BEHAVIOURAL PLASTICITY AND SPECIES INTERACTIONS AS KEY DRIVERS OF TROPICAL FISH RANGE-EXTENSIONS ON TEMPERATE REEFS

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CONTENTS

ABSTRACT

Species invasions have historically driven many natural communities around the world into collapse. As climate changes, species are shifting their distribution to regions with more tolerable conditions, intensifying species invasion rates. By feeling the heat, many marine tropical species are moving towards cooler environments. When extending their ranges they are forced to interact and share habitats and resources with native species, potentially triggering modifications in the structure and functionality of temperate communities. For at least two decades, hundreds of tropical fish species have been recruiting to Australian temperate reefs, but successful colonisation depends on how they respond to and cope with unfamiliar environmental conditions. Temperate ecosystems represent a potential hostile environment for tropical species, due to novel prey, predators, competitors, habitats, and suboptimal temperatures. This thesis provides empirical evidence that behavioural traits and biological interactions are underpinning mechanisms controlling the success of tropical fish establishment in temperate waters, and demonstrates some degree of resistance by temperate fish communities to tropical invasions. By assessing a wide range of behavioural responses of temperate and tropical fishes across a temperature gradient from low to high latitudes along the eastern Australian coast, I reveal that behavioural plasticity, generalism and segregation of tropical and temperate species at their leading and trailing edges, respectively, might facilitate coexistence in temperature mixing zones (Chapter 2). In contrast, tropical fish are more risk-averse at leading edges and such behaviour was associated with reduced foraging, possibly compromising their permanent establishment on temperate reefs under current warming (Chapter 3). I further reveal that physical (low temperature and/or unfamiliarity with temperate environmental conditions) and biological (behaviour and abundance of temperate competitors) effects reduce the efficiency of tropical fishes in their food acquisition, which may compromise their fitness delaying their establishment in temperate environments nowadays (Chapter 4). Whilst warming has led to the expansion of sea-urchin barrens in temperate regions, which creates suitable habitats for tropical fish colonisation, future ocean acidification may inhibit the formation of such habitats, reducing the probability of successful recruitment of tropical fishes and the emergence of novel fish community structures (Chapter 5). Although some biological and physical processes may slow the pace of tropicalisation, under future ocean warming tropical fishes may no longer struggle for survival in cooler-temperate water, which has historically been acting as the main barrier against the tropicalisation of temperate ecosystems. Yet, ocean acidification can slow down the process of tropicalisation at the leading edges of species ranges.

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.

I give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

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"The start point of all achievement is desire"

Napoleon Hill

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CHAPTER I

GENERAL INTRODUCTION

CLIMATE CHANGE AND THE GEOGRAPHIC REDISTRIBUTION OF SPECIES

The Earth's climate naturally fluctuates over time, and extreme climate change events have occurred in the past causing mass extinction and consequently the emergence of new species and communities that form our biodiversity today (Sandel et al. 2011; Blois et al. 2013). Different to past climatic events, the high resource demands of the increasing human population and technological development (industrialisation) led to the intensification of fossil fuel consumption, accelerating the rates and magnitude of climate disturbances as never recorded before (Alley et al. 2003; Meehl & Tebaldi 2004; Rosenzweig et al. 2008; Kerr 2011). Climate change has already disrupted over 80% of ecological processes on Earth, encompassing marine, freshwater and terrestrial ecosystems (Scheffers et al. 2016). Perhaps, one of the main threats imposed by the intensification of climate change is the worldwide redistribution of species (Pecl et al. 2017; Scheffers & Pecl 2019). Almost 59 % of marine and terrestrial species has already extended their distribution across altitude, latitude and deeper waters in order to keep pace with their climatic niche (Parmesan & Yohe 2003; Pecl et al. 2017). When species move to a new geographic area (range-extending species), a quick adaptation to the novel environmental conditions is imperative in order to persist (Angert et al. 2011; Bates at al. 2014). Such "invasion" of range-extending species at recipient communities represents a threat to the native species due to the emergence of novel biotic interactions (Bennett et al. 2015; Alexander et al. 2016, Verges et al. 2016). The uncertainty of the effects of range-extending species on recipient communities and its consequent implications on native communities, social-economic activities and human well-being, should be carefully and urgently investigated as the pace of this shift appears to be rapid.

POLEWARD RANGE SHIFTS

As the Earth warms, poleward redistribution has been the most commonly observed geographic migration of species (Parmesan & Yohe 2003; Parmesan 2006; Kelly & Goulden 2008). However, the pace (range-extending velocity) of marine organisms (72 km per decade) is higher than the terrestrial ones (6 km per decade) (Poloczanska et al. 2013). The strengthening of warm ocean currents combined with the higher connectivity in marine environments and the fact that many marine taxa exhibit a planktonic larval period (e.g. tropical fishes, sea-urchins and corals) have facilitated rapid dispersal of tropical organisms to high latitude regions (Burrows et al. 2011; Donelson et al. 2018). The poleward influx of such marine warm-adapted species has already caused regime shifts in native temperate ecosystems in which recovery to the previous natural stage has become almost impossible (Wernberg et al. 2016). In Japan, the arrival of tropical herbivorous fishes caused the depletion of the principal habitat-forming species (kelp forests), opening up space for the colonization of corals (Nakamura et al. 2013). This is a classic example of the tropicalisation of temperate ecosystems, a phenomenon in which temperate species are replaced by range-extending tropical species. There is evidence that this tropicalisation phenomenon is rapidly occurring as well along the eastern and western Australian temperate coasts, as the abundance of tropical and subtropical herbivorous fishes and corals has increased in the last few decades (Verges et al. 2014; Bennett et al. 2015**;** Booth & Sear 2018). In addition, the overgrazing of warm-adapted sea-urchin (*Centrostephanus rodgersii*) has transformed kelp-dominated ecosystems to impoverished barren-dominated habitats in northern Tasmania (Johnson et al. 2005; Ling 2008; Ling et al. 2009). This shift in tropical species distribution resulted in losses for local fishers who had targeted economically-important temperate fishes and now the fishery system has to adapt to this novel context such as changing in target species (Ojea et al. 2020). Not all range-extending species will cause negative impacts in their novel range-shifted environments (Rodriguez 2006); however, such examples show the vulnerability of native ecosystems to the establishment of novel organisms. During the first stage of the range-extending process, the establishment of species in new areas starts with small numbers of individuals. Thus, by monitoring and managing the arrival stage of redistribution we can anticipate and avoid possible impacts of these natural invaders (Fogarty et al. 2016).

RANGE-EXTENDING VESUS ALIEN SPECIES

The threat of range-extending species establishment into native communities (also called ‘native invaders’), is generally similar to those caused by alien species (Verges et al. 2014). Besides some dissimilarities between range-extending and alien species, such as the pace of invasion, which is higher in alien species (Sorte et al. 2010), there is consensus that both range-extending and alien species drive (1) biodiversity loss by altering population, communities and ecosystem structure, (2) disruption of the functionality of ecosystems, and (3) irreversible economic losses (Mack et al. 2000; Pimentel et al. 2005). Yet, alteration of basal community structures might follow different pathways facilitated by the arrival of new predators and prey, which can alter existing predator-prey interactions in native communities (Peers et al. 2014; Selden et al. 2018). Likewise, the influx of novel competitors has changed the dominance of species due to competitive displacement of inferior native competitors (Millazo et al. 2013; Nagelkerken & Simpson 2013). Consequently, such reshuffling of pre-existing biotic communities may result in changes in ecosystem functioning with unknown implications for the recipient communities (Harborne & Mumby 2011; Nagelkerken & Connell 2015). Alternatively, in some cases, the influx of new preys may enhance the abundance of native predators as resource availability increases (Tablado et al. 2009). Thus, depending on the level of threat, some range-extending species can boost the abundance and diversity of native communities favouring the economy of local human communities (Madin et al. 2012).

SUCCESSFUL SPECIES RANGE SHIFTS

Different species characteristics play an important role in each of the range-extending process such as dispersion, arrival and establishment (Feary et al. 2014). However, range-extending species will only prosper after arriving in novel environments if they become able to reproduce, increase population and then spread (Bates et al. 2014). For example, life-history traits such as propagule pressure (i.e. the quantity of arriving individuals; Lockwood et al. 2005) and pelagic larvae duration, for marine organisms, are key processes determining successful species range shifts in terrestrial and marine ecosystems (Ben RaisLasram et al. 2008; Soeparno et al. 2012), but traits that facilitate dispersal of propagules are no longer relevant after arrival into novel environments. When expanding to new ranges, species must also adjust to novel challenges to establish viable populations by (i) adapting to novel biotic interactions (e.g. predation, competition), (ii) tolerating new abiotic conditions (e.g. colder winter temperatures), and (iii) utilising new resources (e.g. novel habitats) (Angert et al. 2011).

The first response of an organism to prosper in novel environmental conditions and interact with unfamiliar predators and competitors is modifying their behaviour (Lavergne et al. 2010; Tuomainen & Candolin 2011). Behavioural modification may enhance individual performance enabling range-extending species to exploit new resources, escape efficiently from predators and avoid competition with native species (Hill et al. 2001; Reader & MacDonald 2003; Poyry et al. 2009). Additionally, behavioural segregation may reduce the overlap in resource use avoiding competition with native species (Shea & Chesson 2002; Thuiller et al. 2010; van Kleunen et al. 2010). Similarly, behavioural modification and segregation deployed by native species can also be a strategy to cope with invaders (Vermeij 1982; Strauss at al. 2006). Species behaviour is directly associated with the ecological niche that they occupy in the environment (Bergmuller & Taborsky 2010). The larger the behavioural repertoire, the wider is the ecological niche occupied by a species (Whitney &

Gabler 2008). Alternatively, in some stressful cases, species narrow their behavioural repertoire to become more resource-selective in order to avoid competition (Bolnick et al. 2010, Matis et al. 2018). Modification of behaviors involved in foraging, swimming speed, competitor and predator avoidance, social learning and resource use are all strategies used by species to cope with these unfavourable environments (Peers et al. 2014; Nagelkerken &Munday 2016; Smith et al. 2018), although behavioural change is not always beneficial (Sih et al. 2004a; Sih et al. 2004b). Consequently, there is a pressing need to understand whether behavioural plasticity and segregation are mechanisms used by range-extending species to thrive in invaded environments as well as the potential of native species to resist invasions.

