloured niches represent different affinities (tropical vs temperate) or species. In the case of niche displacement, the dashed blue line represents where the blue niche was before it was displaced.

Materials and Methods

Study species

The fish species studied were selected based on their ubiquity and ease of capture at known locations, and include tropical pomacentrid damselfishes (*Abudefduf bengalensis**, *A. sexfasciatus**, *A. vaigiensis**, *Chrysiptera brownriggii*, *Dascyllus aruanus*, *Pomacentrus bankanensis*, *P. coelestis*, *P. moluccensis*), tropical butterflyfishes (*Chaetodon auriga**, *C. citrinellus*, *C. flavirostris*, *C. kleinii*, *C. rainfordi*, *C. tricinctus*, and *C. vagabundus*), two temperate sea chubs (*Atypichthys strigatus** and *Microcanthus strigatus**), a temperate pomacentrid damselfish (*Parma microlepis**), and the temperate Port Jackson glassfish (*Ambassis jacksoniensis*) (See Table S1 for fish lengths, weights, sample sizes, and *in situ* densities). Some of these common tropical species, namely *A. sexfasciatus* and *A. vaigiensis*, are often observed to school with the temperate *A. strigatus* and *M. strigatus* (Smith et al. 2018; Figueira, Curley & Booth 2019). All above species were included in the stable isotope analysis, but due to their small sample sizes in some regions, only species indicated with '*' could be used for stomach contents analysis, and consequently for calculation of diet breadth and niche breadth.

The tropical species are commonly found in warm Indo-Pacific waters, including the Great Barrier Reef (Masuda et al. 1984; Getlekha et al. 2016). The temperate species *M. strigatus* is found from Japan down into tropical and temperate Australia and east towards the Hawaiian Islands, while temperate species *A. jacksoniensis*, *A. strigatus*, and *P. microlepis* are found in south-eastern Australia only. The tropical species used in this study that were observed at Sydney and further south (Fig. 2; *A. bengalensis*, *A. sexfasciatus*, *A. vaigiensis*, *C. auriga*, *C. citrinellus*, *C. flavirostris*, *C. vagabundus*, *P. bankanensis*, and *P. coelestis*) are considered vagrants as they only occur at these locations on a seasonal-basis. Their presence drops quickly as water temperature decreases throughout the seasons, and their presences are also much lower at the cold-water Merimbula site than the warmer Sydney site (Table S2). The remainder of the tropical species were not observed as far south as Sydney. Furthermore, the peak temperatures (below which abundances start to decline) of all the selected tropical species (Booth et al. 2018) are lower than the mean winter temperatures at the two study sites (Table S2). All species studied are omnivorous (Randall 1985; Myers 1991; Lieske & Myers 1994). The East Australian Current (EAC) transports larvae of coral reef fishes from tropical regions to southern sub-tropical and temperate regions (Booth et al. 2007; Smith et al. 2016).

Field collection

Field sampling was conducted in February and March of 2017 and 2018 in four different regions (Fig. 2; true coral reefs, and North, Middle, and South regions of range extensions). Sample locations include 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"); and One Tree Island (two sites) and Lord Howe Island (three sites) ("coral reef") (Fig. 2). One Tree Island and Lord Howe Island were sampled in 2017 only, and only tropical species were present and captured there. These coral reef locations were chosen based on their latitude and geographical spacing, as well as *a priori* knowledge that our species of interest reside there (Booth et al. 2007). Sample sizes of each species at each site are shown in Table S1 and species' seasonal ranges are shown in Table S2. Fish were caught using hand nets at depths of 1-3 m using ethanol and clove oil, to anesthetize the fish. The fish were immediately killed using the *iki jime* method, and placed on ice before being frozen. All samples were frozen within four hours of collection and remained frozen at -30 ˚C before processing.

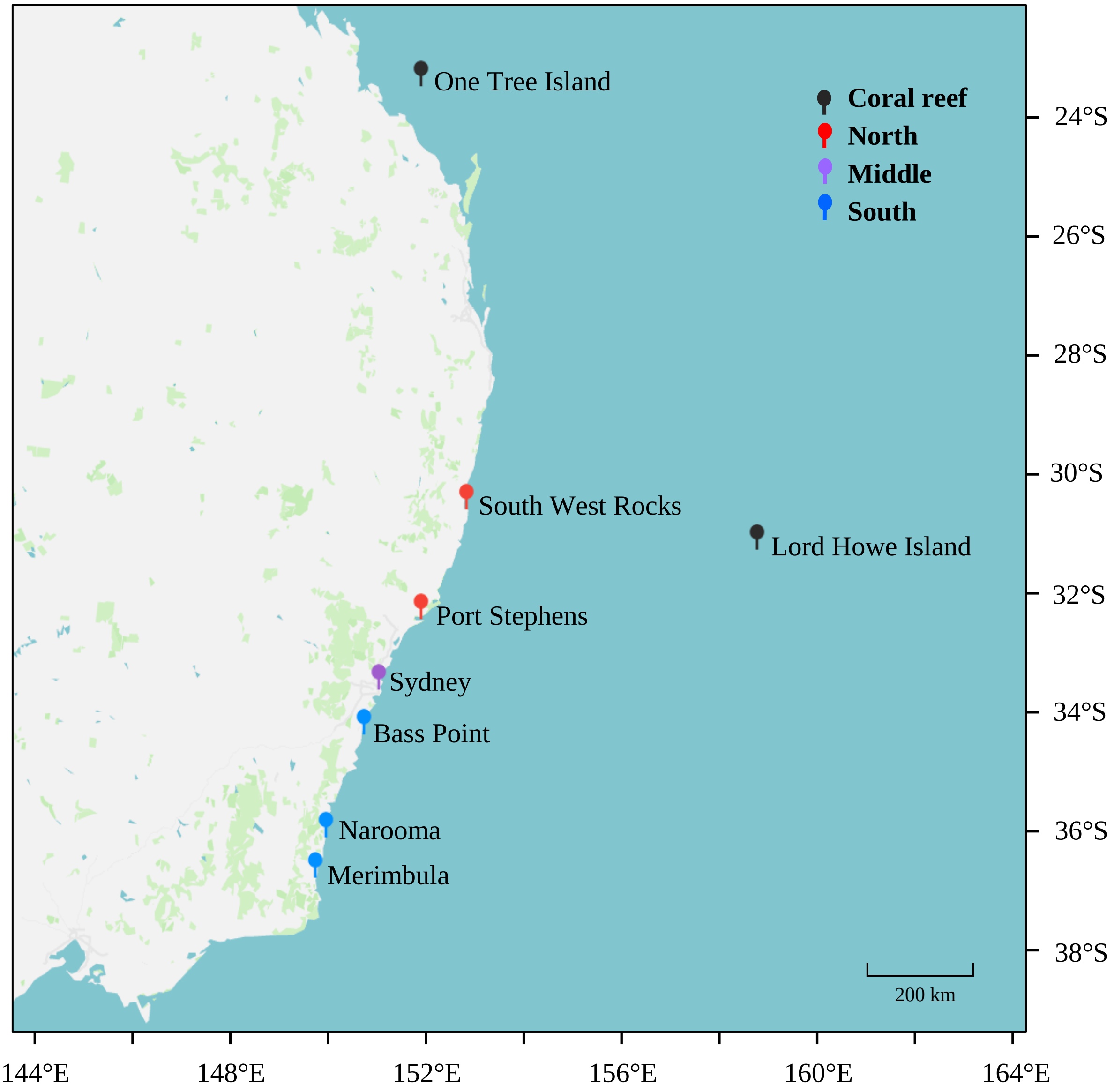

Fig. 2: Sample locations along the southeast coast of Australia, including South West Rocks (two sites; 30°52'34"S, 153°04'02"E and 30°53'00"S, 153°02'17"E) and Port Stephens (two sites; 32°42'56"S, 152°10'58"E and 32°44'55"S, 152°10'19"E) (included in region "North", red marker); Sydney (two sites; 33°42'07"S, 151°18'28"E and 33°47'44"S, 151°17'25"E) (included in region "Middle", purple marker); Bass Point (34°35'54"S, 150°53'18"E), Narooma (36°12'54"S, 150°07'51"E), and Merimbula (two sites; 36°44'13"S, 149°58'58"E and 36°53'40"S, 149°55'25"E) (included in region "South", blue marker); and One Tree Island (23°30'30"S, 152°05'30"E) and Lord Howe Island (31°33'15"S, 159°05'06"E) ("Coral reef", black marker). Tropical species were collected from study sites spanning 1,500 km (13˚ latitude), while temperate species were collected along 730 km (6˚ latitude) of coastline. Temperate species were not present at One Tree Island or Lord Howe Island.

Sample preparation

The scales and skin were removed from the right lateral side of each fish. After a thorough cleaning of the scalpel blade, a pea-sized piece of white muscle tissue, free of bone, organs, and scales, was removed and placed into a labelled tube, and immediately re-frozen. Stomachs and guts were removed and frozen separately for subsequent stomach content analysis, with the exception of stomachs collected in 2017, which were stored in 70% ethanol.

The fish tissue was freeze-dried for at least 36 hours to remove moisture. A small metal ball was then placed into each individual tube, and the tissue was ground into a fine powder using a ball mill. This ensured that the sample was homogeneous, and therefore representative of the organism's true δ^{15}N and δ^{13}C content (Eurich et al. 2019). Powdered samples were then weighed into tin capsules and analysed for stable isotope content using a Nu Instruments Nu Horizon Continuous Flow IRMA (CF-IRMA).

Stable Isotope Analysis (SIA)

Stable isotope analysis (SIA) can be used to estimate an individual's position in trophic space (Layman et al. 2007a), track migration routes (Hobson 1999), and assess shifts in diet (Phillips & Eldridge 2006). These questions can be answered by analysing the type and abundance of prey and associated carbon and nitrogen stable isotopes that have been incorporated into muscle tissue over the past few weeks or months (Fry 2006; Newsome et al. 2007; Fitzgerald et al. 2017). In this way, the accumulation and transformation of organic matter can be traced within a community over time (Fanelli et al. 2015). SIA utilises δ^{15}N, the ratio of ^{15}N:^{14}N, as an indicator of trophic position and δ^{13}C, the ratio of ^{13}C:^{12}C, as an indicator of what the individual's source of prey has been over the past few weeks or months (Cabana & Rasmussen 1994; Campbell et al. 2005; Newsome et al. 2007). δ^{15}N increases ~3.4‰ on average (Post 2002) at each trophic transfer due to nitrogen fractionation, with different prey items resulting in different fish tissue signatures (DeNiro & Epstein 1978; Checkley & Entzeroth 1985; McCutchan et al. 2003). δ^{13}C varies little between trophic levels (0-1‰), as carbon fractionation is primarily influenced by prey type (DeNiro & Epstein 1978; Post 2002; Newsome et al. 2007).

Here, stable isotope analysis was used to display the trophic niche of 1) temperature affinity groups, and 2) individual species in isotopic (δ^{15}N and δ^{13}C) space. At the affinity level, species were grouped into 'tropical' or 'temperate' affinities. Trophic niche areas of the two affinities and of individual species were calculated for each region (North, Middle, and South) using convex hulls in the rKIN package available in *R* (Albeke 2017). Individual fish were plotted in isotopic space (i.e. isospace) and a convex hull (100% of data points used) was created to encapsulate the data points for each species or affinity, depending on the analysis (Layman et al. 2007a; Syväranta et al. 2013). In addition to convex hulls, standard Bayesian ellipses (95% confidence interval of the bivariate means) were used to calculate the niche area (SEAc) of individual species using the *R* package SIBER (Jackson et al. 2011; Jackson et al. 2012; Jackson & Parnell 2019). Standard ellipses can correct for small sample size, such is the case for some of the species used in this study, making them a more suitable tool for individual species niche area analysis than convex hulls alone.

In addition to niche area, we also calculated the degree of overlap between niches. For overlap between affinities, percentages were calculated using convex hulls in the program rKIN (Albeke 2017), with overlap expressed as the percent that each species area is being overlapped. Affinity overlap percentages are from the perspective of the temperate species, as it is the temperate recipient community that is being invaded and is under investigation. For individual species, niche overlap was calculated using ellipses in the *R* package nicheROVER (Lysy, Stasko & Swanson 2014). Ten random elliptical projections were created for each species at each region based on posterior distribution. Overlap was then determined based on the probability of one species falling into the niche of another (Swanson et al. 2015). Because niches are not symmetrical**,** there are two possible values for each species pair, one for the percent probability that hypothetical group “X” is being overlapped by group “Y”, and the other for the percent probability that group “Y” is being overlapped by group “X”. For example, if a large ellipse was directly on top of a smaller ellipse in isospace, one could calculate the probability of overlap from the perspective of the large ellipse, e.g., 15% probability of overlap, whereas the overlap probability from the perspective of the small ellipse would be 100%. Niche areas which overlap by > 60% are thought to be sharing a significant amount of niche space (Schoener 1968; Wallace 1981; Guzzo et al. 2013). The niche range, or the maximum/minimum difference of both δ^{15}N and δ^{13}C values, was also calculated for each species, and then averaged across affinity for each region, to identify whether the fish are occupying a similar isotopic breadth across the regions.

Stomach Content Analysis

Stomach content analysis is used to provide direct evidence of prey items consumed in the hours leading up to the fish’s collection (Rybczynski et al. 2008). Stable isotope signatures provide a measure of where in δ^{15}N and δ^{13}C isospace fishes are situated, but stomach content analysis reveals on what taxa, and in what quantities, tropical and temperate fish are feeding (Svensson et al. 2017). Only stomachs collected in 2018 were used for stomach content analysis, due to disintegration of the 2017 stomachs that were stored in ethanol. As such, some species did not have a large enough regional sample size (e.g. *A. bengalensis* in the Middle and *C. auriga* in the North) to be used in diet analyses (stomach contents, Levins' index of niche breadth, and Pianka's index of diet overlap) in all regions. Only species with at least 3 replicate stomachs were included for the diet analyses. However, all species were still used in the isotopic niche analyses, as stable isotope data from both 2017 and 2018 were included.

The stomachs of all fish were emptied of their contents. Contents that were too digested to be distinguished, as well as gastric juices, were excluded from analysis. Food items were divided into broad categories, including algae, seagrass, crustaceans, worms, gastropods, eggs, zooplankton, detritus, hydroids, fish larvae, parasites, nudibranchs, and terrestrial insects and seeds (Layman et al. 2007b). For example, both fleshy green algae and branching red algae were grouped into the broad category 'algae'. If a stomach was composed of 10% zooplankton, 10% algae, 30% gastric juice, and 50% unknown matter, it would be classified as containing 50% zooplankton and 50% algae to standardise diets solely based on identifiable prey items consumed. The prey categories in the stomachs of each species were averaged for each region to calculate diet overlap among species and across regions using Pianka's index (Pianka 1973). Pianka's diet overlap is calculated using the following equation:

(Equation 1)

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where:

O_{jk} = Pianka's index of diet overlap between species *j* and species *k*
p_{ij} = proportion resource *i* is of the total resources used by species *j*
p_{ik} = proportion resource *i* is of the total resources used by species *k*
n = total number of resource states

Pianka's values range from 0-1, with 0 indicating total segregation, and 1 indicating total diet overlap (Vieira & Port 2007). Similar to isotope niche overlap, Pianka's values > 0.6 are considered to represent a significant diet overlap (Zaret & Rand 1971; Wathne, Haug & Lydersen 2000). Statistical analyses were performed by grouping Pianka's values into either intra-affinity overlap (tropical-tropical or temperate-temperate), or inter-affinity overlap (tropical-temperate). ANOVA was then performed to test if there was a significant difference in overlap between each of these three groups. As such, ANOVA only had region (North, Middle, South) and affinity group (tropical-tropical, temperate-temperate, and tropical-temperate) as factors.