Range-extension theory hypothesises that at lower latitudes biotic interactions set species limits while at high latitudes abiotic factors are more important (Darwin's hypothesis on range limits: Darwin 1859; Dobzhansky 1950). However, biotic and abiotic forces can act in synergetic or antagonist ways, independent of latitude. The cool temperatures of high latitude regions and interactions with native predators and superior native competitors combined with the absence of familiar resources (habitat, food) may decrease survival of range-extending animals, and hence limit their population establishment (Pigot & Tobias 2013; Figueira et al. 2019). However, the climatic barrier of high latitude ecosystems may be ameliorated by positive interactions with native species, availability of suitable habitats and abundance of more nutritious food (Smith et al. 2018; Miranda et al. 2010; Siren & Morelli 2019). Therefore, the outcome of species range-extensions and contractions depends on the strength and interactive effects of biotic and climatic conditions (Cahill et al. 2012; Ockendon et al. 2014; Siren & Morelli 2019). Yet, there is little consensus on the extent to which abiotic and biotic factors determine range limits and how this differs at trailing and leading edge limits (Louthan et al. 2015; Alexander et al. 2018; Godsoe et al. 2018), especially in marine systems (Donelson et al. 2018). Although evidence for the impact of biotic interactions on species extension bounds at high and low latitudes are rare, previous studies (e.g. Araujo & Luoto 2007**;** Godsoe et al. 2017) have emphasized the need to integrate ecological theory to better understand how and under what conditions biotic factors influence range limits, especially considering increasing threats from climate change (Guisan et al. 2013; Parmesan 2006).

Predation is a strong top-down force governing the stability and structure of natural communities (Holt 1977). Whilst native communities gain new prey and predators through climate-driven range expansions, range-extending species are relieved from natural predators but encounter unknown prey and predators in their invaded ranges (Carthey & Blumstein 2017). The emergence of such new predator-prey interactions will determine the persistence of range-extending species and the future of the historically native ecosystem structure, and hence affect human use of these resources, such as recreational and commercial fisheries (Louthan et al. 2015; Figueira et al. 2019). The outcomes of predator-prey interactions depend on the ability of range-extending individuals to maintain efficient escape performance from unknown native predators under altered climatic conditions (Preuss & Faber 2003; Lyon et al. 2007; Djurichkovic et al. 2019). Although animals can learn how to recognize a threat and escape through previous experiences and social interactions (Hoare & Krause 2003; Kelley & Magurran 2003; Paijmans et al. 2020), the environmental conditions play a crucial role in the organism's defensive performance (Domenici et al. 2007). Changes in temperature, for example, can affect swimming performance through changes in individual's aerobic scope (Farrel 2002; Figueira & Booth 2010, Johansen & Jones 2011) and its underlying physiological mechanism, especially in ectotherms (Hanel & Wiese 1996**;** Wakeling 2006; Domenici et al. 2007; Szabo et al 2008). Predicting the outcome of novel predation-prey interactions in climate-altered environments is key to understanding the potential invasion of range-extending species in recipient communities (Nagelkerken & Munday 2016).

In addition to having to adapt to new predators, range-extending species also need to deal with novel competitors (Wittwer et al. 2015; Alexander et al. 2015). The structure of communities is shaped by interactions between inferior and superior competitive species leading to competitive exclusion, resource partitioning and specialization in niche use (Chesson 2000). The emergence of new competitive interactions is driven by the flexibility of range-extending species to fill unoccupied niches in their invaded ranges as well as their competitive ability (MacDougall et al. 2009; Mayfield & Levine 2010, Li et al. 2015). By occupying an open niche, range-extending species may avoid competition and coexist with native species, hence increasing the species diversity of recipient communities (Hutchinson 1959). In cases when native and range-extending species occupy the same niche and resources are limiting, competitive exclusion is likely to occur (Weiher & Keddy 1999; Chesson 2000). These two predictions of niche occupancy theory are encapsulated in Darwin's naturalization conundrum (Darwin 1859, Rejmánek 1996, Procheş et al. 2008, Thuiller et al. 2010). Species with similar resource requirements may only coexist if resources are not limiting; otherwise, the outcome of competition is driven by relative competitor performance (Mayfield & Levine 2010; Gallien et al. 2015). Whilst range-extending species with superior competitive ability increase their chances to establish in novel environments to the detriment of native species, native species with higher competitive ability may resist the invasion – biotic resistance (Masciocchi et al. 2010; Paini et al. 2008). In biological invasion theory, competition is known to be a key determinant of invasion success because alien species are usually better competitors than native species (Sakai et al. 2001; Vila & Weiner 2004). However, the unknown environment of recipient communities (e.g. low water temperature) can affect some aspects of species behaviour, giving a competitive disadvantage to the range-extending species which in turn would affect their behavioural interactions with local species (Figueira & Booth 2010; Figueira et al. 2019). Many studies discuss biological interactions as underlying mechanisms for species invasion within terrestrial systems (Schlaepfer et al. 2011; Peers et al. 2014; Estrada et al. 2017); yet biotic factors and interactions that facilitate invasion in marine ecosystems have largely been neglected.

Habitat structure can significantly reduce high losses during the pre- and post-period of marine larval settlement – which is a period characterized by high mortality rates generally caused by predation susceptibility (Holbrook & Schmitt 2002; Forrester & Steele 2004; Hixon & Jones 2005) – by providing individuals with refuges, enhancing their survivorship (Beuker

& Jones 1997). As such, finding a suitable habitat to recruit into in temperate ecosystems will be the first challenge faced by range-extending species like coral reef fishes that exhibit dispersive larval stages. Ocean warming has directly and indirectly altered temperate marine habitats (Wernberg et al. 2016), such as driving a phase-shift from kelp-dominated to barren-dominated stage caused by the poleward extension of warm-adapted temperate sea-urchin *Centrostephanus rodgersii* (Ling et al. 2009; Johnson et al. 2005). This shift to barren states might facilitate the presence of tropical fishes on temperate reefs, which tend to avoid macroalgae-forming habitats (Beck et al. 2017). However, similar to warming, ocean acidification has also driven modifications of temperate habitats (Nagelkerken & Connell 2015; Connell et al. 2018). Yet, not much is known of how ocean acidification in combination with warming might transform temperate habitat composition and consequently the rate of topical species range-extension in temperate ecosystems.

AIMS AND BACKGROUND

The goal of this thesis was to study the processes and mechanisms that might facilitate or buffer the successful establishment of tropical range-extending fishes and the consequent emergence of novel communities in their invaded temperate ranges along the southeast Australian coast under ocean warming. Over the past twenty years the temperate eastern coast of Australia has been receiving an increased annual influx of tropical fishes larvae during the summer (~100 species) (Booth et al. 2007) triggered by ocean warming and strengthening of major poleward oceanic currents (East Australia Current) (Ridgeway 2007; Hobday & Pecl 2014), thus making the temperate Australian coast a tropicalisation hotspot (Feary et al. 2014). These tropical range-extending fishes are called ‘tropical vagrant fishes’ because they are still unable to tolerate and survive the cold winter temperatures. As such, they are still temporary inhabitants of Australian temperate ecosystems (Djurichkovic et al. 2019; Figueira et al. 2009; Figueira & Booth 2010). However, as ocean temperatures continue to increase, the abundance, diversity and the number of individuals that overwinter has steadily increased, and predictions are that future permanence will occur as the climate continues warming (Booth et al. 2018). Although there is a growing number of studies predicting the potential success of range-expanding tropical fishes in temperate reefs, the influence of species behavioural plasticity, biotic interactions and other climatic stressors still need to be investigated in depth. To understand what mechanisms might drive the future establishment and impact of tropical vagrant fishes in temperate ecosystems, this thesis focuses predominantly on the combination of abiotic and biotic factors and biological interactions that occur between tropical range-extending and native-temperate fishes. This was investigated through observational surveys and manipulative underwater experiments using video recordings over a latitudinal gradient spanning from subtropical warmer waters to temperate cooler environments regions across the south-eastern Australian coast, comparing tropical vagrants and temperate species performance. The outcomes of my study are presented in four chapters (see also diagram Figure 1):

In the first data chapter (Chapter 2), I study how behavioural adjustments by range-extending tropical reef fish might facilitate their establishment in temperate marine communities. I evaluate 14 behaviours for four tropical and three temperate fish species *in situ* over a latitudinal gradient, spanning from warmer-water locations to newly invaded cool-water environments using underwater video recordings. I use a novel multivariate ellipse-based metric within a Bayesian framework, to unravel behavioural plasticity (i.e. alteration in the behavioural repertoire) and overlap in niche space of co-occurring tropical and temperate fishes by evaluating changes in their total behavioural niche space (e.g. expansion vs. contraction), shifts in their behavioural niche (alteration on the proportion of behaviours used), and changes in their degree of behavioural niche overlap.

In Chapter 3, I reveal how tropical range-extending fishes react to a threat in their invaded temperate ecosystems. These systems at their leading range edges represent potentially hostile environments, including novel predators and shelter habitats and suboptimal temperatures. I compare various antipredator behaviours between tropical and native temperate fish species across a latitudinal gradient along the SE Australian coast and across two seasons (summer vs. winter). Species antipredator behaviour (flight initiation distance, flee distance and escape speed) is instigated by using an artificial fear-eliciting stimulus to mimic a predator attack. To understand if altered antipredator behaviours could be associated by trade-offs in other vital-related behaviours, I quantify foraging, activity levels, and shelter behaviour, all of which also affect species survival and fitness. How tropical fishes behaviourally perform to unknown predators is an important determinant of their invasion rate and is a powerful regulator of their fitness and persistence in temperate ecosystems.

In the Chapter 4, I test whether the competitive ability of a common tropical range-extending fish (*Abudefduf vaigiensis*) vs a co-schooling temperate fish (*Microcanthus strigatus*) is compromised by novel temperate environmental conditions or abundance of potential local competitors at their distributional range edges. To assess this, I use an underwater manipulative experiment to study species interactions and evaluate competitive strength, based on their capacity to perceive, access, consume, and compete for prey that was experimentally provided. This chapter reveals whether competition with native temperate fishes might act in synchrony with the negative abiotic conditions of the temperate environment to buffer tropicalisation.

In Chapter 5, I first evaluate which temperate habitats best facilitate the persistence of tropical fishes. Then I study how single climate stressor effects (ocean warming vs. ocean acidification) shift temperate habitat composition and influence the abundance and community composition of tropical fish recruits. Finally, I develop a conceptual model of how current temperate habitats might be transformed under future climate change and how these regime shifts may change the rate of establishment of tropical fishes. To investigate this, I use a new approach using two different natural laboratories to study ocean warming (tropicalisation hotspots located at south-eastern Australian coast) and ocean acidification (natural CO_2 vents at New Zealand). Because it was not possible to investigate these two stressors simultaneously *in situ,* I use this approach as an “early warning” system to assess the combined consequences of ocean acidification and ocean warming at tropicalisation hotspots across temperate coastal ecosystems. Understanding regime shifts in temperate habitats and their effect on invading tropical reef fishes have direct implications for predicting tropicalisation of temperate ecosystems.

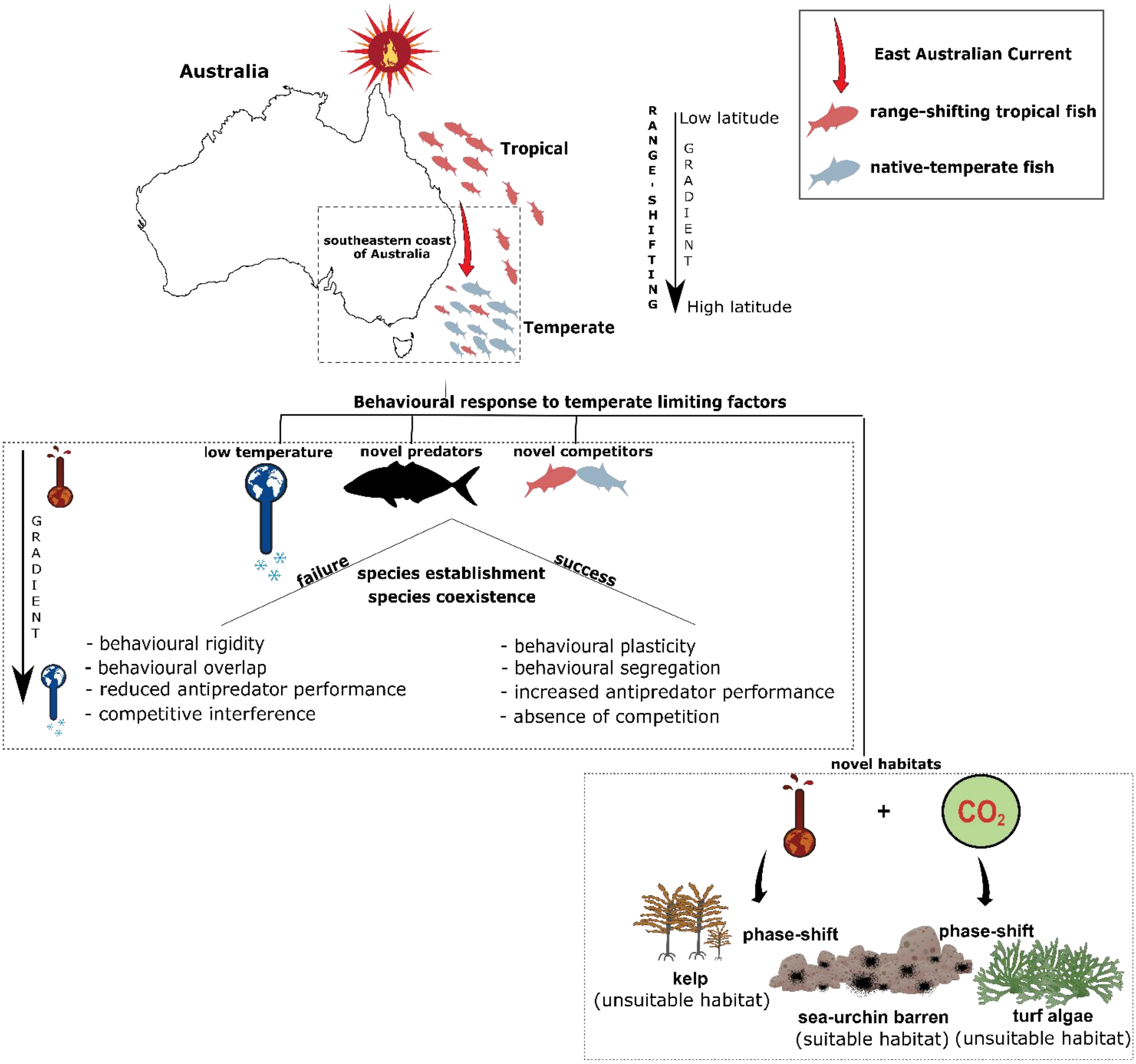

Figure 1. Conceptual diagram illustrating the mechanisms that may facilitate establishment of tropical range-extending fishes in temperate reefs after they arrive at higher latitude regions through the intensification of the East Australian Current. To successfully establish at temperate reefs, tropical species need to efficiently respond to possible limiting factor such as (1) adapt to temperatures below their thermal tolerance (especially during the winter), (2) ability to recognise unknown predators, (3) unknown competitors and (4) find suitable habitats. As often behaviour modification is the first species response to altered environments, this thesis explores how behavioural plasticity and segregation (chapter 2), anti-predator behaviours (chapter 3), and competitive performance (chapter 4) of tropical fishes over a latitudinal gradient spanning from subtropical warmer waters to temperate cooler environments regions combined with temperate habitat shifts driven by ocean warming and acidification (chapter 5) might lead to the failure or success of tropical fishes establishing in temperate invaded ranges under climate change.

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CHAPTER II

BEHAVIOURAL GENERALISM FACILITATES CO-EXISTENCE OF TROPICAL AND TEMPERATE FISHES UNDER CLIMATE CHANGE

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By signing the Statement of Authorship, each author certifies that:

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

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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ABSTRACT

Coral-reef fishes are shifting their distributions poleward in response to human-mediated ocean warming, yet the consequences for recipient temperate fish communities remain poorly understood. Behaviour modification is often the first response of species to environmental change, but we know little about how this might shape the ongoing colonisation by tropical fishes of higher-latitude ecosystems under climate change. In a global hotspot of ocean warming, we quantified 14 behavioural traits in wild fish populations as a proxy of behavioural niche space. We studied the potential of tropical fishes to persist in temperate ecosystems through behavioural plasticity, as well as the potential of temperate species to resist these tropical invasions. We found that tropical fishes modified their behavioural niches as well as increased their overall niche breadth in their novel high-latitude ranges where temperate species predominate, but maintained a moderate to high niche segregation with native temperate species across latitudes. Temperate species also modified their niches, but in contrast to tropical species, experienced an increased niche breadth towards tropical latitudes. Alterations to feeding and schooling behaviours contributed most to niche modifications in tropical and temperate species, while behaviours related to alertness and escape from potential threats contributed least. We here show that at range edges where community structures are being reshuffled due to climate change, behavioural generalism and plasticity are potential mechanisms adopted by tropical range extenders and native-temperate fishes to adjust to novel species interactions under climate change.

INTRODUCTION

Biogeographical species distributions are governed by long-term dynamics of biological-physical factors (MacArthur 1972; Peterson & Lieberman 2012). More recently, however, increased anthropogenic disturbances have facilitated a progressive and rapid global redistribution of species, which is now one of the greatest environmental impacts of climate change on species ranges (Pecl et al. 2017). The impacts of such species range shifts on the biodiversity and ecosystem functioning of recipient native communities are of similar magnitude as those caused by introduced species (Sorte et al. 2010, Verges et al. 2014; Verges et al. 2016). Yet, we still have little understanding of the mechanisms that allow range-extending species to establish in novel ecosystems and their ensuing impacts on local communities (Mack et al. 2000). Life history traits such as propagule pressure (i.e. quantity of arriving individuals; Lockwood et al. 2005) is a key process determining successful species range shifts in marine and terrestrial ecosystems (Ben Rais Lasram et al. 2008; Soeparno et al. 2012). However, traits that facilitate dispersal of larval propagules are no longer relevant once species have arrived in their novel environments (Monaco et al. 2020). To establish viable populations, animals need to tolerate or adapt to novel local conditions (Angert et al. 2011), with behavioural modifications playing a crucial role in how they interact with their novel environment. Behavioural plasticity should, therefore, increase the ability of species to persist under altered biotic and climatic conditions (Chapple et al. 2012). Although there is an increasing effort to identify the mechanisms that enable successful species range shifts, and their potential impacts on recipient communities, the critical roles of species behaviours and species interactions are still poorly understood.

One of the central tenets of species invasion success is that species that are flexible in their resource use and have broad niches are more likely to prosper in novel or dynamic environments (Warren et al. 2001; Cassey et al. 2004; Sol et al. 2005; Slatyer et al. 2013; Ducatez et al. 2015). Although some generalist species become more resource selective to avoid competition (Bolnick et al. 2010, Matis et al. 2018), species with more specialised requirements might have greater difficulty finding suitable or unoccupied niches, and hence have reduced probability of establishing a viable population within their new geographical range or modified environments (Gilman et al. 2010). Individual behaviours underpin the functional role and the ecological niche space of a species in its environment (Bergmüller & Taborsky 2010). This means that range extending species with a broad behavioural repertoire would be favoured in novel ranges over those with a narrow repertoire, as it allows them to exploit resources within a broad spectrum of ecological conditions and avoid conflict with local species (Wright et al. 2010; Feary et al. 2013; Sunday et al. 2015). Thus, tropical species that are behavioural generalists (e.g. showing diversification in feeding and predator avoidance strategies) have a higher likelihood to persevere in temperate ecosystems than tropical specialist species with a more constrained behavioural repertoire (Donelson et al. 2019).