Niche breadth represents the range of resources that a species uses (Slatyer, Hirst & Sexton 2013) and can be used to determine feeding strategies, and separate species into specialists or generalists. Niche breadth was calculated using Levins' method (Levins 1968) and standardized using Hurlbert's method (Hurlbert 1978). Levins' standardized niche breadth equation is as follows:

(Equation 2)

$$B_A = \frac{\frac{1}{\sum p_j^2} - 1}{n - 1}$$

where:

B_A = Levins' standardized niche breadth
p_j = proportion of individuals using resource state j
j = resource state
n = number of possible resource states

Levin's standardized index produces niche breadths ranging in value from 0-1, with species exhibiting a value < 0.3 considered to be specialists and values of 0.3-1 considered to be generalists (Novakowski, Hahn & Fugi 2008; Nagelkerken et al. 2009; Sa-Oliveira, Angelini & Isaac-Nahum 2014). A food specialist consumes a narrow range of food sources, while a generalist consumes a wide variety of food sources (Amundsen, Gabler & Staldvik 1996). Note that Levins' index does not take into account the possibility of variation in resource abundance and availability.

Statistical analyses

Statistical analyses were performed using the program Primer-e, except the isospace niche areas and overlap analyses which were calculated using the packages rKIN and nicheROVER available in *R* (Lysy, Stasko & Swanson 2014; Albeke 2017). Analysis of variance (ANOVA – type III error) was used to test the effects of region ("Re"; North, Middle, South; fixed factor), affinity ("Af"; tropical, temperate; fixed factor), and species ("Sp"; 18 species for isotope statistics, and 7 species for all other analyses; random factor) on niche space. All analyses were performed on fourth root transformed data, and used either Bray-Curtis or Euclidian resemblance matrices. All residuals were permutated under a reduced model. Where significant differences were found, pairwise tests were used to determine which treatments differed. Because the factor 'species' is nested within factor 'affinity', *post-hoc* tests of any significant Re × Sp (Af) interactions yielded only intra-affinity comparisons, e.g., how a particular tropical species differed across regions, or how a temperate species in the North differed from other temperate species in the North. As such, Re × Sp (Af) *post-hoc* results are not useful in investigating dynamics between tropical and temperate affinities, only changes within each affinity.

Results

Niche segregation

Trophic niches of tropical and temperate species were largely segregated (despite their co-schooling *in situ*), irrespective of latitude (Figs. 1a, 3). The niche convex hulls showed that overlap between tropical and temperate niche space was minimal (28.4% in the North, 8.8% in the Middle, 15.5% in the South). The negligible overlap between tropical and temperate species was driven primarily by tropical *Abudefduf* species overlapping with temperate sea chubs (*Microcanthus strigatus* and/or *Atypichthys strigatus*) in the North and Middle, with *Chaetodon* species also overlapping temperature niche space in the South, respectively, and a combination of all temperate species in the Middle (Fig. S1). In total, only four tropical-temperate species pairs out of a possible 37 combinations exhibited overlap greater than 60%, above which overlap is considered to be significant (Table S3). In the North, the trophic niche of tropical species *A. bengalensis* was overlapped by *M. strigatus* 67.5%, yet none of the trophic niches of temperate species were overlapped significantly by tropical species. In the Middle, temperate species *Parma microlepis* was overlapped by tropical species *Chaetodon auriga*

(69.7%), but no tropical species was overlapped significantly by a temperate species. In the South, temperate species *A. strigatus* overlapped tropical species *A. sexfasciatus* (76.9%) and *C. flavirostris* (98.9%), but similar to the North, no temperate species was significantly overlapped by a tropical species. The considerable overlap between *A. sexfasciatus* and *A. strigatus* in the South is particularly notable because they are known to co-school. Unsurprisingly, species exhibited considerable overlap with other species of the same affinity (i.e. tropical species overlapping with other tropical species), regardless of region. The niche segregation between affinity groups was caused by temperate species having consistently higher $\delta^{15}N$ values (indicative of feeding at a higher trophic level; Fig. 3) than tropical species (3-way ANOVA, $p < 0.001$), but $\delta^{13}C$ values did not differ ($p = 0.077$; Table S4a).

Pianka's index of diet overlap between tropical and temperate species affinities did not exceed 0.6 in any region, the value above which overlap is considered significant (Fig. S3). Diet overlap between species with tropical and temperate affinities was similar to the intra-tropical and intra-temperate dietary overlap (Pianka's index, 2-way ANOVA, $p = 0.620$; Table S4a; Fig. S3), indicating that affinity did not affect diet overlap. In contrast to isotope niche area and Pianka's diet overlap, tropical and temperate species affinities had similar diet compositions (3-way ANOVA, $p = 0.538$; Table S4a; Fig. 4).

Niche range (i.e. maximum minus minimum values) of trophic levels ($\delta^{15}N$; 3-way ANOVA, $p = 0.762$) and of prey origin ($\delta^{13}C$; $p = 0.098$) did not differ between tropical and temperate fishes, indicating that they feed within similar isotopic boundaries (Table S4a; Fig. S4). Species with tropical and temperate affinities had similarly moderately-broad niche breadths (Levins' index, 3-way ANOVA, $p = 0.455$; Table S4a; Fig. 5) with most species-location combinations showing an index of > 0.3 (Fig. S5), indicative of trophic generalism.

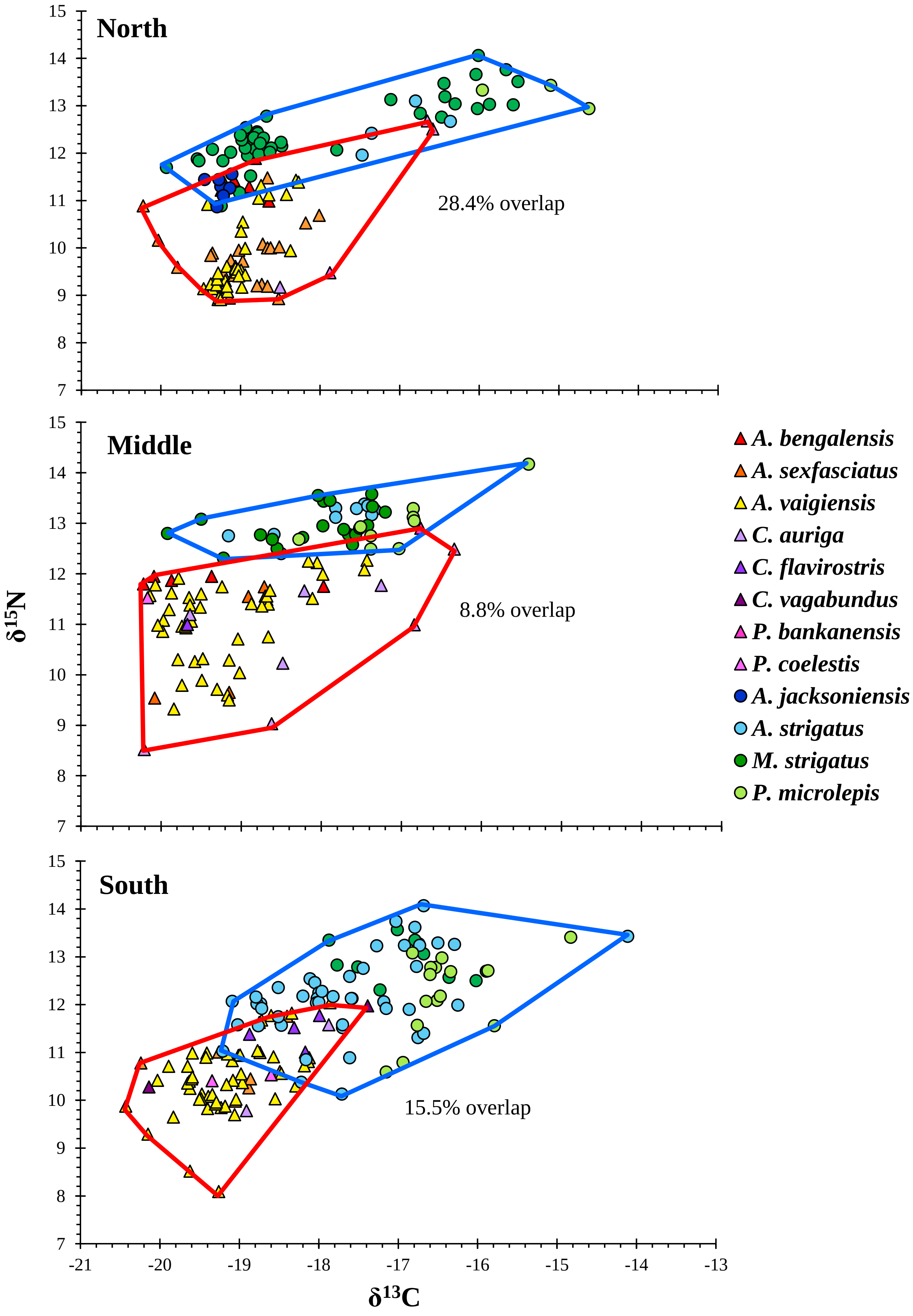
North
28.4% overlap
Middle
8.8% overlap
South
15.5% overlap
δ15N
δ13C
15
14
13
12
11
10
9
8
7
-21
-20
-19
-18
-17
-16
-15
-14
-13
A. bengalensis
A. sexfasciatus
A. vaigiensis
C. auriga
C. flavirostris
C. vagabundus
P. bankanensis
P. coelestis
A. jacksoniensis
A. strigatus
M. strigatus
P. microlepis

Fig. 3: Trophic niche of tropical and temperate affinity groups, displayed in $\delta^{15}N$ and $\delta^{13}C$ space for North, Middle, and South regions (see Fig. 2) based on convex hulls. Tropical fish are indicated with triangles, and temperate fish are indicated with circles. Each marker represents a single fish, and polygons represent convex hulls that encapsulate 100% of data points. The percentage of the temperate niche that is being overlapped by the tropical niche is shown for each region. Percent overlap was calculated using the rKIN package available in *R*. See Fig. S6 for the total niche area size of these convex hulls, and Fig. S1 for standard ellipses of individual species.

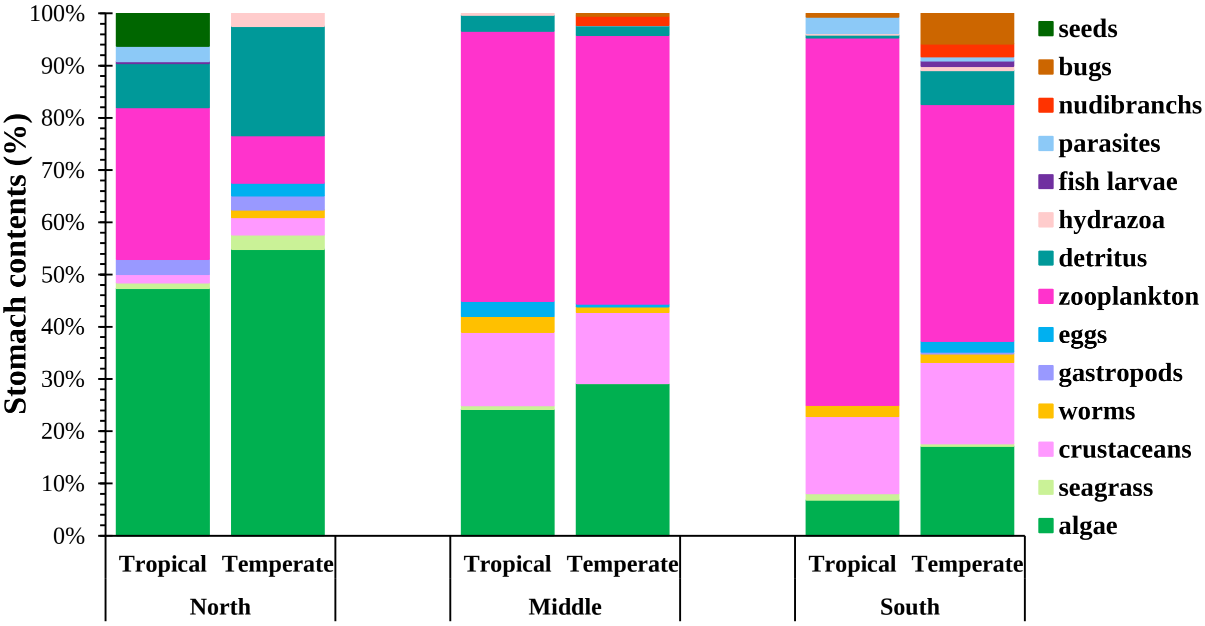

Fig. 4: Proportional stomach contents averaged for fish species within tropical and temperate affinity groups in North, Middle, and South regions from fish collected in 2018. Stomach gastric juice was excluded, as was partially-digested, unidentifiable food. The remaining food items were scaled up to 100%. Affinity means were calculated based on the species means in each region. Algae, seagrass, crustaceans, worms, and gastropods are broad groups and may contain multiple families within the taxa. See Fig. S7 for the stomach contents of individual species.

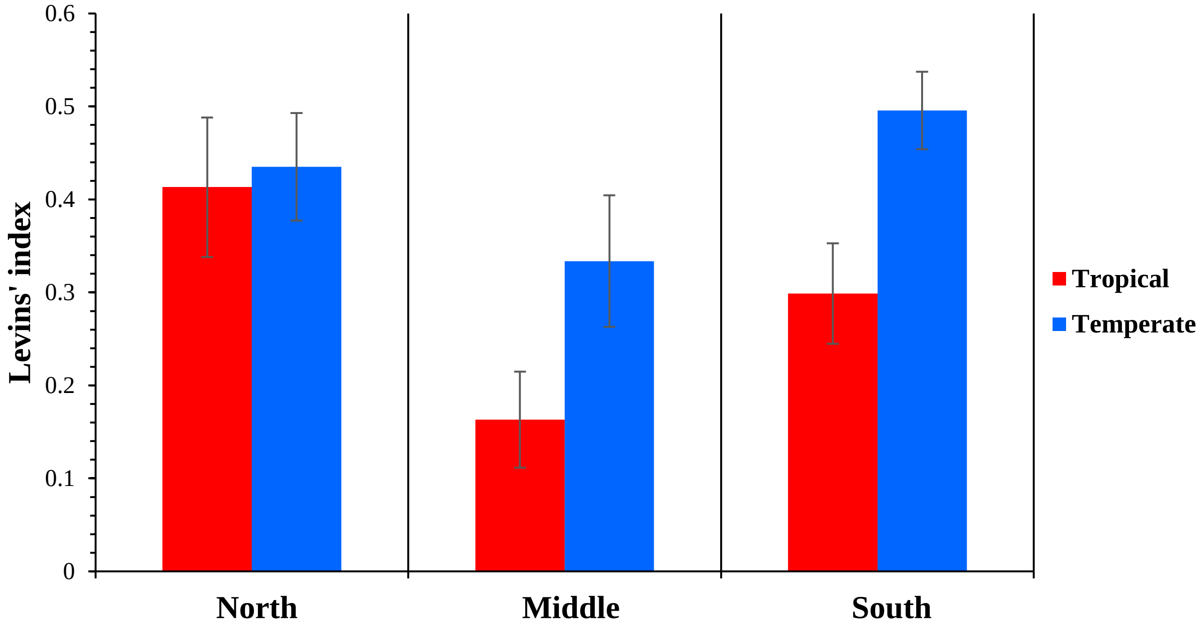

Fig. 5: Mean (± SE) Levins' index of niche breadth (ranging from 0 to 1) for tropical and temperate species across regions. A low value indicates that a species has a very small niche breadth and is a specialist, and higher values (> 0.3) indicate broad niche breadth, or generalism. Affinity values were calculated using species means at each region. See Fig. S5 for the niche breadths of individual species.