Non-native species often reconfigure local community structures following their invasion (Mooney & Cleland 2001; Strayer et al. 2006; David et al. 2017). For example, the range-extension of tropical predators and prey species could alter existing predator-prey interactions in higher-latitude communities (Peers et al. 2014). Furthermore, the influx of novel competitors can change the dominance hierarchy of species, altering the composition of "winner" and "loser" species due to competitive displacement by species with higher competitive ability (Nagelkerken & Simpson 2013, Lauchlan et al. 2019). Such modifications of native communities can be irreversible, especially whether invaders become well established (Harborne & Mumby 2011; Nagelkerken & Connell 2015). It is assumed that invaders are more likely to establish when they do not share the same niches as local species, because this would allow them to occupy unfilled ecological niches in native communities (Thuiller et al. 2010; van Kleunen et al. 2010). For example, range expanding species that are morphologically similar to native species are predicted to have lower success rates in their establishment and persistence, owing to greater interspecific competition with native species (Azzuro et al. 2014; Smith et al. 2016). In contrast, species which are dissimilar in their niches to local species are more likely to succeed in invaded areas by avoiding direct competition with resident species (Shea & Chesson 2002). Hence, the degree to which tropical species overlap in their behavioural niches with temperate species can provide strong insights in the degree to which they will experience resource competition with already established species and their likelihood to increase their population sizes in temperate ecosystems under climate change.

The potential of range-extending species to impact local communities depends on how local species ('natives') will interact and respond to the incursion of these novel 'intruders' (Berthon 2015). In some cases, natives will fail to adjust, resulting in local or global extinction (Case & Bolger 1991; Fritts & Rodda 1998). Alternatively, natives may possess traits (pre-adaptation) that may diminish the impacts of invaders, allowing their successful coexistence (Vermeij 1982; Strauss at al. 2006). Ecological insights into the dynamic of invasion are typically studied by comparing traits of invaders with those of the native (recipient) community (Belmaker et al. 2009; Edelist et al. 2013; Elleouet et al. 2014). Such comparisons allow an understanding of how invasions might alter local communities and whether the structure and fundamental niche of the recipient community influences invasion success (Parker et al. 2006; Lockwood et al. 2013; Ricciardi et al. 2013). Understanding the similarity in behavioural niche of invasive-tropical and native-temperate species is key to identifying the mechanisms underlying successful establishment of tropical species in temperate ecosystems under changing climate.

Natural climate change laboratories – e.g. southeast Australia that is a hotspot of range-shifting tropical species mediated by ocean warming (Ridgway 2007; Hobday & Pecl 2014) – allow for a unique investigation of the performance of sympatric novel tropical and native temperate species under ongoing climate change in the wild. Over the last two decades, hundreds of tropical fish species have been newly recorded along temperate Australian coasts, and the expectations are that this number will continue to further increase with the intensification of ocean warming and strengthening of poleward ocean currents (Figueira & Booth 2010; Booth et al. 2018). Although studies increasingly focus on identifying the mechanisms that facilitate tropical species range expansions (e.g. Figueira et al. 2009; Basford et al. 2015; Djurichkovic et al. 2019; Paijmans et al. 2020), the way in which these species alter their behaviours (i.e.

phenotypic flexibility) to adjust to their novel environments is poorly understood. Behavioural modifications could include foraging, swimming speed, competitive performance, and social interactions (Tuomainen & Candolin 2011). In addition, we know little about how native temperate species alter their behaviours to adjust to these invasions.

Here we study how behavioural traits of range-extending tropical reef fish might facilitate their establishment in temperate marine environments by testing two underlying mechanisms: 1) their behavioural phenotypic plasticity (i.e. behavioural repertoire), and 2) their degree of behavioural overlap with native temperate species. We assessed this for 4 tropical and 3 temperate fish species *in situ* over a 730-km latitudinal gradient, spanning from warmer-water latitudes to newly invaded cool-water environments. We used a novel multivariate ellipse-based metric within a Bayesian framework, to unravel behavioural plasticity and overlap in behavioural niche space of co-occurring tropical and temperate fishes by evaluating: 1) changes in the breadth of their behavioural niches (e.g. expansion vs contraction), 2) shifts in the composition of their behavioural niches (alteration in the predominant behaviours expressed), and 3) differences in their degree of behavioural niche overlap (Fig. S1). This approach enhances our understanding of the likelihood of tropicalisation success as a function of species behavioural niche space and phenotypic plasticity, and their potential effects on temperate species and ecosystems under climate change.

METHODOLOGY

STUDY SITE

Ten sites at five locations were selected over a latitudinal gradient along the SE Australian coastline (Fig. 1) and sampled during the summers of 2017 and 2018 when recruitment of tropical fishes peaks (reaching up to 25% of the total benthic fish density). Four sites at the two lowest latitude locations were sampled ("low" latitude) and these represented subtropical temperatures and biotic features (fish species and habitat composition) closest to that of the native ranges of tropical fish: two sites at South West Rocks and two sites at Port Stephens. Three sites at one location were selected at Sydney, which is considered here as the middle-latitude ("middle"): Shelly Beach, Little Manly and Narrabeen. Finally, three sites at two locations were selected at higher latitude and represented cooler areas with unfamiliar environmental features for tropical fishes ("high" latitude): Narooma (one site) and Merimbula (two sites). The sites were chosen based on an 18-yr study of ongoing tropical fish settlement on shallow rocky reefs along the coast of SE Australia (Booth et al. 2007; Booth et al. 2018). From the perspective of tropical fishes, the low latitude region is considered as a native area, while the middle and high latitudinal regions are considered as range-extension areas.

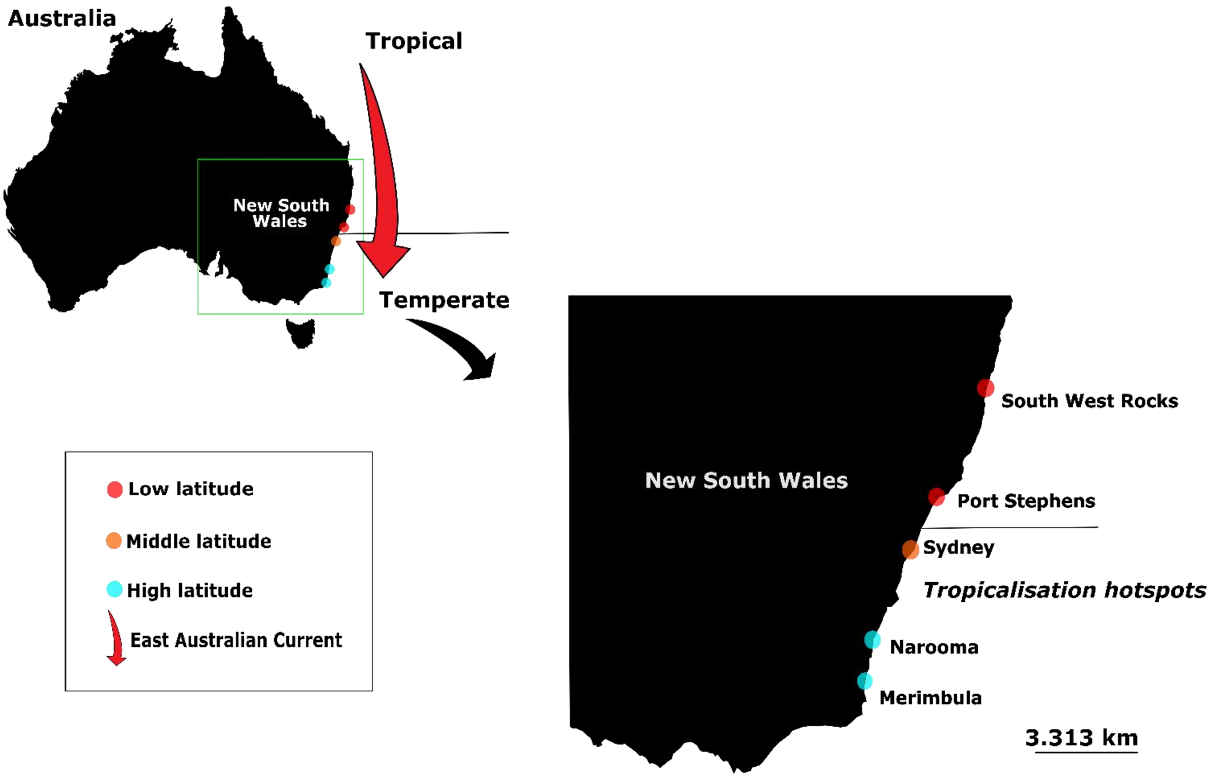

Figure 1. Map showing the 5 locations of the *in situ* behavioural video recordings. Red circles show the locations in the 'low latitude' region: two sites at South West Rocks (30°52'34"S, 153°4'2"E and 30°53'0"S, 153°2'17"E) and two sites at Port Stephens (32°42'56"S, 152°10'58"E and 32°44'55"S, 152°10'19"E). Orange circle indicates the 'middle latitude' region, with three sites: Shelly Beach (33°48'1.13"S, 151°17'31.23"E), Little Manly (33°48'23"S, 151°17'8"E) and Narrabeen (33°42'7"S, 151°18'21"E). Blue circles indicate the locations in the 'high latitude' region: one site at Narooma (36°12'54"S, 150°7'51"E) and two sites at Merimbula (36°53'40"S, 149°55'25"E and 36°44'13"S, 149°58'58"E).