Niche expansion/contraction

When grouped into affinities, tropical species had the largest niche in the tropics (One Tree Island, southern Great Barrier Reef; Figs. 1d, S2, S6a); likewise, the largest temperate species niche area was found at the coldest location (i.e. highest latitude sampled). In the regions where tropical and temperate species geographically overlap (North, Middle, and South), tropical species had the largest niche area where temperate species had their lowest (Middle), with tropical species exhibiting a niche area nearly three times the size of the temperate niche area (10.5 vs 3.8, Fig. S6a). Similarly, temperate species exhibited their largest niche area where tropical species exhibited their smallest (South), with the temperate niche almost double the size of the tropical niche (10.9 vs 5.8). When examining species individually (using either convex hulls or standard ellipses), affinity-level patterns were less discernible, although temperate species continued to have a large niche area in the South and several tropical species a large area in the Middle (Figs. S6b, c). The considerable dichotomy in mean tropical and temperate affinity niche areas in the Middle is primarily due to the large niche areas of tropical species *C. auriga* and *A. vaigiensis* (and *A. sexfasciatus* when using standard ellipses) and the small niche areas of all temperate species, particularly *A. strigatus*. Both trophic level (δ^{15}N; 3-way ANOVA, $p < 0.001$) and prey origin (δ^{13}C; 3-way ANOVA, $p < 0.001$) signatures differed regionally, with signatures in the tropics being lower in δ^{15}N and higher in δ^{13}C than all other regions, suggesting that coral reef fishes were consuming isotopically-different prey items from the far north to the South (Tables S4a, b; Fig. S2a). However, the niche range of δ^{15}N (3-way ANOVA, $p = 0.624$) and δ^{13}C ($p = 0.645$) did not differ between regions for either tropical or temperate species (Table S4a; Fig. S4).

Tropical and temperate fish consumed primarily algae, zooplankton, and crustaceans, and overall decreased their consumption of algae and increased their consumption of zooplankton and crustaceans as a function of increasing latitude, i.e. from North to South (Figs. 4, S7; Table S4a). All tropical species had different diet compositions between the latitude extremes (North and South), with one species (*A. vaigiensis*) also differing between North and Middle regions. Only one temperate species *(M. strigatus)* had a different diet composition between the latitude extremes, yet all differed between the Middle and South regions (Fig. S7; Table S4b). Additionally, temperate species decreased the number of food items consumed from the highest latitude (South: 13 items) to the two lower latitudes (North/Middle: 9 and 10, respectively), but tropical species ate a similar number of food items across all three latitudes (9, 8, 9, respectively) (Fig. 4). Neither diet overlap (Pianka's index, 2-way ANOVA, $p = 0.702$; Fig. S3) nor niche breadth (Levins' index, 3-way ANOVA, $p = 0.917$; Fig. 5) varied among regions for temperate or tropical species affinity groups. On the individual species level, the tropical species *A. vaigiensis* and the temperate species *M. strigatus* varied in niche breadth between regions (Fig. S5; Table S4b).

Discussion

Here we show that the novel co-existence of range-extending tropical and local temperate species in temperate ecosystems under climate change is facilitated by trophic niche segregation (see conceptual diagram Fig. 1a). On average, temperate species had consistently higher δ^{15}N values than tropical species in all regions, indicating that temperate species are consuming food sources that are higher up the food chain than the tropical species they co-occur with. Some individual species exhibited some degree of isotopic niche overlap, although only four out of 37 tropical-temperate species combinations exhibited an overlap in niche space of > 60%, above which overlap is considered to be significant. Similarly, there was a low degree of overlap in stomach contents between tropical and temperate species (i.e., based on

Pianka's index < 0.6) in all regions. In contrast, stomach content composition revealed that species of different affinities were foraging on broadly similar prey groups. This similarity in prey groups is likely due to the low resolution of prey identification from stomachs (e.g. broad categories like 'crustaceans' and 'algae'), which may not reflect taxonomic differences in prey species within broader groups consumed. Previous studies have demonstrated that minor prey items (which might not be significantly reflected within bulk stable isotope signatures) can be of great importance in facilitating species co-existence (Nagelkerken et al. 2009; Koussoroplis et al. 2010), and that co-existence can occur between species even when there is no apparent partitioning of food resources (Pratchett 2005). Nevertheless, niche segregation (based on isotopic niche space and Pianka's dietary overlap) was observed across all latitudes studied and indicates that tropical and temperate fishes are therefore less likely to compete for the same prey resources at the initial phases of range-extensions in a warming ocean.

The fishes studied here consumed a wide range of prey groups (8-13 per region), suggesting that they are generalists (Roper 1994). Additionally, affinities exhibited moderately-broad niche breadths (based on Levins' index of > 0.3) across regions, which further indicates a certain degree of trophic generalism (Hurlbert 1978; Devictor et al. 2010; Sa-Oliveira, Angelini & Isaac-Nahum 2014). Generalistic feeding strategies are known to play an important role in spatial partitioning and co-existence among species by minimizing competition for trophic space (e.g. pomacentrid fishes) (Eurich et al. 2019). Generalists are thought to have an advantage over specialists, as they are able to consume a wider array of food sources and are therefore better equipped to deal with food shortages (Wilson et al. 2008; Clavel, Julliard & Devictor 2011). Additionally, generalists are thought to be less vulnerable to climate change as they have higher trophic niche plasticity and may be better able to accommodate changes in resource availability and habitat (Travis 2003; Slatyer, Hirst & Sexton 2013; Sunday et al. 2015; Afonso Silva et al. 2017). As such, trophic generalists, such as the tropical vagrants and temperate locals that were examined in this study and are known to frequently co-occur or school together under increasing ocean warming (Smith et al. 2018), will likely be the most successful feeding strategists, or "winners", under future climate change (Warren et al. 2001; Wilson et al. 2008; Ho et al. 2009). Our findings therefore provide strong support that trophic generalism is mediating the co-existence of tropical fishes with various local species in temperate waters under ongoing global warming.

Across broad spatial scales (from tropical coral reefs to temperate kelp systems), tropical fishes exhibited a niche contraction with increasing latitude (as per Fig. 1d), whilst at smaller spatial scales (i.e. within their novel temperate ranges) they showed niche expansion where local species experienced niche contraction. In the regions where species of both affinities co-occurred, tropical species exhibited their largest niche area in the region where the temperate niche area was the smallest, and vice versa. This suggests that tropical and temperate fish may be unable to maintain large trophic niches simultaneously, although this may simply be an artefact of small and unequal sample sizes. Previous studies have suggested that an expanding niche area may be a result of ecological release, or a sudden population increase due to the disappearance of limiting factors (Svanbäck & Bolnick 2007; Bolnick et al. 2010), while others posit that an expansion of niche area may be due to competition (Schulter, Price & Grant 1985; Namgail et al. 2009). In the case of competition, a narrow niche may prove harmful for the local temperate fish, as a previous study has shown that a small niche area and high overlap with non-native species can lead to a decline in native fish populations in a freshwater lake (Córdova-Tapia, Contreras & Zambrano 2015). A study of marine snails living along their range edge showed that thermal stress, as is possibly experienced by our tropical species in the South (cool water) and temperate species in the North (warm water), led to increased diet variation and therefore trophic niche expansion (Reddin, O'Connor & Harrod 2016), highlighting the effect that range edges may have on feeding plasticity. Our findings highlight that species that extend their ranges from coral reefs with high prey diversity to less-diverse temperate areas may need to adjust to novel environments by contracting their trophic niche. However, on smaller spatial scales local (a)biotic conditions may alter trophic dynamics and lead to opposite outcomes in terms of niche expansion versus niche contraction. These initially variable and plastic dynamics at the leading edges of range extensions are typical of species invading new environments (irrespective of climate change) (Broennimann et al. 2007; Michel & Knouft 2012; Fernández & Hamilton 2015), but as oceans continue to warm such spatial refuges where local species can resist invasion are likely to slowly disappear with more definite outcomes in terms of which species will become winners versus losers under climate change (Moyle & Light 1996; Byers 2002; Hellmann et al. 2008).

It is important to note that stable isotope signatures may be confounded by environmental stressors unrelated to changes in diet, potentially leading to inaccurate depictions of trophic niche space (Karlson et al. 2018). A study of freshwater snails showed that high temperatures, such as those experienced by temperate species along their trailing range edge, may enrich δ^{15}N and δ^{13}C values (Ek et al. 2015). Other factors that may contribute to differential incorporation of stable isotopes include body size, growth rate, and protein turnover (Martínez del Rio et al. 2009). Because tropical species are not yet established in the southern study sites, fish were caught opportunistically, making it difficult to control for body size. Temperature extremes may affect metabolic rate (Clarke & Johnston 1999; Gillooly et al. 2001), causing altered stable isotope tissue incorporation to increase for reasons unrelated to food intake (Carleton & Rio 2005). For these reasons, other factors might have also partially contributed to some of the variability in trophic niche segregation as displayed by our study species.

Conclusions

How tropical and temperate species fill and share trophic niches within novel mixed communities resulting from global change is a key determinant of future species persistence and biodiversity. We demonstrate that range-extending tropical and local temperate fish species exhibit segregated trophic niches, mediated by trophic generalism and local-scale dietary plasticity. We conclude that range-expanding species adjust their trophic niches at their leading edges and occupy open niche space thereby avoiding significant dietary overlap with local species, despite operating under suboptimal environmental and biotic conditions that are characteristic of novel ranges at the initial stages of climate change.

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Supplementary Information

Table S1: Details of (**a**) the sample size (*n*) of each species collected as well as their mean *in situ* density (den) per 1000 m^2 at One Tree Island, Lord Howe Island, South West Rocks, Port Stephens, Sydney, Bass Point, Narooma, and Merimbula based on multiple fish surveys (as per Beck et al. 2014) conducted during the approximate time as the fish collections (February, March, and April of 2017 and 2018); (**b**) mean fish length (L in cm) and weight (W in g). Location abbreviations: One Tree Island (OTI) and Lord Howe Island (LHI) (Coral reef); South West Rocks (SWR) and Port Stephens (PS) (North region); Sydney (SYD) (Middle region); and Bass Point (BP), Narooma (NAR), and Merimbula (MER) (South region). If surveys were not performed at a particular site, species densities are not provided (i.e. empty rows). Tropical species include *Abudefduf bengalensis*, *A. sexfasciatus*, *A. vaigiensis*, *Chrysiptera bronwnriggii*, *Chaetodon auriga*, *C. citrinellus*, *C. flavirostris*, *C. kleinii*, *C. rainfordi*, *C. tricinctus*, *C. vagabundus*, *Dascyllus aruanus*, *Pomacentrus bankanensis*, *P. coelestis*, and *P. moluccensis*. Temperate species include *Ambassis jacksoniensis*, *Atypichthys strigatus*, *Microcanthus strigatus*, and *Parma microlepis*.

(a)

Species	**OTI**		**LHI**		**SWR**		**PS**		**SYD**		**BP**		**NAR**		**MER**	
	n	den	*n*	den	*n*	den	*n*	den	*n*	den	*n*	den	*n*	den	*n*	den
A. bengalensis	1				5	12.5		9.5	5	0				0		0.5
A. sexfasciatus	5		12		18	279	4	5.9	4	1.2	2		1	12.8	6	1.8
A. vaigiensis	1		1		25	504	10	149	43	40.1	9		11	116	29	6.0
C. brownriggii			12			0		0		0				0		0
C. auriga	1		7			7.3	3	6.5	8	0.4				3.2	2	1.1
C. citrinellus			1			12.7		4.7		0.3				0		0
C. flavirostris	1		3			89.2		9.5	1	0.2				0	4	1.0
C. kleinii			1			6.7		4.7		0				0		0
C. rainfordi	1					0		0		0				0		0
C. tricinctus			4			0		0		0				0		0
C. vagabundus	6					12.7		0		0.1				0	2	0.1
D. aruanus	4					0		0		0				0		0
P. bankanensis						9.3		0	1	0.2				0		0
P. coelestis	10					3.8	1	0	1	1.3			1	0	1	0.4
P. moluccensis	8					0		0		0				0		0
A. jacksoniensis					7	0		0		0				0		0
A. strigatus						340	4	62.6	10	0	5		13	1897	28	0
M. strigatus					33	166	13	149	20	0	4		7	436		1.9
P. microlepis						9.6	3	12.6	9	0	1			49.5	14	0

(b)

Species	**OTI**		**LHI**		**SWR**		**PS**		**SYD**		**BP**		**NAR**		**MER**	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
A. bengalensis	5.7	3.6			11	82			3.8	1.7						
A. sexfasciatus	3.6	0.8	1.9	0.6	2.7	2.4	2.2	0.4	2.4	0.8	2.3	0.8	3.0	1.1	2.2	0.5
A. vaigiensis	4.4	1.5	n/a	2.6	2.5	1.5	2.8	0.7	2.7	1.4	2.4	0.6	2.0	0.4	2.2	0.6
C. brownriggii			2.1	0.6												
C. auriga	3.5	1.2	4.9	3.1			2.9	1.2	2.9	1.4					3.6	0.9
C. citrinellus			3.8	1.6												
C. flavirostris	3.5	1.8	4.0	3.3					2.4	0.5	4.7	4.3			3.5	1.4
C. kleinii			3.9	1.6												
C. rainfordi	3.1	1.1														
C. tricinctus			3.6	1.8												
C. vagabundus	3.7	0.9													2.8	0.7
D. aruanus	3.1	1.1														
P. bankanensis									4.1	3.1						
P. coelestis	3.4	0.7					2.2	0.4	4.1	1.4			2.9	0.8	2.5	0.3
P. moluccensis	2.2	0.3														
A. jacksoniensis					2.7	0.3										
A. strigatus							4.6	2.4	4.3	2.5	3.6	0.8	4.8	4.0	3.4	0.9
M. strigatus					4.4	4.2	4.3	4.8	4.4	2.8	5.2	3.8	5.2	6.6		
P. microlepis							4.7	4.6	5.1	5.6	4.8	6.5			3.9	3.3

Table S2: Seasonal presence at temperate locations of tropical species used in this study, acquired through underwater surveys conducted from 2003-2017. Values are based on the numbers of years that each species was observed during that season's surveys divided by the total number of years that surveys were conducted during that season, and are expressed as a percentage (%). sum = summer, aut = autumn, win = winter, spr = spring. T_{peak} is the temperate (°C) observed at the peak of species abundance, with lower values suggesting higher cold tolerance (Booth et al. 2018). The mean winter temperature of Sydney (SYD) and Merimbula (MER) are 19.3 °C and 16.9 °C, respectively, and are based on of sea surface temperatures acquired from NOAA. N/A = not available.