STUDY SPECIES

Only the most commonly observed tropical coral reef fish species were used in this study to allow for sufficient replication within each region, while the temperate native species were chosen based on their known interactions and schooling with the respective tropical fishes (see Smith et al. 2018). A total of 7 species (4 tropical vagrants and 3 temperate native species) were investigated. The four tropical fish species selected and the number of replicates (i.e. individual fishes sampled for behaviours) were: two water-column omnivorous feeders (1) sergeant major, *Abudefduf vaigiensis* (low = 22, middle = 22, high = 20) and (2) scissor tail, *Abudefduf sexfaciatus* (low = 8, middle = 6, high = 7), and two grazing benthic herbivores (3) dusky surgeonfish, *Acanthurus nigrofuscus* (low = 19, middle = 17) and (4) convict surgeonfish, *Acanthurus triostegus* (low = 19, middle = 18). Because the two surgeonfishes could not be found in sufficient numbers ($n \geq 5$) at the high latitude sites, they were not included in the analysis for this location. The three temperate native species selected and their number of replicates were one pelagic omnivore (1) mado, *Atypichthys strigatus* (low = 6, middle = 10, high = 8) and one benthic omnivore (2) stripey, *Microcanthus strigatus* (low = 21, middle = 17, high = 17), and one territorial benthic herbivore (3) white-ear damselfish, *Parma microlepis* (low = 9, middle = 20, high = 20) (Fig. S3).

DATA COLLECTION AND STUDY DESIGN

Behaviours of each fish were quantified from underwater video recordings. First, visual surveys were performed to locate recruits and juveniles at the selected sites. Then, underwater cameras (GoPro's) attached to dive weights were placed on the reef substratum at a distance of ~ 50 cm from the target fish. This distance was based on a trade-off between being able to film recruits of tropical fishes with a relatively small body size (< 5 cm) on temperate reefs versus maintaining some distance to avoiding disturbing them with the presence of a camera. Usually recruits and early-stage individuals of these species are site-attached, allowing suitable recordings of their behaviours *in situ*. Based on Nanniga et al. (2017), after placing the camera, the first 3 min of recording was considered as acclimation time to the recorder before behaviours were quantified for a total of 10 min. per recording. We did not observe any clear disturbance of the fish by the presence of the camera. To evaluate whether species behaviour differed over a range of climatic and biotic conditions, recordings were conducted over a latitudinal temperature gradient ranging from native to non-native habitats for both tropical and temperate fish assemblages (see under Study area above).

FISH BEHAVIOUR

Fourteen behavioural variables within seven behavioural traits were quantified for each individual fish from the video footage (Table S1): (1) water column position (proportion of time spent on the bottom vs. midwater), (2) boldness/shyness (estimated by the proportion of time a fish was away from shelter vs. sheltered or near to shelter). In this case individuals were considered bold when they were > 5 times their body length away from the nearest shelter, while shy individuals were considered when a fish spent more time sheltering inside a crevice or under an overhanging rock and/or foraging near to shelter at a distance from 0–5 times their body length. (3) alertness (number of times that an individual showed a rapid increase in their swimming speed, often when larger temperate fishes approached), (4) feeding behaviour (evaluated when an individual was biting and measured as: I) the proportion of time a fish spent feeding, and II) the number of bites taken (e.g. bite rate) on the substratum vs particles in the water column), (5) schooling interactions (proportion of time solitary, or schooling with conspecifics, heterospecific tropical species, heterospecific temperate species, and mixed-species groups), (6) agonistic behaviour (number of times chasing or escaping from other individuals), and (7) activity levels (proportion of time that the individual was moving). All these behaviours were measured in each latitude independent on the type, amount and distance to food and shelter availability. Although the amount and distance to shelter and food items can affect species behaviour, these variables were considered as been intrinsic of each latitudinal region.

All observations were consecutively quantified from the videos using the software VLC media player (version 2.1.3) and for each focal individual all 14 behaviours were analysed. To avoid pseudo-replication only one individual of each species was analysed in each video recording when they were schooling with conspecifics. Due to the variable time that individuals spent in front of the camera, each individual was analysed for a max. of 2 min. so as to standardise the data collection and effort. Observation times of a few minutes per individual have been found to suffice for a representative estimate of an individual's behaviour (McClanahan et al. 1999; Biro et al. 2010; Francini-Filho et al. 2010). Behavioural traits were analysed using two different approaches (see Table S1 for more details), either through continuous counts (e.g. bite rates, alertness, chasing, escaping) or in each 10-sec intervals during the observation time (e.g. water column position, boldness, feeding, schooling interactions), which were then transformed to proportion of time (%) spent performing the behaviours.

STATISTICAL ANALYSES

To assess the multidimensional behavioural niche space (i.e. behavioural repertoire) of species across a latitudinal gradient the SIBER R-package was used. Because of the high multivariate space of our data set (14 behaviours) and because SIBER only works with two axes, we first performed a Redundancy Analysis (RDA) on the 14 behaviours to reduce the multidimensional data set to bidimensional coordinates (i.e. along two axes, Table S2). This allowed us to establish the relative position in the behavioural space for each individual per species (these values are based on the relative importance of behavioural traits in the initial dataset; Villeger et al. 2008, Laliberte & Legendre 2010). As behavioural observations were measured on different scales (e.g. count and percentage data), we first standardised the data and then used the Hellinger transformation to avoid zero inflation in the RDA (Paliy et al. 2016) to calculate a distance matrix that was used as the basis for the RDA. RDA outputs are similar to those obtained from Principal Component Analysis (Legendre & Legendre 1998). However, RDA is a constrained ordination that assesses how much variation in the response variables (behaviours) can be explained by variation in the explanatory variables (species and latitudes) (Paliy et al. 2016). The first two RDA axes together accounted for 68% of the observed variation in behavioural data for the tropical and temperate species. The order of the behaviours that showed the best representation of the two principal RDA axes are listed in (Table S2).

The two axes that were extracted from the RDA analysis were then used to create standard ellipse areas (SEA) representing relative behavioural niche breadths in a bivariate space, where the standard ellipse area represents the bivariate standard deviation. We generated Bayesian credible intervals of the standard ellipse area for each species at each latitude (low, middle, and high). Species with larger ellipse areas therefore exhibit a higher variability among individuals in behavioural trait space, and can therefore be considered as a behaviourally more generalistic species (Fig. S1). In contrast, species with smaller ellipse areas express only a restricted range of behavioural traits, tending towards behavioural specialisation. Bayesian estimation of standard ellipses (SEA_b) allows for an unbiased estimate of relative niche area even for small sample sizes, in contrast to metrics such as convex hulls, which are sensitive to small sample size (Jackson et al. 2011). SEA were corrected (SEA_c) to minimize bias caused by small sample sizes (Jackson et al. 2011, 2012).

The SEA_c was used to compute the overlap between species of tropical and temperate fish populations within each latitude and the overlap of each individual species across latitudes. We consider a significant species overlap to have a proportion of >60%, the same criteria as used in the Schoener diet overlap index (Schoener 1968; Guzzo et al. 2013). We then used a Bayesian approach (SEA_b) as described in Jackson et al. (2011) to obtain confidence intervals for behavioural niche space. These confidence intervals allow for statistical comparisons of the sizes of behavioural niche areas among species within latitudes. All analyses were performed using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011).

Competitive interactions, measured as number of chases per minute, were compared between tropical and temperate species using permutational ANOVAs to evaluate aggressive behaviour between individuals of the same species (conspecifics), heterospecific tropical species, and heterospecific temperate species, respectively.

RESULTS

BEHAVIOURAL NICHE SHIFTS ACROSS LATITUDES

Both tropical and temperate species reshuffled their behavioural niche as a function of latitude (Fig. 2, Fig. S1a). In general, behavioural niche space (based on standard ellipse areas) of individual species showed low to moderate overlap among latitudes (19–60% overlap, Table 1). Only 5 out of 17 species-latitude comparisons showed relatively high overlap (62–70%, Table 1) in behavioural niche space. Feeding, schooling interactions, and to a lesser extent activity levels appear to be the most important behavioural traits driving latitudinal differences in behavioural niche space within individual tropical and temperate species (Fig. S3).