	T_{peak} (°C)	**Sydney %**				**Merimbula %**			
		sum	aut	win	spr	sum	aut	win	spr
		☀	🍃	❄	✿	☀	🍃	❄	✿
A. bengalensis	22.4	94	94	69	25	47	73	0	0
A. sexfasciatus	22.5	100	100	62	0	54	55	0	11
A. vaigiensis	21.8	100	100	92	50	100	90	0	22
C. brownriggii	N/A	0	0	0	0	0	0	0	0
C. auriga	21.6	88	100	15	0	100	90	0	11
C. citrinellus	21.0	63	69	8	0	27	27	0	0
C. flavirostris	21.6	100	88	8	0	80	73	0	11
C. kleinii	N/A	0	0	0	0	0	0	0	0
C. rainfordi	N/A	0	0	0	0	0	0	0	0
C. tricinctus	N/A	0	6	0	0	27	0	0	0
C. vagabundus	N/A	44	38	8	0	60	55	0	0
D. aruanus	N/A	0	0	0	0	0	0	0	0
P. bankanensis	23.9	63	81	0	0	0	0	0	0
P. coelestis	22.2	100	94	54	0	73	36	0	0
P. moluccensis	N/A	0	0	0	0	0	0	0	0

Table S3: Niche area overlap between individual species pairs for North, Middle, and South regions based on ellipses, calculated using the nicheROVER package available in *R*. Overlap is defined as the probability of one species falling into the niche of another (Swanson et al. 2015). There are two overlap values for each species pair; one indicating the percent probability that the niche of the species in the column is being overlapped by the species in the row, and vice versa. For example, in the North, there is a 4.6% probability that *A. sexfasciatus* has its niche overlapped by *A. bengalensis*, yet a probability of 40.6% that *A. bengalensis* will have its trophic niche overlapped by *A. sexfasciatus*. N/A is displayed where a species is paired with itself. Values in **bold** represent niche overlap between tropical and temperate species of > 60%, above which overlap is generally considered to be significant (Schoener 1968; Wallace 1981; Guzzo et al. 2013).

		Tropical fishes					Temperate fishes			
		A. bengalensis	*A. sexfasciatus*	*A. vaigiensis*	*C. flavirostris*	*C. auriga*	*M. strigatus*	*A. strigatus*	*P. microlepis*	*A. jacksoniensis*
North	*A. bengalensis*	N/A	40.6	51.7		0.1	**67.5**	3.0	0	24.7
	A. sexfasciatus	4.6	N/A	62.7		5.2	2.3	0.7	0	2.0
	A. vaigiensis	10.1	88.7	N/A		0.7	4.1	1.2	0	1.3
	C. auriga	0.1	21.1	1.2		N/A	25.4	26.1	4.0	0
	M. strigatus	9.0	2.2	3.2		3.7	N/A	24.1	4.3	3.0
	A. strigatus	0.6	0.7	0.8		17.1	86.2	N/A	4.0	0.1
	P. microlepis	0	0	0		3.9	41.7	8.7	N/A	0
	A. jacksoniensis	58.3	49.7	14.3		0	71.9	1.6	0	N/A
Middle	*A. bengalensis*	N/A	32.1	77.0		42.4	4.6	1.2	11.6	
	A. sexfasciatus	4.7	N/A	83.9		86.6	8.7	4.1	8.0	
	A. vaigiensis	8.2	60.5	N/A		78.6	8.5	3.3	8.4	
	C. auriga	2.3	27.2	44.7		N/A	5.8	1.9	8.5	
	M. strigatus	0.5	23.0	34.7		42.2	N/A	59	41.6	
	A. strigatus	0.2	24.3	30.1		41.1	94.6	N/A	41.8	
	P. microlepis	1.6	12	19.1		**69.7**	67.5	22.9	N/A	
South	*A. sexfasciatus*		N/A	88.5	23.5		0.3	**76.9**	3.3	
	A. vaigiensis		74.5	N/A	17.3		0.4	58.4	0.9	
	C. flavirostris		73.7	85.3	N/A		1.4	**98.9**	8.9	
	M. strigatus		0.4	0.3	0.9		N/A	94.7	62.4	
	A. strigatus		23	27.2	19.2		35.8	N/A	39.2	
	P. microlepis		2.6	0.7	2.3		47.3	83.6	N/A	

Table S4: Results of analysis of variance (ANOVA) tests. Factors include region (Re), affinity (Af), and species (Sp), where species is a random factor and nested within affinity. Diet overlap is only based on two factors as it compares overlap between affinity groups (tropical-tropical, temperate-temperate, and tropical-temperate). Analyses were performed using either Bray-Curtis or Euclidian resemblances. Analyses were univariate or multivariate*. Significant effects are indicated in **bold**. *Post-hoc*† tests are shown (b).

(a) ANOVA/MAVOVA results

Factors	**df**	**MS**	***F***	***P***
†*$\delta^{15}N$ isotopes*				
Re	4	21.89	24.48	**0.001**
Af	1	55.45	28.97	**0.001**
Sp (Af)	17	2.080	2.150	**0.032**
Re × Af	2	0.955	0.897	0.421
Re × Sp (Af)	21	1.179	2.310	**0.001**
†*$\delta^{13}C$ isotopes*				
Re	4	47.46	25.04	**0.001**
Af	1	21.04	3.497	0.077
Sp (Af)	17	6.725	3.182	**0.004**
Re × Af	2	0.470	0.195	0.824
Re × Sp (Af)	21	2.747	3.674	**0.001**
$\delta^{15}N$ range				
Re	2	0.895	0.497	0.624
Af	1	0.169	0.102	0.762
Sp (Af)	8	1.679	0.933	0.533
Re × Af	2	1.611	0.896	0.442
$\delta^{13}C$ range				
Re	2	0.866	0.460	0.645
Af	1	3.692	9.754	0.098
Sp (Af)	8	0.607	0.323	0.937
Re × Af	2	1.014	0.539	0.601
*†*Stomach contents*				
Re	2	8380	1.336	0.317
Af	1	5147	0.789	0.538
Sp (Af)	5	8194	4.939	**0.001**
Re × Af	2	5351	0.853	0.536
Re × Sp (Af)	5	6802	4.100	**0.001**
Diet overlap (Pianka's index)				
Re	2	74.43	0.226	0.702
Af groups	2	113.3	0.344	0.620
Re × Af groups	4	155.6	0.473	0.539
†*Niche breadth (Levins' index)*				
Re	2	0.012	0.086	0.917
Af	1	0.092	0.818	0.455
Sp (Af)	5	0.131	2.318	0.061
Re × Af	2	0.100	0.748	0.535

Re × Sp (Af)	5	0.142	2.329	**0.039**

(b) [†]***Post-hoc* pairwise tests.**

i. $\delta^{15}N$ and $\delta^{13}C$ ANOVA, within factor ‘region’.

	$\delta^{15}N$		$\delta^{13}C$	
Group	**t**	***P***	**t**	***P***
North, Middle	1.259	0.266	2.937	**0.030**
North, South	0.605	0.584	1.057	0.368
North, Lord Howe Island	2.708	**0.016**	10.51	**0.003**
North, One Tree Island	5.102	**0.001**	4.073	**0.002**
Middle, South	0.756	0.496	2.985	**0.018**
Middle, Lord Howe Island	5.627	**0.001**	8.173	**0.001**
Middle, One Tree Island	6.437	**0.001**	7.636	**0.001**
South, Lord Howe Island	5.645	**0.002**	8.413	**0.001**
South, One Tree Island	7.996	**0.001**	4.614	**0.002**
Lord Howe Island, One Tree Island	4.419	**0.005**	2.974	**0.015**

ii. Stomach content and niche breadth ANOVA; within Re × Sp (Af) ‘region’.

		Stomach contents		**Niche breadth**	
Level	**Group**	**t**	***P***	**t**	***P***
Tropical	*A. bengalensis*				
	North, Middle	No test	No test	No test	No test
	North, South	No test	No test	No test	No test
	Middle, South	No test	No test	No test	No test
	A. sexfasciatus				
	North, Middle	0.524	0.699	0.378	0.712
	North, South	2.777	**0.014**	1.574	0.147
	Middle, South	2.074	0.085	1.754	0.129
	A. vaigiensis				
	North, Middle	1.863	**0.044**	1.67	0.104
	North, South	3.624	**0.001**	0.223	0.821
	Middle, South	1.448	0.123	2.256	**0.028**
	C. auriga				
	North, Middle	No test	No test	No test	No test
	North, South	No test	No test	No test	No test
	Middle, South	No test	No test	No test	No test
Temperate	*M. strigatus*				
	North, Middle	6.144	**0.001**	2.483	**0.016**
	North, South	1.631	**0.049**	0.857	0.399
	Middle, South	2.576	**0.007**	2.745	**0.014**
	A. strigatus				
	North, Middle	No test	No test	No test	No test
	North, South	No test	No test	No test	No test
	Middle, South	1.642	**0.044**	0.659	0.518
	P. microlepis				
	North, Middle	1.992	**0.033**	0.029	0.975
	North, South	1.407	0.125	0.760	0.459
	Middle, South	0.031	**0.031**	1.041	0.305

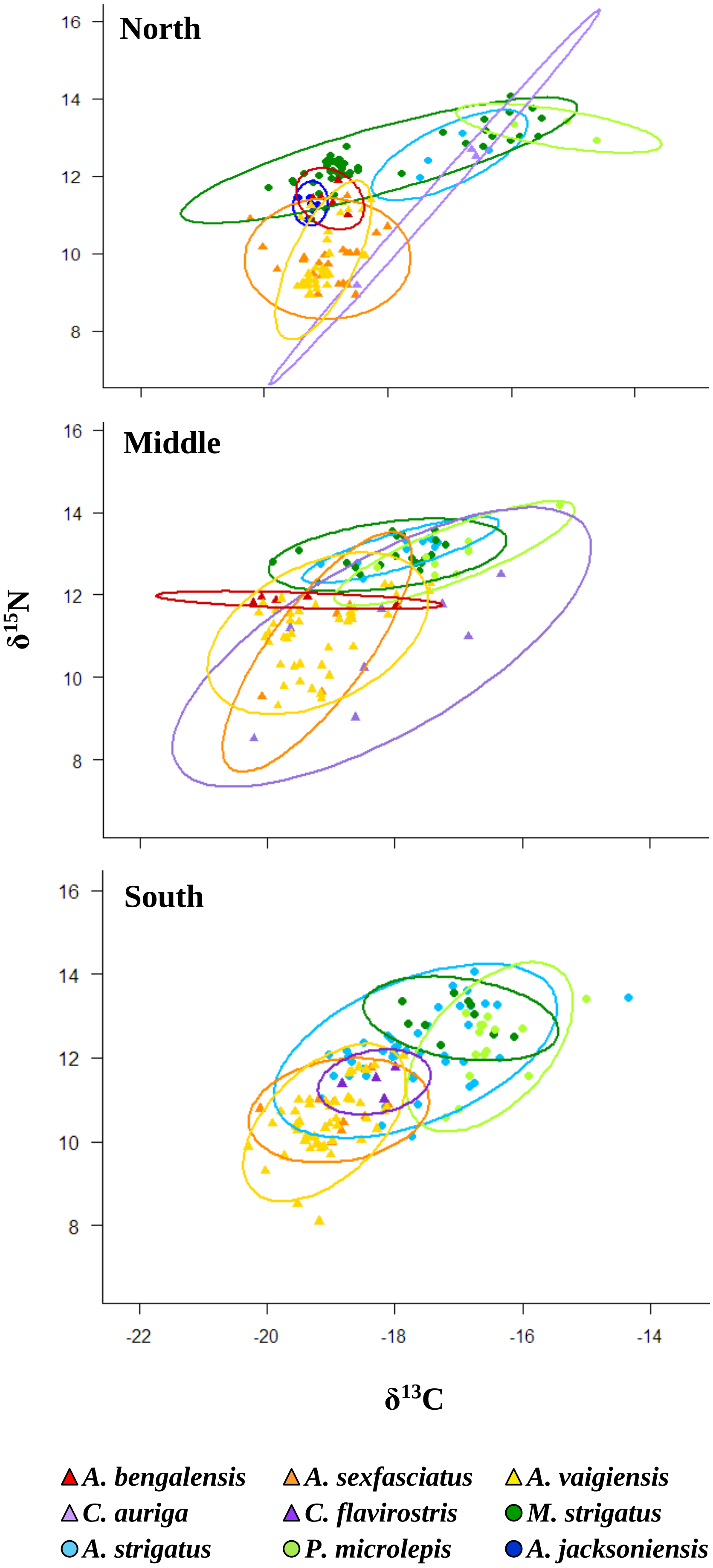
North
Middle
South
16
14
12
10
8
-22
-20
-18
-16
-14
$\delta^{15}N$
$\delta^{13}C$
▲ A. bengalensis
▲ A. sexfasciatus
▲ A. vaigiensis
▲ C. auriga
▲ C. flavirostris
● M. strigatus
● A. strigatus
● P. microlepis
● A. jacksoniensis

Fig. S1: Trophic niche of individual tropical and temperate species, displayed in δ^{15}N and δ^{13}C space for North, Middle, and South regions presented as standard ellipses (95%) using the package SIBER available in *R (Jackson & Parnell 2019)*. Each point represents a single fish, with tropical species represented by triangles, and temperate species by circles. Note that not all species were found in great enough quantity to form their own ellipses (minimum 3 individuals) and were therefore omitted from these graphs. All species, however, are included in the convex hulls shown in Fig. 3.

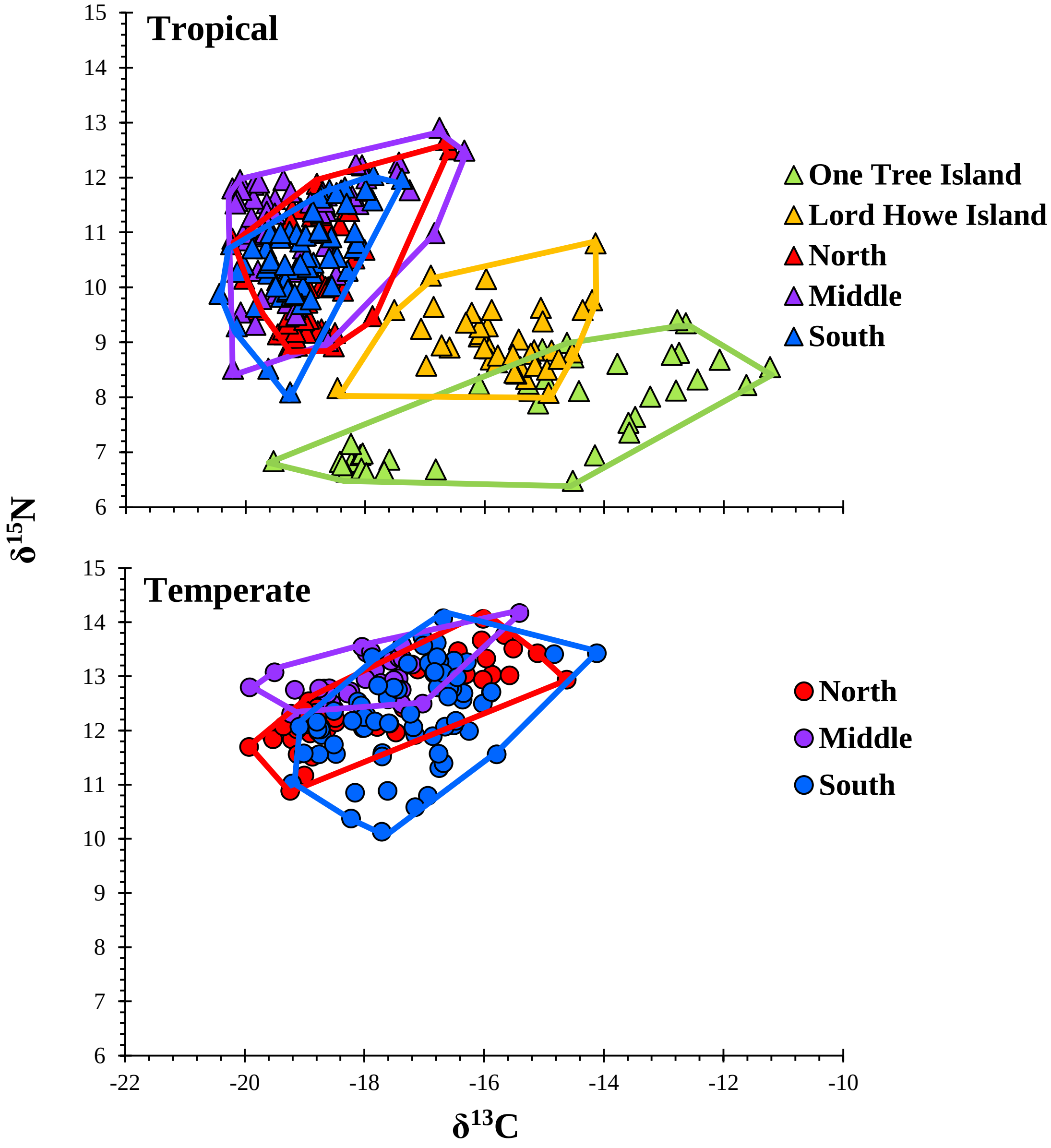

Fig. S2: Trophic niches of tropical and temperate species, displayed in δ^{15}N and δ^{13}C space for One Tree Island and Lord Howe Island, as well as the North, Middle, and South regions. Each point represents a single fish, and polygons represent convex hulls that encapsulate 100% of data points using the *R* package rKIN (Albeke 2017). Tropical species are indicated with coloured triangles, while temperate species are indicated with coloured circles. Temperate species were not found at One Tree Island and Lord Howe Island.

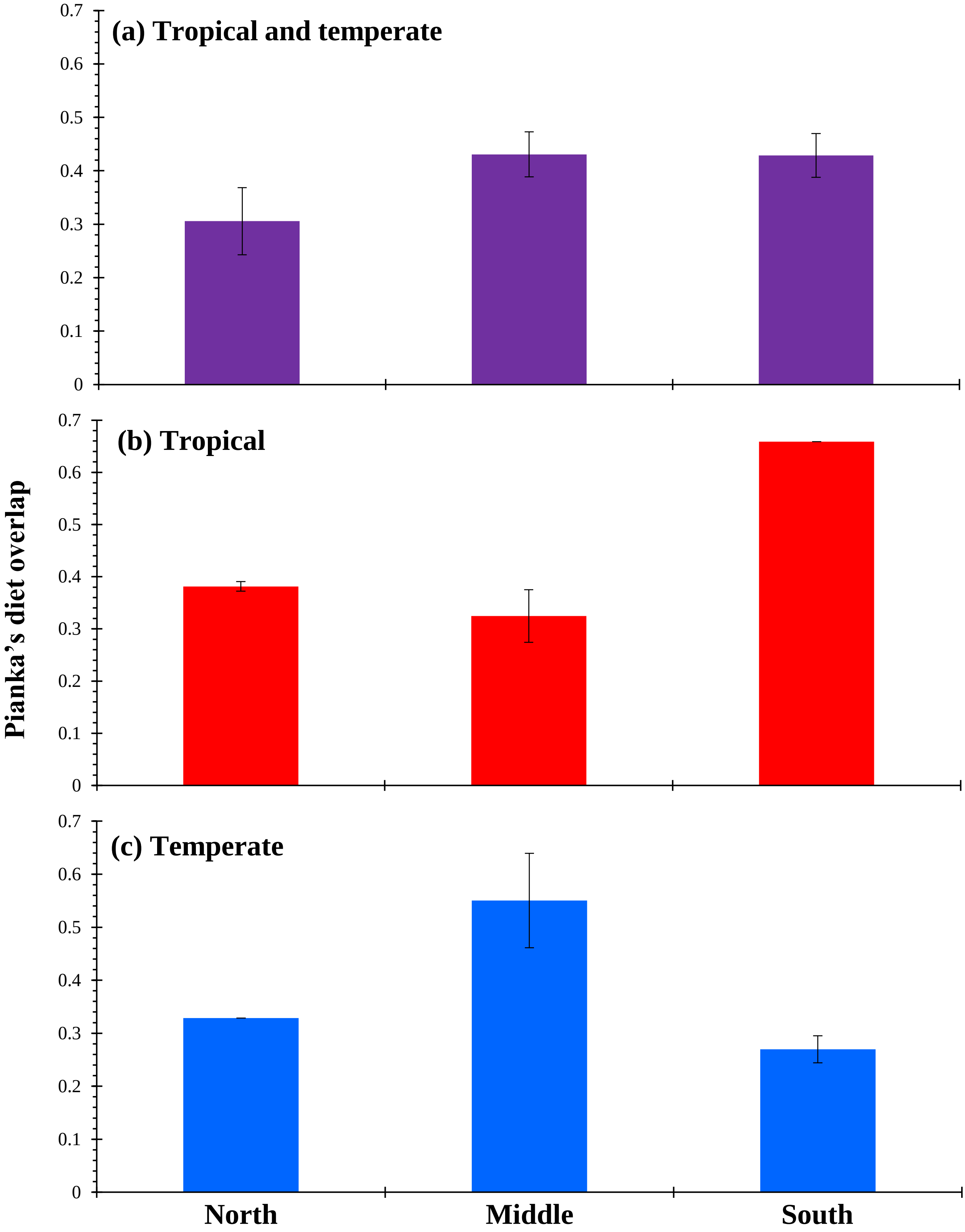

Fig. S3: Mean (± SE) Pianka's index of diet overlap between: (**a**) tropical and temperate species, (**b**) among tropical species, and (**c**) among temperate species, for the North, Middle, and South regions of east Australia. Mean values are calculated as the mean of the species means, and are based on stomach contents. A Pianka's value of 0 indicates no overlap, whereas a value of 1 indicates complete overlap. Overlap values > 0.6 are considered significant.

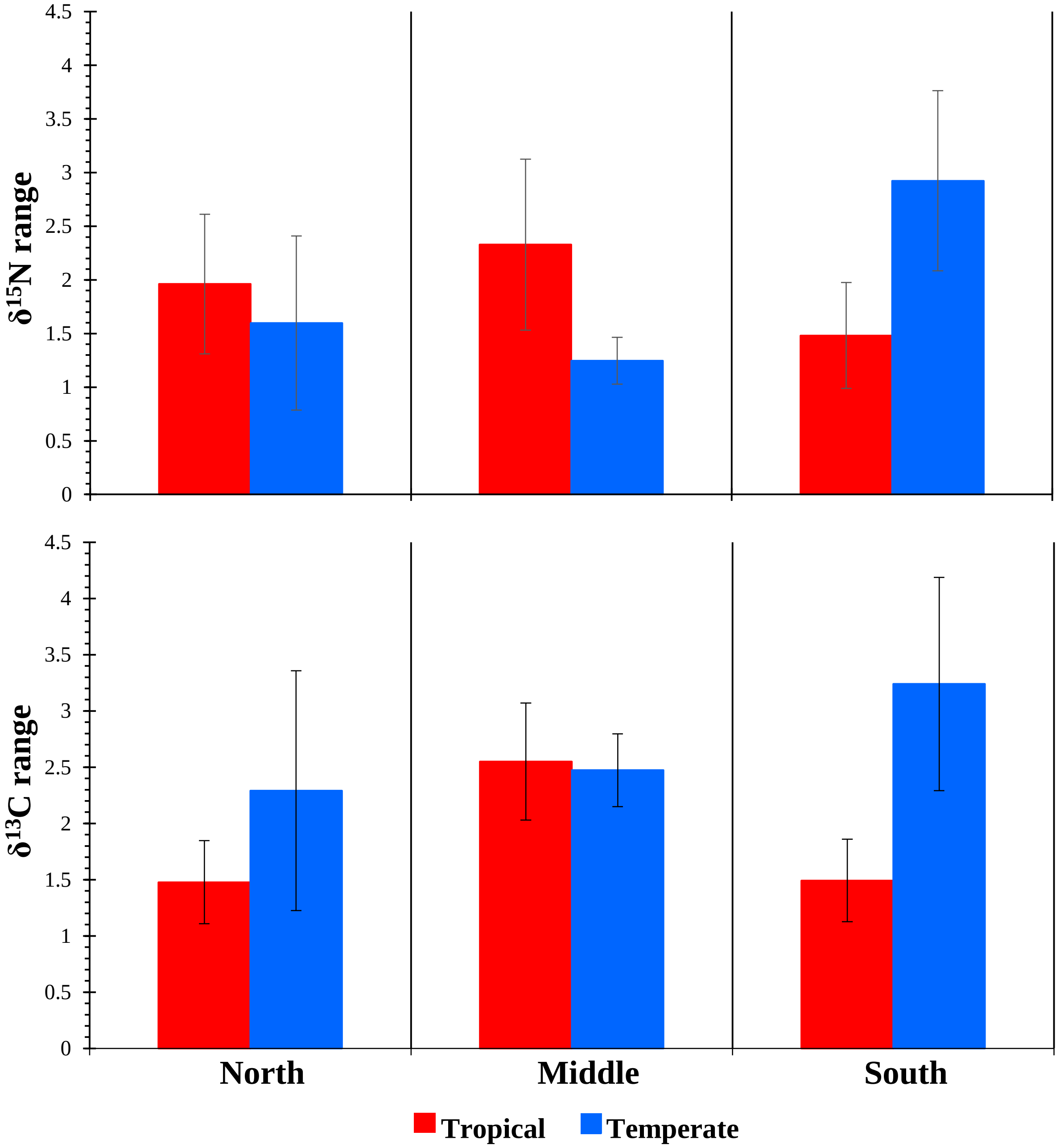

Fig. S4: Mean (± SE) niche range of $\delta^{15}N$ and $\delta^{13}C$ signatures for the North, Middle, and South regions. Ranges were calculated by subtracting the minimum isotope value of a species from its maximum value, and then calculating an affinity mean across species.

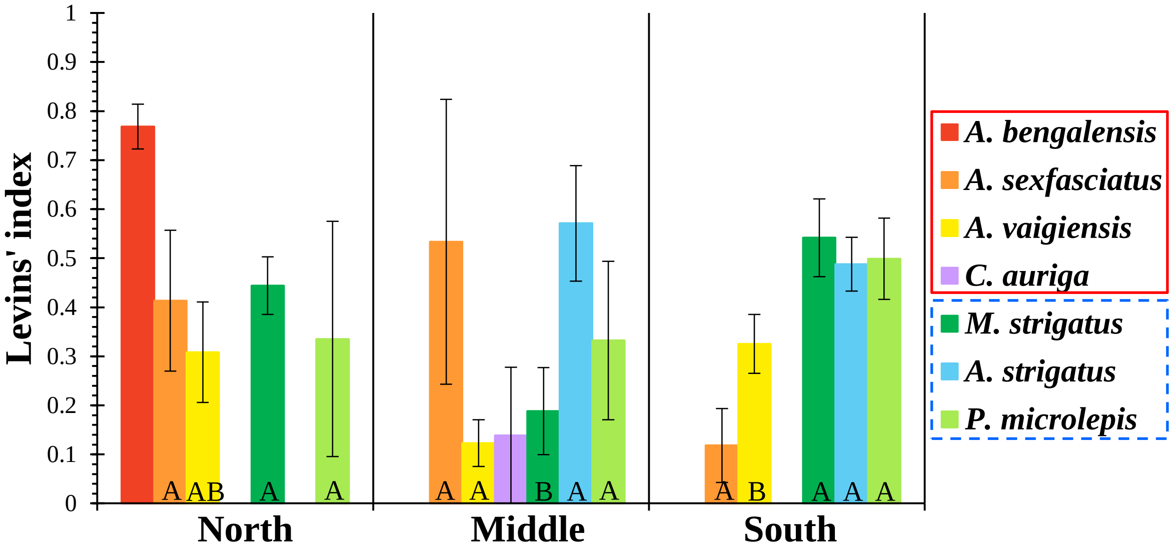

Fig. S5: Mean (± SE) Levins' index of niche breadth (which ranges between 0 and 1) for regions North, Middle, and South, based on stomach contents. A low value indicates that a species has a very small niche breadth and is a specialist, and higher values (>0.3) indicate broad niche breadth, or generalists. Tropical species are outlined in red, with columns grouped to the left, and temperate species are outlined in dashed blue, with columns grouped to the right. Different letters inside each bar represent significant differences obtained from *post-hoc* statistical tests (Table S4b). **AB** labels correspond to intra-species differences, and therefore should be interpreted between columns of the same colour only. Species that were collected from one region only do not have letters inside their bars.

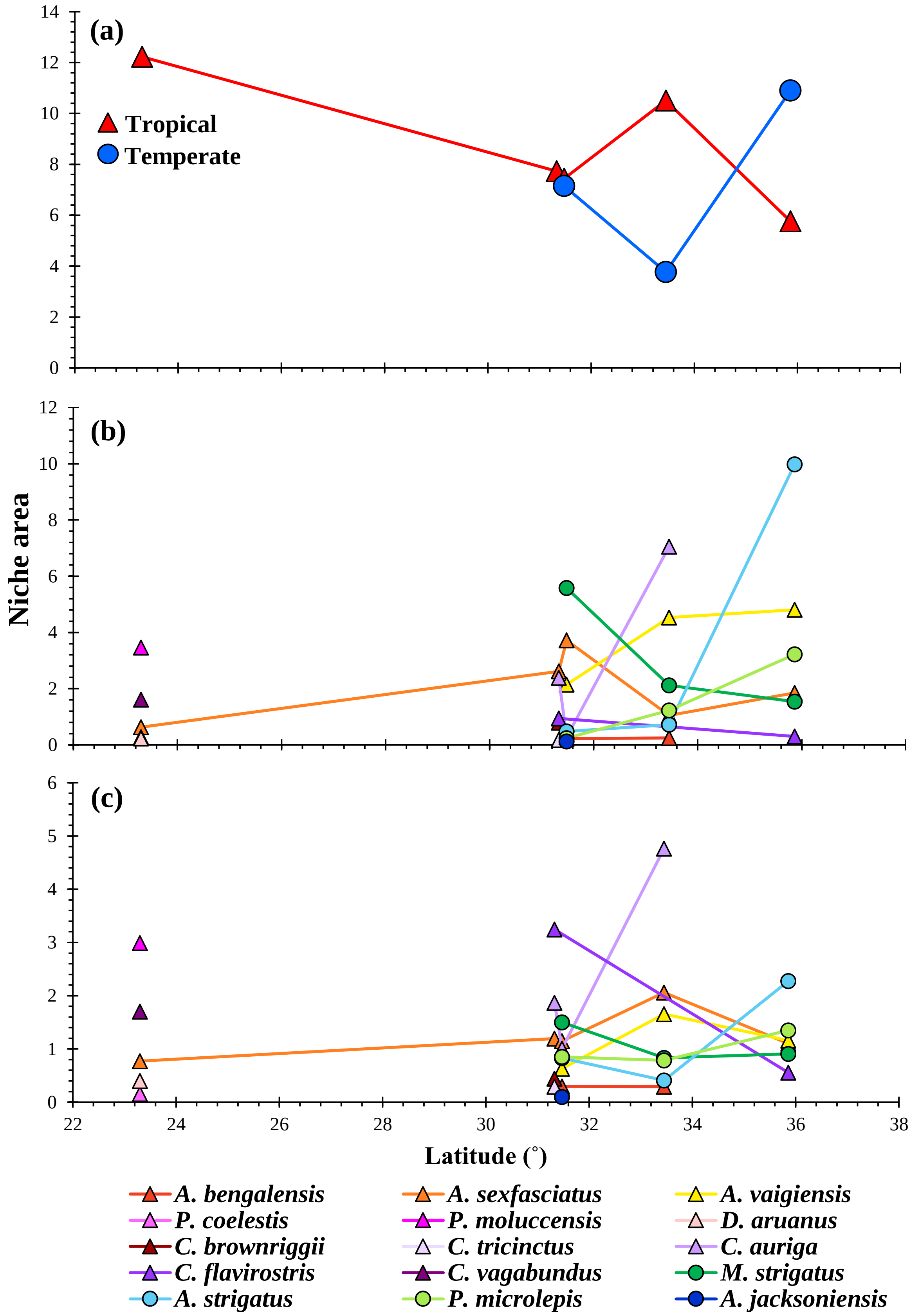

Fig. S6: Trophic niche area of tropical and temperate affinity groups and species, based on stable isotope analysis: **(a)** niche area of affinity groups from Fig. 3, based on 100% convex hulls (rKIN package); **(b)** niche area of individual species, based on 100% convex hulls (rKIN package); **(c)** niche area of individual species from Fig. S1, based on 95% standard ellipse corrected for small sample size (SEAc; SIBER package). Tropical species are shown with triangles, and temperate species are shown with circles. Niche areas are unit-less. Locations include One Tree Island (23.30˚S), Lord Howe Island (31.33˚S), and the regions North (31.48˚S), Middle (33.45˚S), and South (35.86˚S), based on the average latitude of their respective sampling sites. Temperate species were not present at One Tree Island or Lord Howe Island.