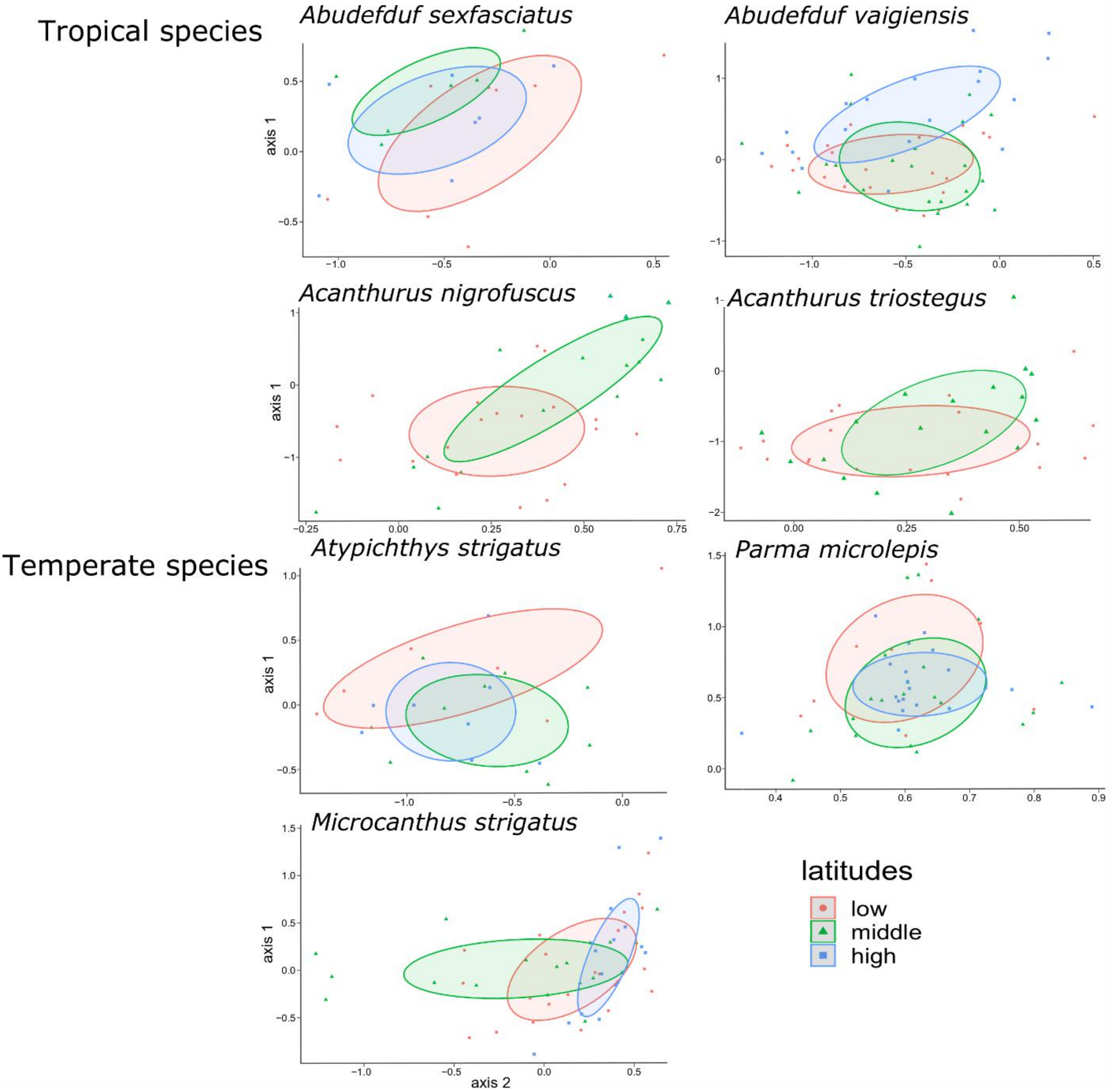

Figure 2. Behavioural niche space based on the 14 behaviours measured for each tropical vagrant and native-temperate species at three different latitudes (low = equatorward, middle and high = poleward). The standard ellipses (SEAc) for each species are based on a 40% confidence interval. The data points represent each observed fish (sample) per species. See Table 1 for overlap in niche space.

Table 1. Behaviour similarity among latitudes based on the overlap (%) of the standard ellipses area (SEAc) of each species per latitude. Bold numbers indicate the latitudes that showed a negligible behavioural shift (behaviour similarity between latitudes > 60%) following the criterion used by Schoener 1968 and Guzzo et al. 2013.

Affinity	**Species**	**Latitude**	**Overlap (%)**
Tropical	*Abudefduf sexfasciatus*	low vs. middle	42
		low vs. high	**68**
		middle vs. high	**68**
	Abudefduf vaigiensis	low vs. middle	**70**
		low vs. high	45
		middle vs. high	46
	Acanthurus nigrofuscus	low vs. middle	50
	Acanthurus triostegus	low vs. middle	59
Temperate	*Atypichthys strigatus*	low vs. middle	30
		low vs. high	37
		middle vs. high	**61**
	Parma microlepis	low vs. middle	56
		low vs. high	39
		middle vs. high	**62**
	Microcanthus strigatus	low vs. middle	41
		low vs. high	37
		middle vs. high	19

BEHAVIOURAL NICHE EXPANSION ACROSS LATITUDES

The behavioural niche breadth (behavioural repertoire) of tropical vagrant fishes showed an expansion with increasing latitude (i.e. from warm to colder waters), except for a deviation of *A. sexfasciatus* at low latitude (Fig. 3, Fig. S1b, Table S3). Temperate native fishes showed the opposite pattern, with an increase in niche space towards lower latitudes (i.e. from cold to warmer waters).

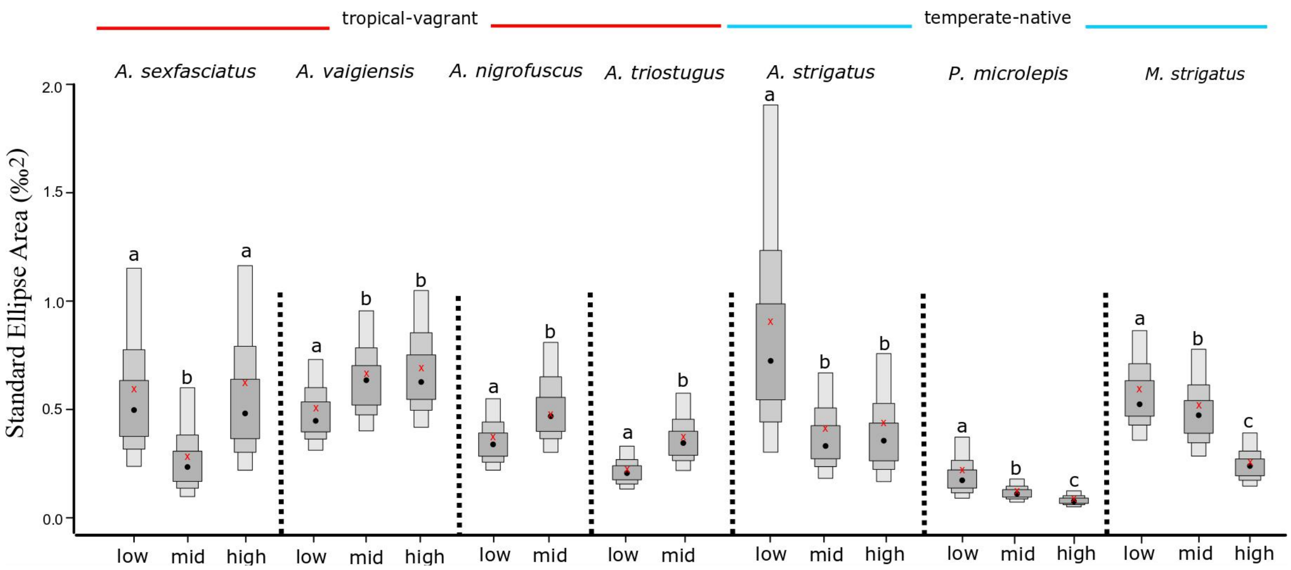

Figure 3. Bayesian estimation of the size of the standard ellipses areas (SEAb) based on 14 behaviours (i.e. behavioural niche space) of tropical and temperate species at each latitude (low, mid = middle, high). Shown are Bayesian estimates (• = mode) with 50%, 75% and 95% credible intervals (shaded boxes), and maximum likelihood estimates of the means (x). Different letters above the bars indicate significant differences (increase or decrease) in behavioural niche breadth among latitudes for each species (see Table S3 for statistical results).

BEHAVIOURAL NICHE OVERLAP BETWEEN TROPICAL AND TEMPERATE SPECIES

Behavioural niche space of tropical and temperate species exhibited a low to moderate overlap independent of latitude, ranging from 0% to 53% in the low latitude, 0% to 61% in the middle, and 1% to 59% in the high latitude, respectively (Fig. 4, Fig. S1c, Table 2). Moderate niche overlap between tropical and temperate species was driven at all three latitudes by co-schooling planktonic feeders, viz. the tropical *Abudefduf vaigiensis* and *Abudefduf sexfasciatus* with the temperate *Atypichthys strigatus*, whilst significant niche overlap (61%) between tropical and temperate species was only found for one pair (*Abudefduf vaigiensis* vs *Atypichthys strigatus* at middle latitude) out of all 30 species-pair combinations across latitudes. Moderate and significant overlap in behavioural niche space between these co-schooling tropical and temperate zooplanktivores was driven by feeding and schooling behaviours at all three latitudes, but especially in the middle (Fig. S4).

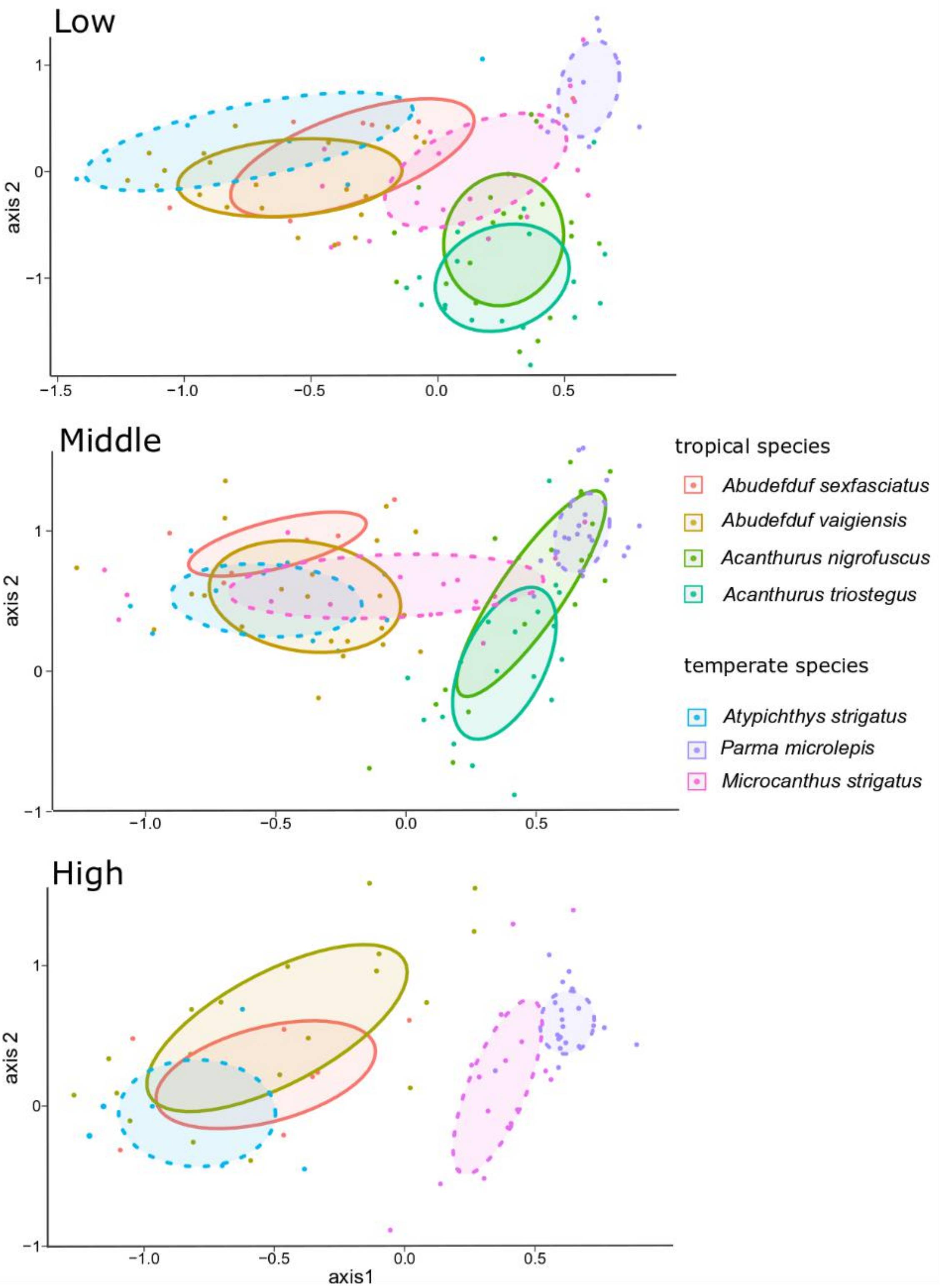

Figure 4. Standard ellipse areas (SEAc) showing the degree of overlap in behavioural niche space among and within tropical species (solid circles) and temperate species (dashed circles) across a latitudinal gradient. SEAc were calculated from the two axes extracted from a multivariate analysis (RDA) based on 14 species behaviours per latitude. The data points represent each observed fish (sample) per species. The ellipses are based on a 40% confidence interval. See Table 2 for degree of niche overlap.