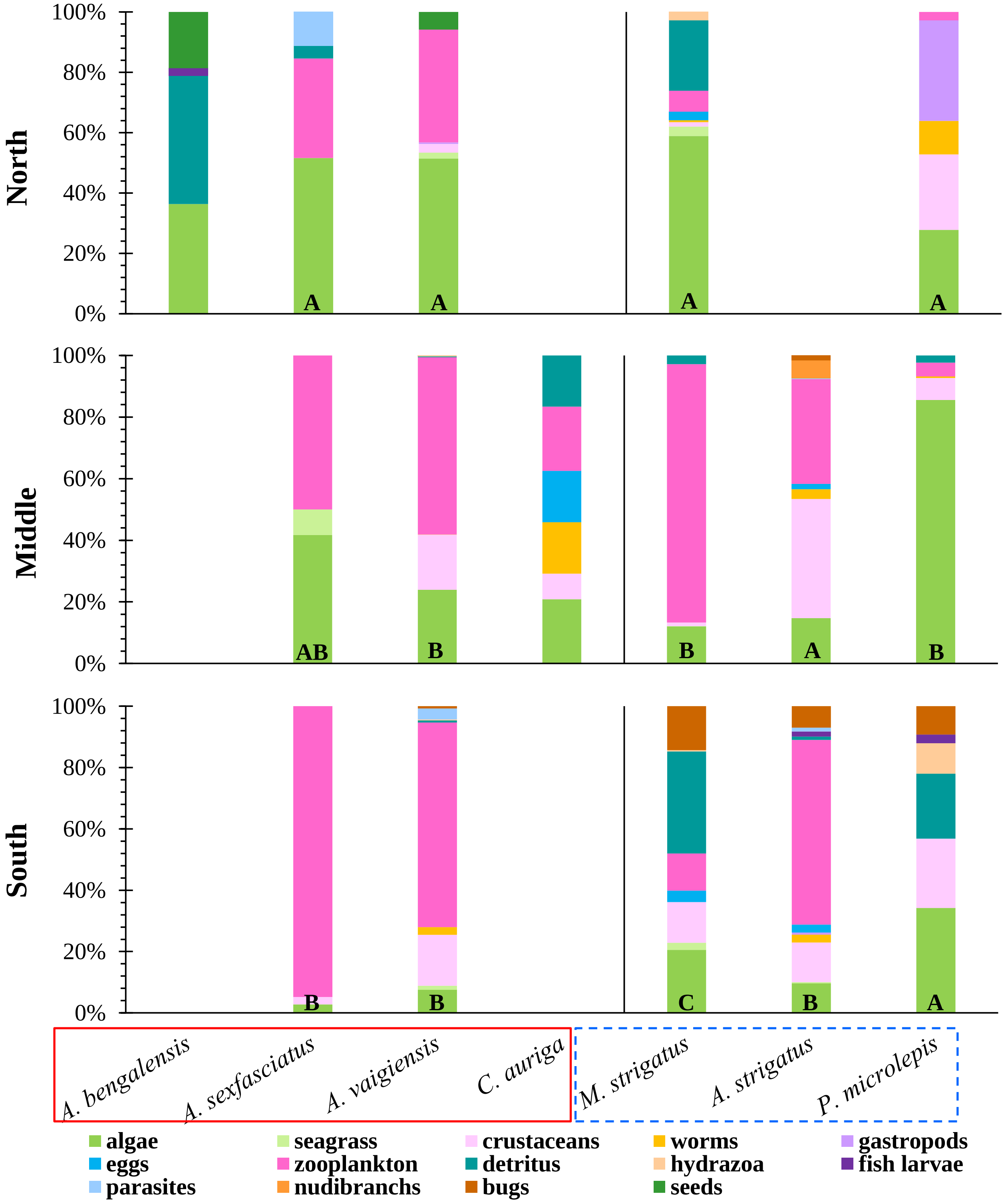

Fig. S7: Stomach contents (proportion volume) averaged for each species in North, Middle, and South regions. Algae, seagrass, crustaceans, gastropods, and worm groups all contain multiple families, but are grouped together for visual clarity. Tropical species are outlined in red and displayed on the left, and temperate species are outlined in dashed blue and on the right. Data gaps are a result of either small sample size or the species not being found at that region. Letters inside each bar represent significant differences obtained from *post-hoc* statistical tests (Table S4bii). **ABC** labels correspond to intra-species differences and should be read from top panel to bottom panel. Bars without a letter represent species that were only found in one region.

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Chapter 3 – Range-extending coral reef fishes trade-off growth for maintenance of body condition in cooler waters

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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

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, Essl & Rabitsch 2011), a change in water depth (Perry et al. 2005), or a change in latitude (Booth, Bond & Macreadie 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, Williams & Carlton 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, Bond & Macreadie 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, Cucherousset & Olden 2017). Consequences could also be physiological in nature, such as changes in feeding performance and growth (Bolger & Connolly 1989; Amara et al. 2007). 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, Sass & Stafford 2007) and survival of an organism (Bolger & Connolly 1989; Lambert & Dutil 1997; Schulte-Hostedde, S. Millar & Hickling 2001). Survival, growth, and reproduction are usually higher in fish with better condition (Millar & Hickling 1990; Lloret, Shulman & Love 2014; Brosset et al. 2016), linking body condition with future population success (Jakob, Marshall & Uetz 1996; Van Beveren et al. 2014).

Temperature plays a crucial role in the physiology and therefore ecological success of range-extending species (Angilletta, Niewiarowski & Navas 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 (Pörtner et al. 2001; Green & Fisher 2004; Enders et al. 2006) which can lead to decreased swimming ability and activity levels due to energy redistribution to other, more critical physiological processes (Batty & Blaxter 1992; Lyon, Ryan & Scroggie 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, Wethey & Helmuth 2014), with maintenance taking precedence (Jokela & Mutikainen 1995; Heino & Kaitala 1999; Kooijman 2001). In situations where organisms are unable to maximise all of their life-history traits simultaneously, trade-offs may occur among physiological processes (Stearns 1992; Brosset et al. 2016), 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 (Ridgway 2007; Hobday & Pecl 2014). 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.

Materials & Methods

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.

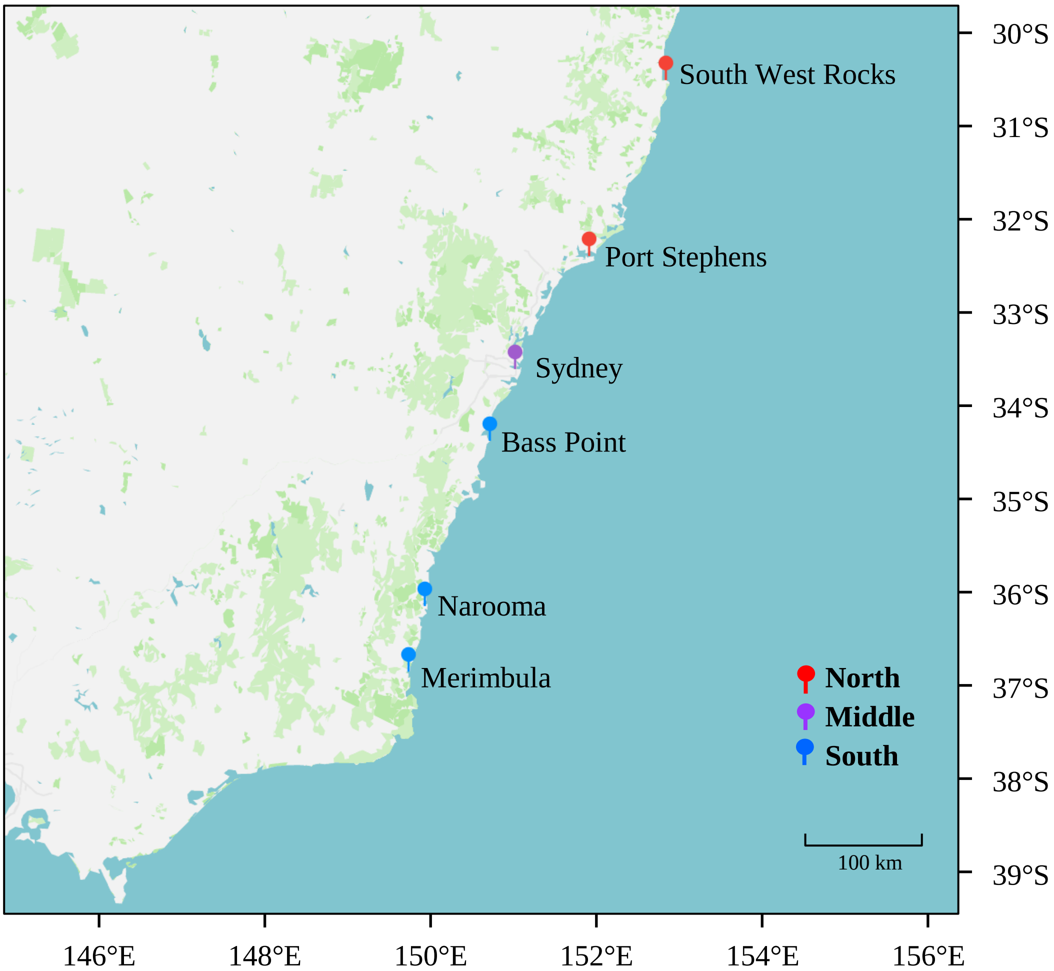

Fig. 1: Sample locations in a natural warming hotspot along 730 km (6˚ latitude) of the southeast coast of Australia. Locations include South West Rocks (two sites) and Port Stephens (two sites) (included in region "North", **red** marker); Sydney (two sites; included in region "Middle", **purple** marker); 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.

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).

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).

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; Sullivan, Zhang & Bonner 2014; Perkins et al. 2018). 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).

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, Kritzer & Ackerman 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).

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) (Mazzaro, Pesarin & Salmaso 2001; Anderson, Gorley & Clarke 2008). 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 Re × 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 (Winer, Brown & Michels 1991; Underwood 1996).

Results

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 × 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).

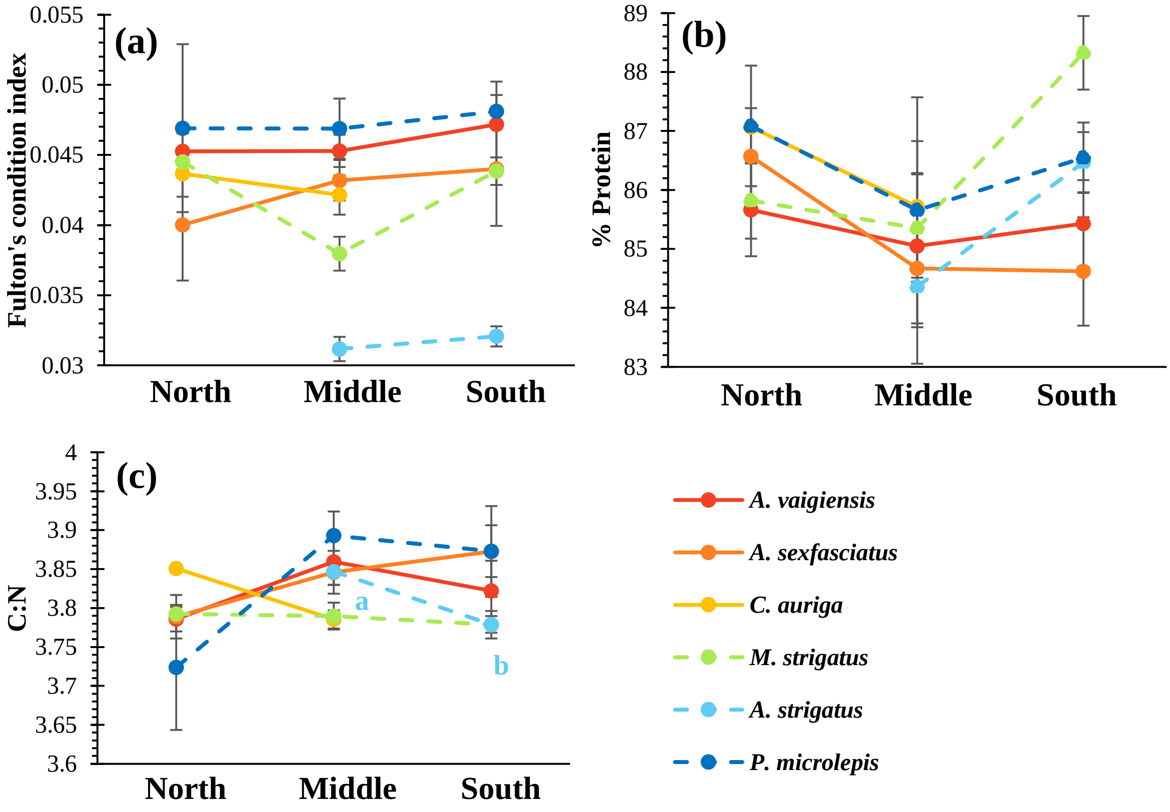

Fig. 2: Mean (± SE) measures of condition of tropical (solid lines) and temperate (dashed lines) fish species. Condition proxies are based on Fulton's condition index (**a**), muscle tissue protein content (**b**), and the atomic ratio of carbon to nitrogen in muscle tissue (C:N) (**c**). **ab** letters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

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).

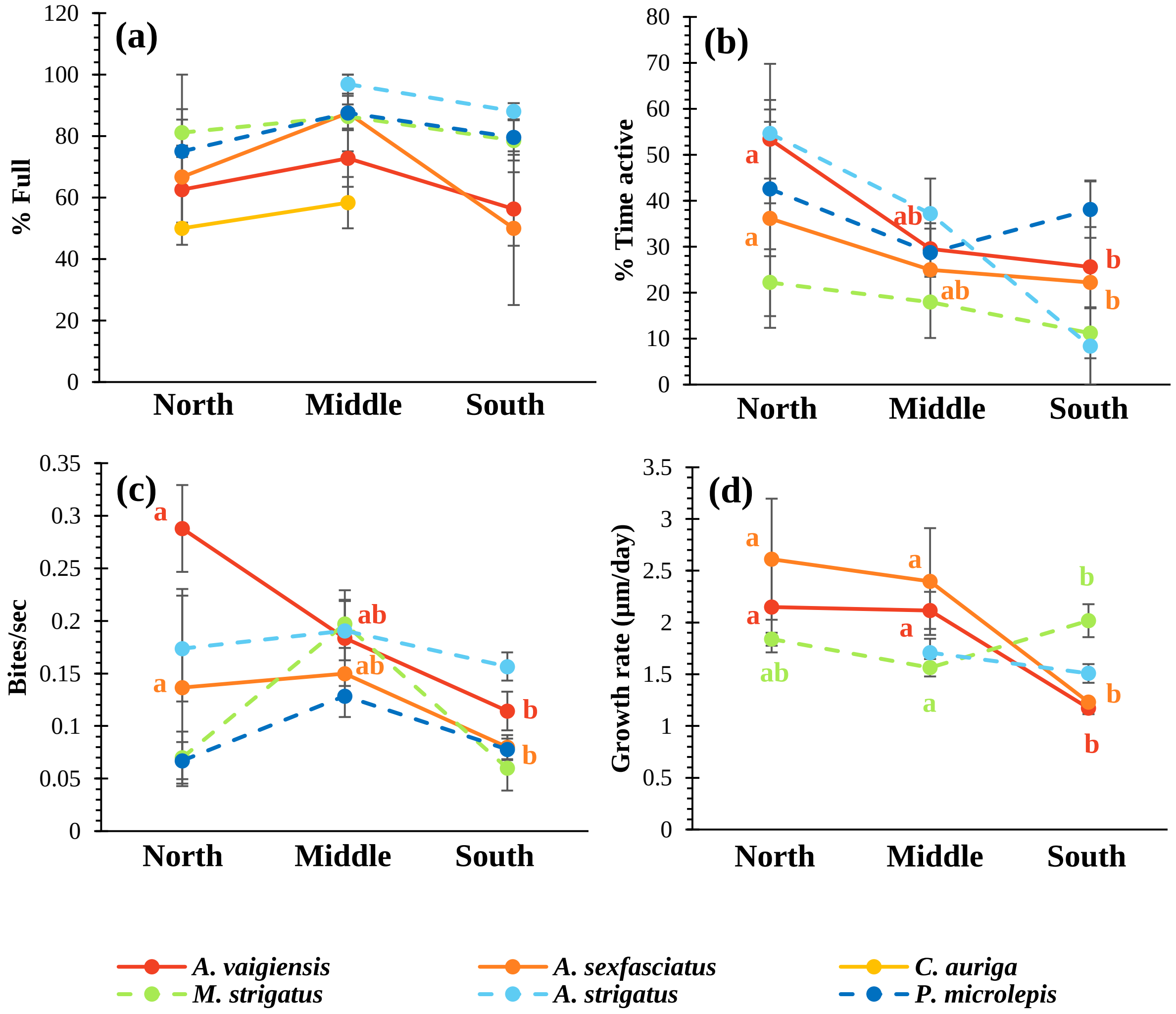

Fig. 3: Mean (± SE) measures of performance of tropical (solid lines) and temperate (dashes lines) fish species. Performance was measured as: stomach fullness (**a**), percent time active *in situ* (**b**), *in situ* bite rate (**c**), and growth rate (daily otolith growth increments) (**d**). Stomach 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 signifiant differences. See Fig. S2 for location-specific data.

Discussion

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, Ryan & Scroggie 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, Cao & Fu 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, Kuyper & Breeman 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 (Jokela & Mutikainen 1995; Heino & Kaitala 1999; 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.

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, Munday & Nilsson 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, Early & Bellemare 2013), potentially increasing their vulnerability to further ocean warming.

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.

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.

Acknowledgements

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Supplementary Information

Table S1: Sampling location and site coordinates along 730 km (6˚ latitude) of the southeast coast of Australia. Includes mean seawater winter temperatures based on long-term NOAA sea surface temperature data. See Fig. 1 for locations.

Region	**Location**	**Temp (°C)**	**Site**	**Latitude (°S)**	**Longitude (°E)**
North					
	South West Rocks	20.3	1	30°52'34"	153°04'02"
			2	30°53'00"	153°02'17"
	Port Stephens	19.6	1	32°42'56"	152°10'58"
			2	32°44'55"	152°10'19"
Middle					
	Sydney	19.3	1	33°42'07"	151°18'28"
			2	33°47'44"	151°17'25"
South					
	Bass Point	18.3	1	34°35'54"	150°53'18"
	Narooma	17.4	1	36°12'54"	150°07'51"
	Merimbula	16.9	1	36°44'13"	149°58'58"
			2	36°53'40"	149°55'25"

Table S2: Information on the seasonal presence of tropical species used in this study, acquired through underwater surveys conducted from 2003-2017. Values are based on the numbers of years that each species was observed during that season's surveys divided by the number of years that surveys were conducted during that season, and are expressed as a percentage (%). The mean winter temperatures of Sydney (SYD) and Merimbula (MER) are 19.3 °C and 16.9 °C, respectively, and are based on sea surface temperatures acquired from NOAA.

	Summer %		**Autumn %**		**Winter %**		**Spring %**	
	SYD	MER	SYD	MER	SYD	MER	SYD	MER
A. sexfasciatus	100	54	100	55	62	0	0	11
A. vaigiensis	100	100	100	90	92	0	50	22
C. auriga	88	100	100	90	15	0	0	11

Table S3: Results of non-parametric two-way ANOVA tests. All test were univariate and included factors region "Re" and species "Sp", as well as their interaction "Re × Sp". Results are shown for temperate (**a**) and tropical (**b**) affinities. **Bold** values indicate significant effects.

(a) Temperate fishes

Variables	df	SS	MS	*F*	*P*
Fulton's index (body condition)					
Re	2	0.000	0.000	0.689	0.504
Sp	2	0.002	0.001	14.93	**<0.001**
Re × Sp	3	0.000	0.000	0.418	0.740
Error	93	0.007	0.000		
% protein (body condition)					
Re	2	1.384	0.692	2.947	0.057
Sp	2	0.393	0.196	0.838	0.436
Re × Sp	3	0.393	0.132	0.562	0.641
Error	93	21.83	0.235		
C:N ratio (body condition)					
Re	2	0.049	0.024	6.113	**0.003**
Sp	2	0.022	0.011	2.720	0.071
Re × Sp	3	0.056	0.019	4.653	**0.004**
Error	93	0.373	0.004		
Stomach fullness (performance)					
Re	2	1053	526.7	1.525	0.223
Sp	2	1240	619.9	1.795	0.172
Re × Sp	3	83.43	27.81	0.081	0.970
Error	93	32122	345.4		
Activity levels (performance)					
Re	2	4843	2422	1.695	0.319
Sp	2	5364	2682	4.264	**0.018**
Re × Sp	4	5847	1462	2.324	0.062
Error	80	50314	628.9		
Bite rate (performance)					
Re	2	0.212	0.106	3.208	0.101
Sp	2	0.237	0.119	6.419	**0.002**
Re × Sp	4	0.134	0.034	1.818	0.134
Error	82	1.516	0.018		
Growth (performance)					
Re	2	0.160	0.080	0.634	0.534
Sp	1	0.226	0.266	2.115	0.151
Re × Sp	1	0.965	0.965	7.658	**0.007**
Error	68	8.567	0.126		

(b) Tropical fishes

Variables	df	SS	MS	*F*	*P*
Fulton's index (body condition)					
Re	2	0.000	0.000	0.521	0.601
Sp	2	0.000	0.000	1.725	0.200
Re × Sp	3	0.000	0.000	0.232	0.873
Error	24	0.000	0.000		
% protein (body condition)					
Re	2	0.183	0.091	1.133	0.339
Sp	2	0.052	0.026	0.323	0.727
Re × Sp	3	0.073	0.024	0.302	0.823
Error	24	1.934	0.081		
C:N ratio (body condition)					
Re	2	0.005	0.002	0.429	0.656
Sp	2	0.001	0.000	0.078	0.925
Re × Sp	3	0.016	0.005	0.933	0.440
Error	24	0.134	0.006		
Stomach fullness (performance)					
Re	2	844.6	422.3	0.523	0.599
Sp	2	2032	1016	1.259	0.302
Re × Sp	3	340.6	113.5	0.141	0.935
Error	24	19370	807.1		
Activity levels (performance)					
Re	2	34.13	17.07	18.49	**0.019**
Sp	1	4.649	4.649	0.598	0.460
Re × Sp	2	1.846	0.923	0.119	0.897
Error	25	194.7	7.786		
Bite rate (performance)					
Re	2	0.118	0.059	4.891	**0.015**
Sp	1	0.038	0.038	3.185	0.080
Re × Sp *pooled					
Pooled	27	0.326	0.012		
Growth (performance)					
Re	2	4.639	2.320	4.301	**0.027**
Sp	1	0.345	0.345	0.639	0.433
Re × Sp	2	0.090	0.045	0.083	0.920
Error	21	11.33	0.539		

Table S4: Results of *post-hoc* tests when the 'Re × Sp' interaction (**a**) or 'Re' (**b**) was significant (see Table S3) for temperate species (**a**) and the tropical affinity (**b**) groups. Significant factors are shown in **bold**. Signifiant interactions between regions are also depicted using **a** and **b** labels in the graph associated with each test (Figs. 2, 3). 'No test' indicates that analyses were not performed for that region, e.g. small sample size of *A. strigatus* in the North region, and growth rate analyses were not performed on *P. microlepis*.

(a) Temperate *post-hoc* test results

Variables	**C:N**		**Growth**	
Re × Sp	**Std. Error**	**p**	**Std. Error**	**p**
A. strigatus				
North – Middle	No test	No test	No test	No test
North – South	No test	No test	No test	No test
Middle – South	0.021	**0.003**	0.167	0.225
M. strigatus				
North – Middle	0.018	0.987	0.124	0.099
North – South	0.022	0.802	0.146	0.397
Middle – South	0.025	0.901	0.173	**0.031**
P. microlepis				
North – Middle	0.083	0.133	No test	No test
North – South	0.078	0.165	No test	No test
Middle – South	0.051	0.921	No test	No test

(b) Tropical *post-hoc* test results

Variables	**Activity levels**		**Bite rate**		**Growth**	
Re	**Std. Error**	**p**	**Std. Error**	**p**	**Std. Error**	**p**
North – Middle	1.434	0.388	1.471	0.164	0.324	0.903
North – South	19.90	**0.030**	3.108	**0.004**	0.387	**0.028**
Middle – South	2.241	0.268	1.734	0.103	0.367	**0.046**

Table S5: Summary table showing how each performance indicator changed for temperate and tropical fish from North (warm) to South (cold). '=' indicates no change across regions, while '↓' indicates a decrease and '↑' indicates an increase from North to South. NT = no test, due to inadequate sample size or lack of data. '↓↑' indicates a decrease from North to Middle followed by an increase in the South, while '=↑' indicates no change from North to Middle, but an increase from Middle to South. 'NT↓' indicates no test from North to Middle, followed by a decrease from Middle to South. Body condition* was measured using Fulton's condition index, % protein of muscle tisse, and C:N ratio in muscle tissue. Performance[†] was assessed using stomach fullness data, activity level, bite rate, and growth. See Tables S3 and S4 for statistical results.

	Temperate fishes			**Tropical fishes**		
Physiological process	***M. strigatus***	***A. strigatus***	***P. microlepis***	***A. vaigiensis***	***A. sexfasciatus***	***C. auriga***
Fulton's index*	=	=	=	=	=	=
% protein*	=	=	=	=	=	=
Tissue C:N*	=	NT↓	=	=	=	=
Stomach fullness[†]	=	=	=	=	=	=
Activity level[†]	=	=	=	↓	↓	NT
Bite Rate[†]	=	=	=	↓	↓	NT
Growth[†]	=↑	NT=	NT	↓	↓	NT

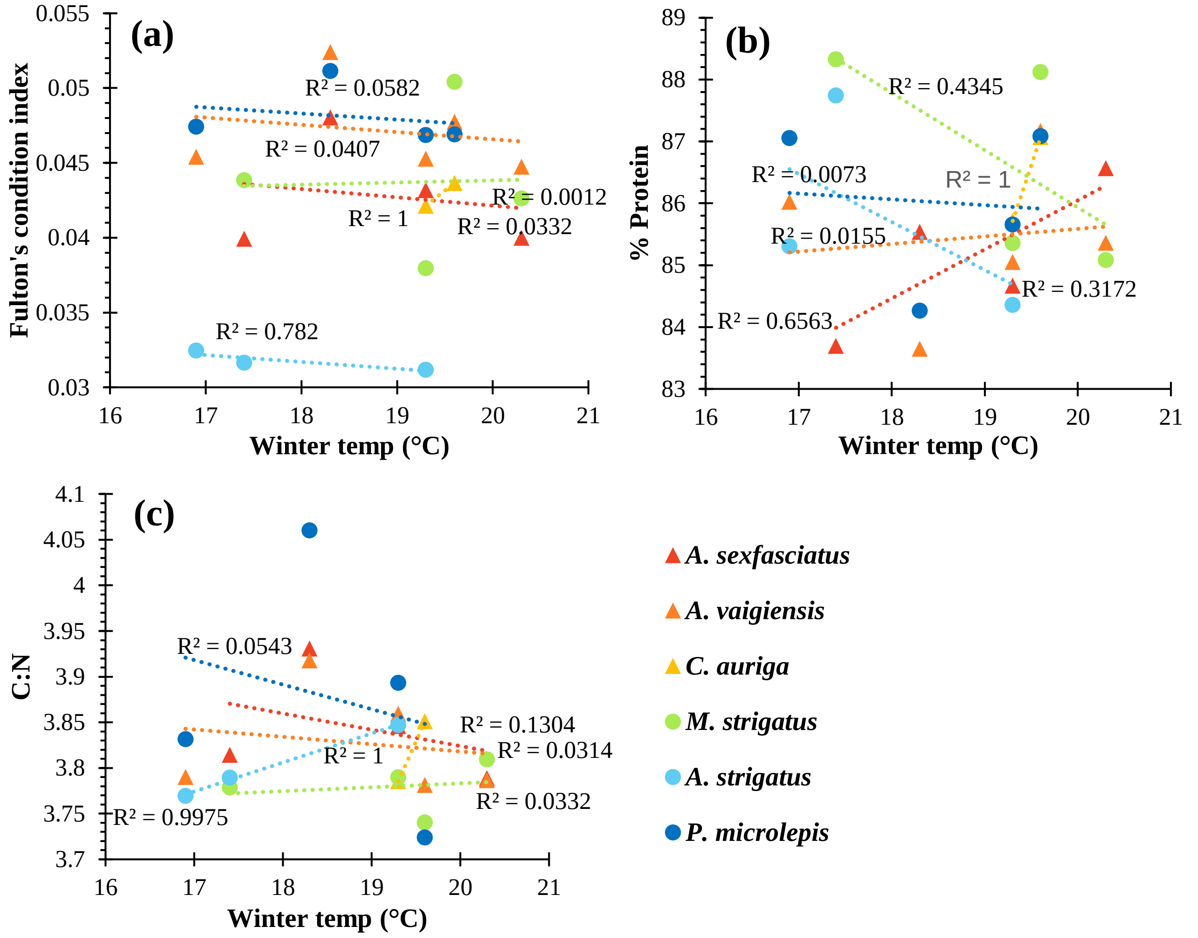

Fig. S1: Mean measures of condition of tropical (triangles) and temperate (circles) fish species at each location (See Table S1). Condition proxies are based on Fulton's condition index (**a**), muscle protein content (**b**), and the atomic ratio of carbon to nitrogen in muscle tissue (C:N) (**c**). Locations (mean winter temperature) include South West Rocks (20.3 °C), Port Stephens (19.6 °C), Sydney (19.3 °C), Bass Point (18.3 °C), Narooma (17.4 °C), and Merimbula (16.9 °C). Fitted linear regression lines and associated R^2-values are included.