Table 1. Behaviour similarity among latitudes based on the overlap (%) of the standard ellipses area (SEAc) of each species per latitude. Bold numbers indicate the latitudes that showed a negligible behavioural shift (behaviour similarity between latitudes > 60%) following the criterion used by Schoener 1968 and Guzzo et al. 2013.

a)

Low latitude Affinity	Pairs of species		Overlap (%)
Tropical vs. Tropical	***Abudefduf sexfasciatus***	***Abudefduf vaigiensis***	**60***
	Abudefduf sexfasciatus	*Acanthurus nigrofuscus*	18
	Abudefduf sexfasciatus	*Acanthurus triostegus*	8
	Abudefduf vaigiensis	*Acanthurus nigrofuscus*	14
	Abudefduf vaigiensis	*Acanthurus triostegus*	10
	Acanthurus nigrofuscus	***Acanthurus triostegus***	**70***
Tropical vs. Temperate	*Abudefduf sexfasciatus*	*Atypichthys strigatus*	53
	Abudefduf sexfasciatus	*Parma microlepis*	15
	Abudefduf sexfasciatus	*Microcanthus strigatus*	42
	Abudefduf vaigiensis	*Atypichthys strigatus*	43
	Abudefduf vaigiensis	*Parma microlepis*	2
	Abudefduf vaigiensis	*Microcanthus strigatus*	31
	Acanthurus nigrofuscus	*Atypichthys strigatus*	9
	Acanthurus nigrofuscus	*Parma microlepis*	12
	Acanthurus nigrofuscus	*Microcanthus strigatus*	41
	Acanthurus triostegus	*Atypichthys strigatus*	0
	Acanthurus triostegus	*Parma microlepis*	5
	Acanthurus triostegus	*Microcanthus strigatus*	25
Temperate vs. Temperate	*Atypichthys strigatus*	*Parma microlepis*	6
	Atypichthys strigatus	*Microcanthus strigatus*	24
	Parma microlepis	*Microcanthus strigatus*	24

b)

Middle latitude Affinity	Pairs of species		Overlap (%)
Tropical vs. Tropical	*Abudefduf sexfasciatus*	*Abudefduf vaigiensis*	37
	Abudefduf sexfasciatus	*Acanthurus nigrofuscus*	0
	Abudefduf sexfasciatus	*Acanthurus triostegus*	0
	Abudefduf vaigiensis	*Acanthurus nigrofuscus*	0
	Abudefduf vaigiensis	*Acanthurus triostegus*	12
	Acanthurus nigrofuscus	*Acanthurus triostegus*	56
Tropical vs. Temperate	*Abudefduf sexfasciatus*	*Atypichthys strigatus*	37
	Abudefduf sexfasciatus	*Parma microlepis*	0
	Abudefduf sexfasciatus	*Microcanthus strigatus*	30
	Abudefduf vaigiensis	***Atypichthys strigatus***	**61***
	Abudefduf vaigiensis	*Parma microlepis*	0
	Abudefduf vaigiensis	*Microcanthus strigatus*	47
	Acanthurus nigrofuscus	*Atypichthys strigatus*	5
	Acanthurus nigrofuscus	*Parma microlepis*	26
	Acanthurus nigrofuscus	*Microcanthus strigatus*	18
	Acanthurus triostegus	*Atypichthys strigatus*	6
	Acanthurus triostegus	*Parma microlepis*	20
	Acanthurus triostegus	*Microcanthus strigatus*	20
Temperate vs. Temperate	*Atypichthys strigatus*	*Parma microlepis*	0
	Atypichthys strigatus	*Microcanthus strigatus*	49
	Parma microlepis	*Microcanthus strigatus*	12

c)

High latitude Affinity	Pairs of species		Overlap (%)
Tropical vs. Tropical	*Abudefduf sexfasciatus*	*Abudefduf vaigiensis*	59
Tropical vs. Temperate	*Abudefduf sexfasciatus*	*Atypichthys strigatus*	59
	Abudefduf sexfasciatus	*Parma microlepis*	2
	Abudefduf sexfasciatus	*Microcanthus strigatus*	9
	Abudefduf vaigiensis	*Atypichthys strigatus*	43
	Abudefduf vaigiensis	*Parma microlepis*	1
	Abudefduf vaigiensis	*Microcanthus strigatus*	7
Temperate vs. Temperate	*Atypichthys strigatus*	*Parma microlepis*	0
	Atypichthys strigatus	*Microcanthus strigatus*	0
	Parma microlepis	*Microcanthus strigatus*	20

AGGRESSIVE BEHAVIOURS AMONG SPECIES

Aggressive behaviours of most tropical and temperate species towards other individuals was always highest against their own species, and very low towards heterospecific tropical or heterospecific temperate species, independent of latitude. *Parma microlepis* was the only species that showed high aggression towards other species (Fig. S5).

DISCUSSION

We here show that behavioural niche shifts and niche expansion are potential mechanisms adopted by sympatric tropical vagrant and native-temperate fishes to adjust to changing community structures under climate change. Whilst tropical fishes showed behavioural phenotypic plasticity at poleward temperate latitudes, temperate species exhibited a behavioural niche shift and expansion at warmer compared to cooler regions. As such, temperate species show niche expansion at their trailing warm-water edges where tropical species are invading, whilst tropical species show niche expansion at their leading edges where they are invading novel temperate ecosystems. This suggests that at range edges where community structures are being reshuffled due to climate change, phenotypic plasticity in behaviours might be a mechanism to avoid competition and significant niche overlap (Menge 1979; Huey et al. 2012). In these temperature mixing zones where temperate and tropical species increasingly co-exist, elevated species diversity is often observed (Horta e Costa et al. 2014), with ensuing competition for resources (Hawkins et al. 2009). Behavioural niche expansion reflects increased generalism, which might be beneficial under environmental change (Whitney & Gabler 2008) and increased competition (Svanback & Bolnick 2007; Huss et al. 2008). Generalists are more flexible in resource use than specialists, facilitating species adaptation and coexistence (Clavel et al. 2011; Slayter et al. 2013; Ducatez et al. 2015). As such, tropical and temperate species that are behavioural generalists are more likely to persist under climate change, with tropical fishes persisting in non-native temperate areas and temperate species resisting tropicalisation.

Behavioural niche segregation facilitates the persistence of tropical fishes in temperate reefs by allowing their coexistence with native species. Such segregation can also provide advantages to temperate fishes under invasion of tropical species. Overall, tropical fishes showed only a low to moderate degree of behavioural niche overlap with temperate native species, independent of latitude. Feeding and schooling behaviours contributed most to the behavioural differences between tropical and temperate species suggesting that they might rely on different prey resources despite their co-schooling (Kingsbury et al. 2019). It has been postulated that species that highly overlap in any of their n-dimensional niche space (e.g. climatic, diet) with other species are more susceptible to competition (Hutchinson 1957). When resources are sparse, and species share niches, extinction may eventually occur if they do not shift their niches (Human & Gordon 1996). Conversely, high resource availability may allow coexistence regardless of significant niche overlap (Sale 1974; Connell 1980). The observed behavioural segregation between tropical and temperate species might result from them having evolved separately, allowing them to coexist even when resources are scarce due to intrinsic species characteristics that allow them to utilise a different range of resources (Connell 1980). Additionally, aggressive behaviour was almost absent among tropical and temperate species, with the highest rates of aggressiveness observed towards individuals of the same species. When the competitive ability between species is small, species can coexist despite occupying relatively similar niches (Mayfield & Levine 2010). Our findings therefore suggest that the behavioural segregation and the low incidence of inter-species aggression could facilitate the coexistence of tropical and temperate native fishes in temperate ecosystems.

Feeding behaviour (foraging position) and schooling interactions (school composition) were the behaviours most responsible for behavioural niche alteration across latitudes for both tropical and temperate species. A possible explanation is the difference in prey availability across these regions. Optimal foraging theory predicts that individuals modify their behaviour to maximise their physiological integrity (fitness) as prey availability changes (Stephens & Krebs 1986; Sih & Christesen 2001). A study using stable isotopes performed at the same sites and on the same species showed that prey types consumed by tropical and temperate species differed regionally (from low to high latitudes) (Miranda et al. 2018; Kingsbury et al. 2019), which can explain the changes in their foraging behaviour as observed in the present study. Although some species may exhibit maladaptive behaviours under environmental change with resulting fitness loss (e.g.

increased anxiety) (Sih et al. 2004), the tropical vagrant and temperate species that we examined showed more favourable behavioural choices at cooler non-native areas and warmer regions, respectively. On temperate reefs, some tropical vagrant fishes form schools with local temperate species, suggesting that these species are flexible in employing social interactions with unknown species (see Figure S6). This novel co-schooling can increase survivorship of tropical vagrants in temperate ecosystems (Smith et al. 2018; Pajimans et al. 2019). Schooling with native fishes provides a source of information about the new environment and enables learning (e.g. recognition of unfamiliar prey and predators) (Hoare & Krause 2003), a strategy that is advantageous to range-extending tropical social species in temperate regions. By adopting such adaptive behaviours (i.e. flexibility in schooling, foraging and boldness), tropical fishes can maintain their fitness, and reduce predation risk and competition, facilitating their survivorship in novel temperate ecosystem under climate change.