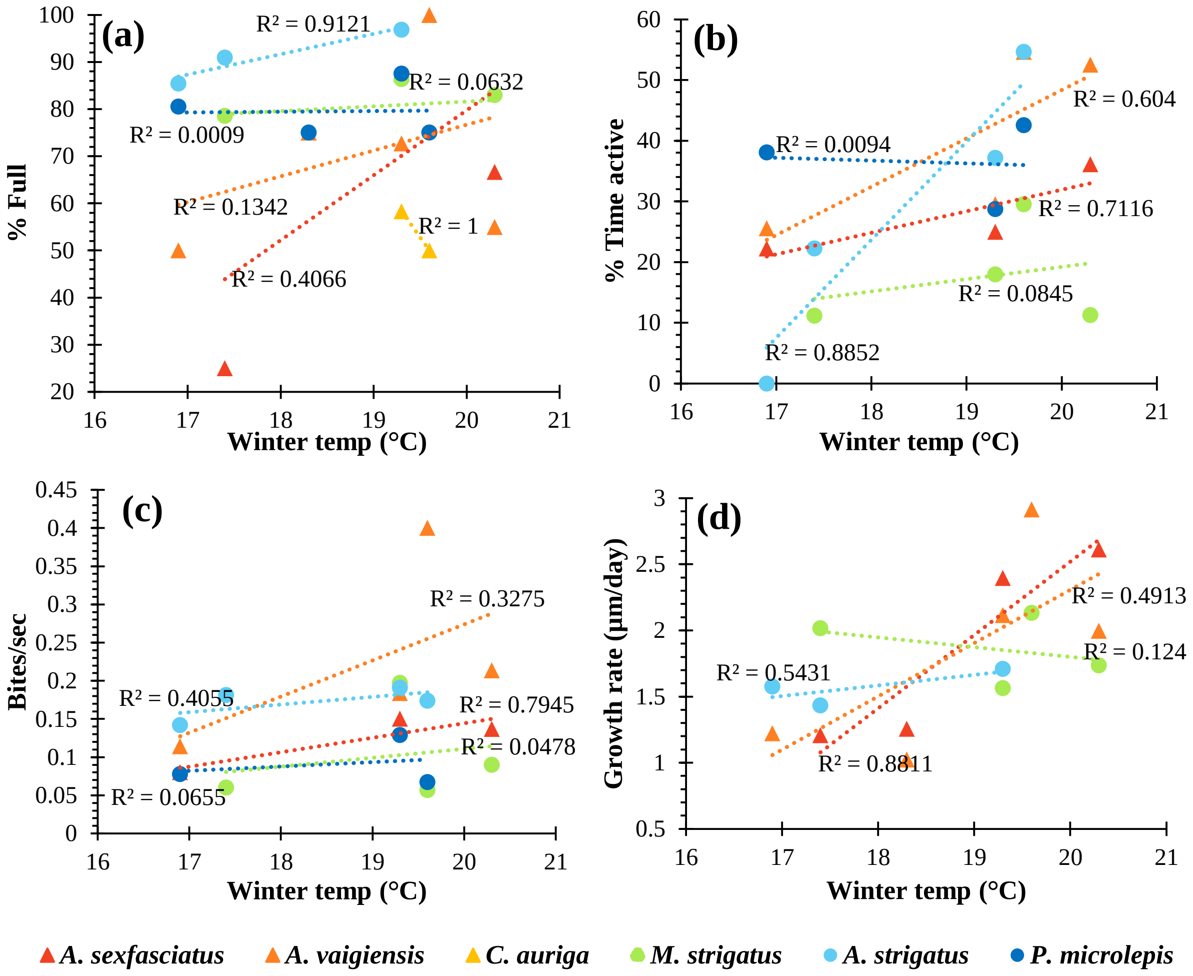

Fig. S2: Mean measures of performance of tropical (triangles) and temperate (circles) fish species at each location (see Table S1). Performance was measured as: stomach fullness (**a**), percent time active *in situ* (**b**), *in situ* bite rate (**c**), and growth rate (daily otolith growth increments) (**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. Locations (mean winter temperature) include South West Rocks (20.3 °C), Port Stephens (19.6 °C), Sydney (19.3 °C), Bass Point (18.3 °C), Narooma (17.4 °C), and Merimbula (16.9 °C). Fitted linear regression lines and associated R^2-values are included.

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Chapter 4 – General discussion

Trophic interactions between tropical and temperate species in coastal communities along a latitudinal gradient in southeast Australia were examined. These novel communities are composed of tropical vagrant and local temperate species, with such species assemblages potentially leading to altered species interactions. To determine if species were competing for food, I used stable isotope analysis to display trophic niches in isotope space. I discovered that tropical range extenders did not overlap in niche space with local temperate species, although both affinities foraged on broadly similar food items. This niche segregation is crucial in preventing trophic competition, and illustrates that these groups are successfully co-existing under current climate conditions. This co-existence is likely due to generalist feeding strategies, as both affinity groups consumed a wide variety of food items along the latitudinal gradient. This result is corroborated by a recent study that also found that tropical range-extending fishes employ generalist feeding strategies (Miranda et al. 2019). Under future climate change, trophic generalists are predicted to be the 'winners' by outcompeting specialists (Warren et al. 2001; Wilson et al. 2008; Ho et al. 2009). Although there was little diet overlap between tropical and temperate species in these mixed communities, they appeared unable to maintain a large trophic niche area simultaneously with one another. If this dynamic continues as tropical species advance poleward, a narrow niche area may be harmful, as low niche area and high spatial overlap with non-native species has previously led to a decline in native fish population abundance (Córdova-Tapia, Contreras & Zambrano 2015). Additionally, were resource availability and composition to change under future warming as prey species shift at a rate different to that of the study species, the current niche segregation of tropical and temperate species may be altered.

The genus *Abudefduf* (family Pomacentridae) used in the present study are site-attached tropical fish that primarily breed on coral reefs (Foster 1987), and are among the most abundant tropical fish seen in temperate communities along southeast Australia (Booth et al. 2007; Figueira, Curley & Booth 2019). In a study of pomacentrids, coral-associated juveniles had a narrower trophic niche breadth than their adult counterparts when living on reefs, due to reliance on specific coral species, and subsequently suffered declines in abundance following coral loss (Wilson et al. 2008). As water temperatures continue to rise and juveniles become less reliant on coral reefs for food and habitat as they enter southern temperate communities (Feary et al. 2014), their niche breadths may expand, increasing their trophic generality and possibly decreasing their vulnerability to climate change.

Additionally, *Abudefduf* species are habitat generalists, and when paired with a generalist feeding strategy, may result in even greater resilience under future climate conditions (Matis et al. 2018). *Abudefduf* species may benefit when shoaling with temperate fish by growing larger and surviving longer than those shoaling in con-specific schools of *Abudefduf* individuals only (Smith et al. 2018). Perhaps it is this schooling behaviour, combined with temperature tolerance and generalist strategies – both habitat and feeding – that may explain why *Abudefduf* species are successful in co-existing with temperate species in these mixed communities.

In addition to examining trophic niche partitioning, I wanted to investigate how these novel community assemblages affect species performance. In Chapter 3, I examined the effects of cool water in the South on vagrant tropical and resident temperate species. As I hypothesised, tropical fish experienced reduced growth and feeding performance along their leading range edge in the South, likely due to cool water temperature and its effect on metabolic rates. Under such sub-optimal conditions, tropical species faced a trade-off between growth and body condition, favouring the maintenance of body condition due to its hierarchical importance (Jokela & Mutikainen 1995; Heino & Kaitala 1999; Kooijman 2001). In contrast to my hypothesis, temperate species did not exhibit increased growth rates along their warm trailing edge, and instead only exhibited slight changes in body condition and growth that did not follow a distinct pattern.

Tropical species exhibited no change in nutritional quality in temperate communities compared to tropical communities, as seen through protein content and the ratio of carbon to nitrogen in muscle tissues. Temperate species exhibited some changes in nutritional quality, with some species displaying low nutritional values in the South, and other species showing high values in the South. In order to ascertain if this variation in nutritional value is correlated to the presence of tropical range-extending species, it would be necessary to study temperate fish in a community devoid of tropical species. Although the species used in this study are not fishery species, our findings are still important as they may be a food source to commercially-viable species, such as the occasional predation of *Abudefduf* species by triple fins as well as various grouper species (Froese & Pauly 2017), and changes in nutritional value could have consequences further up the food chain. These results indicate that tropical species are not experiencing altered nutritional quality in cooler high latitudes, an important finding if these species are going to continue to exist under future climates.

Although tropical species did not exhibit any changes in nutritional value, or any other measure of body condition, between tropical communities in the North and temperate communities in the South, environmental conditions in the South are not particularly favourable for tropical fish, evident from their trade-off between growth and maintenance of body condition. Because trade-offs are not made under perfect circumstances (Axelsen et al. 2000; Urban 2007; Brosset et al. 2016), it can be said that conditions in the South were not ideal for tropical species. Additionally, tropical species rarely overwinter in the high latitude communities of the South (Figueira & Booth 2010; Booth et al. 2018) due to temperature constraints, again suggesting sub-optimal conditions.

Under current climate conditions, low temperatures are the limiting factor preventing tropical fish from permanently establishing in temperate communities (Eme & Bennett 2008; Figueira & Booth 2010; Booth et al. 2018). If a species range edge is set by a low temperature threshold, warming is predicted to increase performance (e.g. activity, growth, and immune response), survival rates, and fecundity, ultimately leading to population increases (Pörtner & Farrell 2008). Poleward range extensions occur faster than range contractions (Poloczanska et al. 2013), indicating that until maximum temperature thresholds are met, habitats will experience species overlap and diversity will increase at mid-latitudes (García et al. 2016). As winter water temperatures continue to rise, tropical fish are expected to increasingly survive through winters, as far south as Sydney (our Middle region) by 2080 (Figueira & Booth 2010; Booth et al. 2018), and continue to advance their ranges poleward while temperate species slowly retreat (Hawkins et al. 2009; Horta e Costa et al. 2014). Additionally, as temperate waters warm, tropical species will likely be more adept at escaping temperate predators (Figueira, Curley & Booth 2019), assuming tropical predators have not also undergone a range shift. Tropical species living in temperate communities will once again exist in optimal temperature conditions, and it is likely that maintenance trade-offs will no longer occur, resulting in stronger species interactions with local temperate species which may accelerate the retreat of the latter at their trailing edges.

In addition to cool waters negatively affecting tropical fish, newly-arrived tropical species may be at a disadvantage compared to locally established species, irrespective of condition level. In a study of tropical pomacentrid ‘residents’ (effectively our temperate fish) and ‘intruders’ (effectively our vagrant tropical fish), the effects of condition on survival were examined (Poulos & McCormick 2015). Similar levels of aggression were seen between low-condition residents and high-condition intruders, indicating that residency may provide an advantage even when body conditions are low. Intruders also had a higher likelihood of mortality than residents when both had low body conditions (Poulos & McCormick 2015). Additionally, when residents were the same size or larger than intruders, residents had a great advantage over intruders, and were the consistent ‘winners’ in competitions for space (Poulos & McCormick 2015). Temperate species may also be aided by priority effects, which occur when resident individuals have an influence on invading species, simply by having arrived first, and this increases with the amount of time between arrivals (Shulman et al. 1983; Almany 2004; Geange & Stier 2010). A study of two fly species showed that the second species to arrive in the environment, regardless of which of the two species it was, suffered decreased body size, development delays, and ultimately higher mortality rates (Shorrocks & Bingley 1994). This did not occur when the two species arrived in the community at the same time. Since tropical species are arriving in temperate communities well after temperate species have already established, the low growth rates found in tropical species could also be due to priority effects, and not solely the results of cool water temperates in the South.

The main objective of this thesis was to assess the ecological effects of tropical range extension into temperate communities. Previous studies have focused on the effects of water temperature (Figueira & Booth 2010; Beck et al. 2016), ocean currents (Booth et al. 2007), and fish morphology (Smith et al. 2016) on the success of range-extending tropical species and local temperate species, but until now, studies have neglected to explore the direct trophic interactions of vagrant tropical and temperate species in these novel communities and how this affects their performance. My work highlights the importance of *in situ* community-level studies, which are able to capture a more realistic picture of what trophic dynamics are like in these mixed-assemblage communities. This study is valuable because it shows how the presence of tropical fish in temperate communities is affecting the performance of both groups, allowing us to make better predictions about species community structure under future climate scenarios and to better prepare for and mitigate the effects of increasing temperatures and future range shifts.

Future directions

The southeast coast of Australia is home to tropical, temperate, and mixed community assemblages. While this offers a unique natural laboratory to study novel communities *in situ*, it does present some weaknesses. Certain environmental factors, such as temperature and salinity, are not manipulatable. Isotopic signatures may have been influenced by temperature, and can vary across seasons and latitudes (Woodland et al. 2012; Mackey et al. 2015), possibly confounding the observed trophic niche segregation between tropical and temperate species found in Chapter 2, and further supports the approach of using both stable isotope and stomach contact analyses. Additionally, fish fed exclusively on the food sources that were available at that time and place, and may have eaten different items were a different selection available, as may be the case under future climate change. Similarly, the use of stomach content analysis in Chapter 2 and of stomach fullness in Chapter 3 are based on a momentary snapshot of that fish's life, and may have been different were the fish sampled the following day. This study would also benefit from the addition of bioenergetic indices such as muscle fat content, which could reveal subtle changes in body condition that the proxies used in Chapter 3 may have been unable to detect. The addition of laboratory experiments that correct for these factors, such as controlling for temperature, and a longer *in situ* analysis of stomach contents would allow for control over confounding factors and would ultimately benefit this study.

Another possible addition to this study would be an investigation into habitat niche use. While there has been some research tangentially related to this, including a study on generalist versus specialist habitat associations in a mixed tropical-temperate community (Matis et al. 2018), there is a need for further research. Additional investigations into niche partitioning and growth in temperate-only and tropical-only communities would be useful as this would provide a baseline of what trophic niche space, body condition, and performance are like when affinities do not spatially overlap. Sampling communities south of Merimbula (36°S) would be beneficial because as water temperatures rise, these novel mixed communities will extend further and further poleward and trophic niche space may shift to accommodate this. This study would also benefit from additional sampling north of South West Rocks (30°S), as temperate species were not collected north of 30°S.

While this study utilised a broad range of both tropical and temperate species, all species used were coastal generalists, and were primarily juveniles. A study investigating trophic niche partitioning of adult fish, as well as off-shore species, would be beneficial to this field of study. Similarly, the species used in this study are not commercial fishery species, nor are they apex predators, and as such the same niche dynamics may not apply. Additionally, as growth rates and resource availability change under future climate change, inter-specific competition may be altered, presenting a need for on-going investigations (Rose et al. 2001; Lewin, Arlinghaus & Mehner 2006).

Conclusion

The effects of tropical fish range-extensions on tropical and temperate fish species inhabiting these newly-sympatric communities were studied in this thesis. I investigated trophic niche space partitioning and how these novel mixed-community assemblages affect fish body condition and performance along the southeast coast of Australia. Through the use of stable isotope analysis, I found that tropical and temperate species occupied segregated trophic niches that did not overlap considerably. Fishes of both tropical and temperate affinities were unable to maintain a large niche area at the same time, and appeared to alternate between which affinity occupied the larger area. These fish are likely able to co-exist due to their generalist feeding strategies, with both affinity groups consuming a wide variety of food items across all regions studied. I then investigated how tropical vagrants and local temperate species performed in these mixed communities, by examining body condition and performance (feeding performance and growth rate). In the cool waters of the southeast coast, tropical species exhibited decreased growth rates, yet maintained their body condition, likely the result of a growth-maintenance trade-off. Temperate species, although slightly variable in growth and body condition, did not exhibit discernible patterns along the latitudinal gradient examined. In summary, I demonstrate current co-existence of tropical and temperate fish species in these novel mixed communities. As water temperatures continue to rise under future climate change and tropical species exist within their optimal thermal bounds once again, I expect to see fewer maintenance trade-offs, ultimately resulting in stronger interactions with local temperate species.

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