The importance of behavioural niche plasticity has been largely overlooked in climate change studies. Studies of ecological niche breadth and niche overlap have mainly been based on diets, e.g. stomach contents or stable isotope analyses (Newsome et al. 2007; Kingsbury et al. 2019). Only recently, other proxies such as morphology and foraging behaviour have been used to measure ecological niche space, which can be related to habitat use, feeding and locomotion (Azzuro et al. 2014; Brandl & Bellwood 2014; Smith et al. 2016). However, studies using these realised niche metrics mainly focus on feeding ecology and habitat use, ignoring the fact that species show complex adaptive behaviours that reflect an important ecological niche as well (Gouraguine et al. 2019). Furthermore, instead of relying on a single behaviour, as is common in climate change studies (Beck et al. 2016), we use an established approach from stable isotope studies to calculate niche breadth in a multivariate space as a proxy of behavioural plasticity. This novel approach shows that specific behaviours contribute more to the observed differences in niche space and breadth across species and regions, emphasising the importance of using multiple behaviours to test species responses to altered environments or climate change. We show that behavioural plasticity is an important mechanism that could allow coexistence and potential success of tropical vagrant invasions into temperate ecosystems under climate change.

CONCLUSION

We reveal that behaviour plasticity and behavioural generalism may be critical mechanisms deployed by tropical fish species that extend their ranges to higher latitudes under climate change, to reduce competition with local temperate species and cope with novel temperate climate and biotic conditions. Additionally, maintenance of behavioural niche segregation among tropical and temperate fish species combined with flexible schooling behaviour and the low incidence of inter-species aggression, may further mediate successful invasion of tropical fishes into temperate environments under climate change, whilst allowing generalist temperate fish species to persist.

ETHICS

All experiments were performed under animal ethics approval numbers S-2015-222A and S-2017-002 (University of Adelaide) and ETH17-1117 (University of Technology Sydney) and followed the University's animal ethics guidelines.

AUTHOR CONTRIBUTIONS

E.O.C.C, I.N., and D.J.B. conceived and designed the study, E.O.C.C. and C.M.F. collected the data, E.O.C.C. analysed the data. E.O.C.C, I.N., and D.J.B wrote the article.

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SUPPLEMENTARY INFORMATION

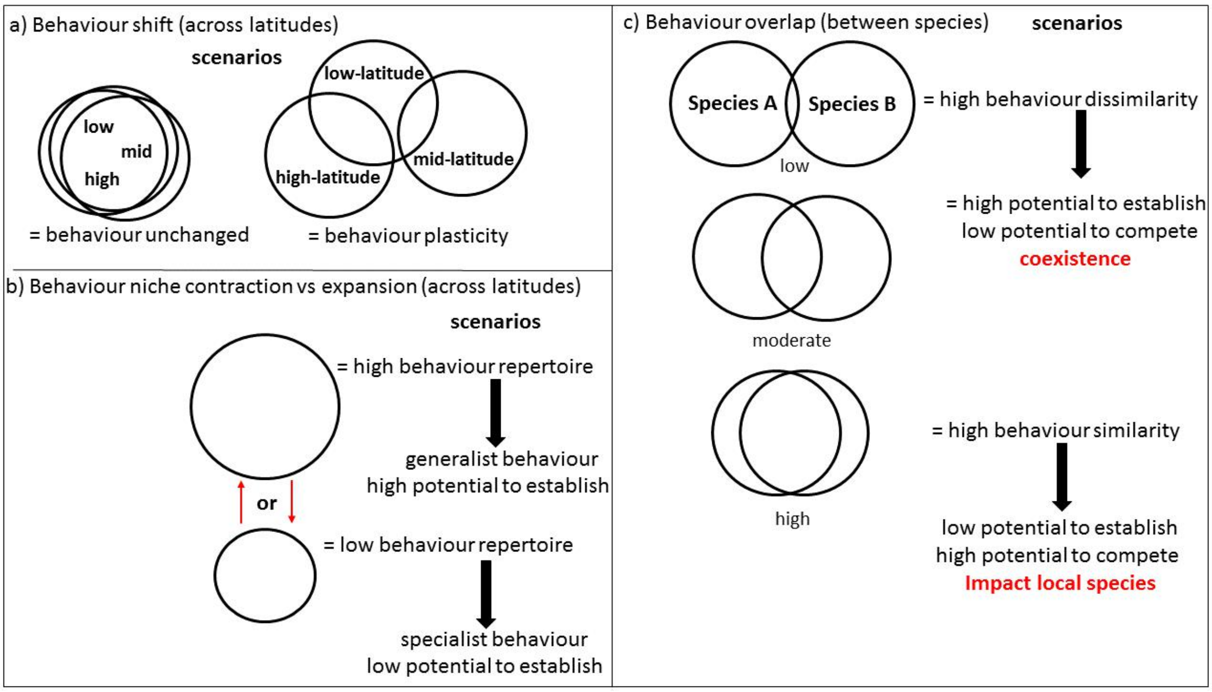

Figure S1. Conceptual diagram of possible mechanisms of behavioural niche plasticity under climate change. a) behavioural niche shift across latitude based on the positioning in niche space (individual ellipses), b) behavioural niche contraction (decreased behavioural repertoire) vs expansion (increased behavioural repertoire), indicating the extent to which a species is specialised or generalised in their behavioural niche, and c) behavioural niche overlap measured as the percentage of behavioural niche space shared between two species.

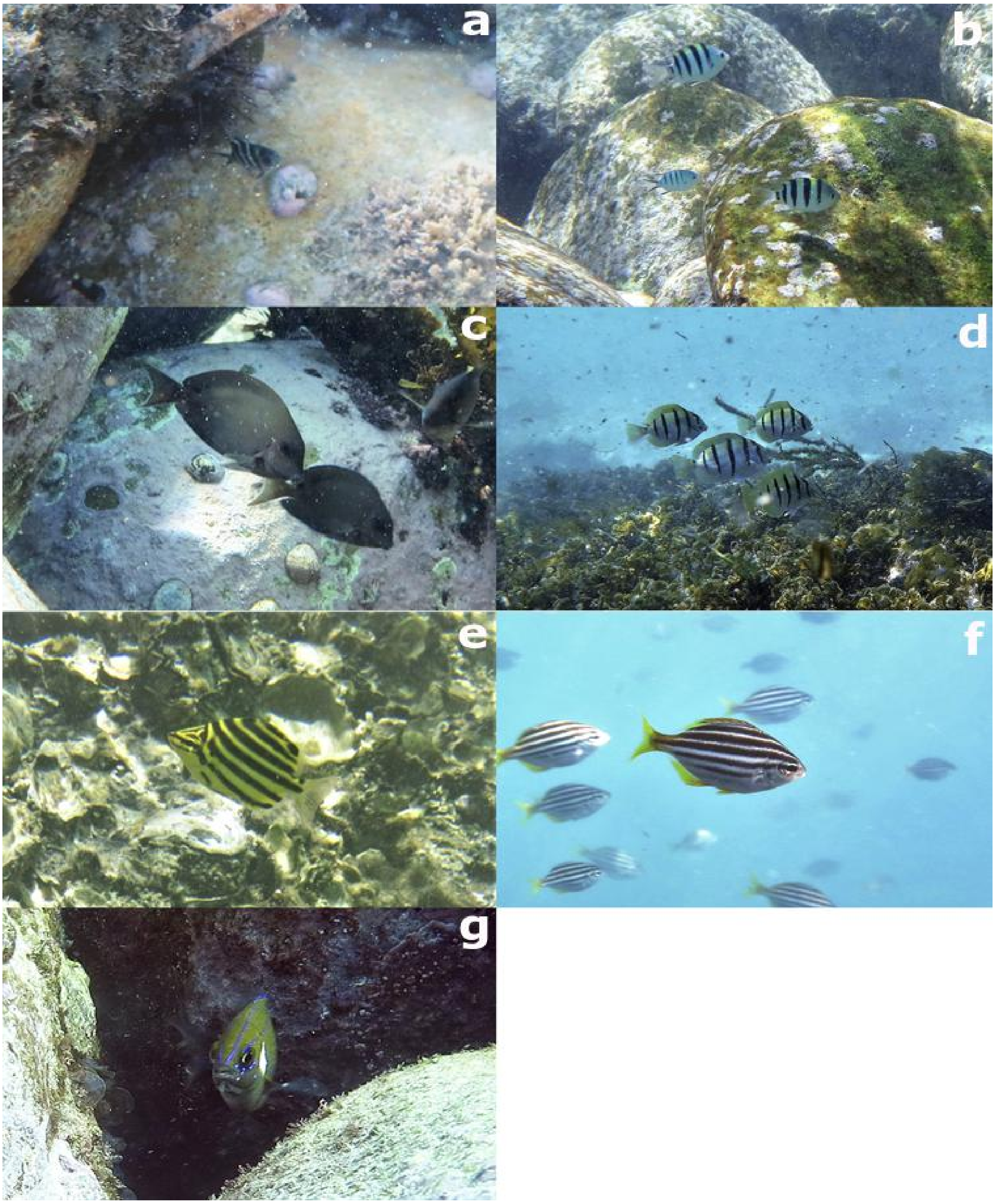

Figure S2. Tropical-vagrant and temperate-native fish species investigated in this study. Tropical fishes: a) scissor tail *Abudefduf sexfasciatus*, b) sergeant major *Abudefduf vaigiensis* (the two larger fish), c) dusky surgeonfish *Acanthurus nigrofuscus*; d) convict surgeonfish *Acanthurus triostegus*; and temperate fishes: e) stripey *Microcanthus strigatus*, f) mado *Atypichthys strigatus*, and g) white-ear damselfish *Parma microlepis*.

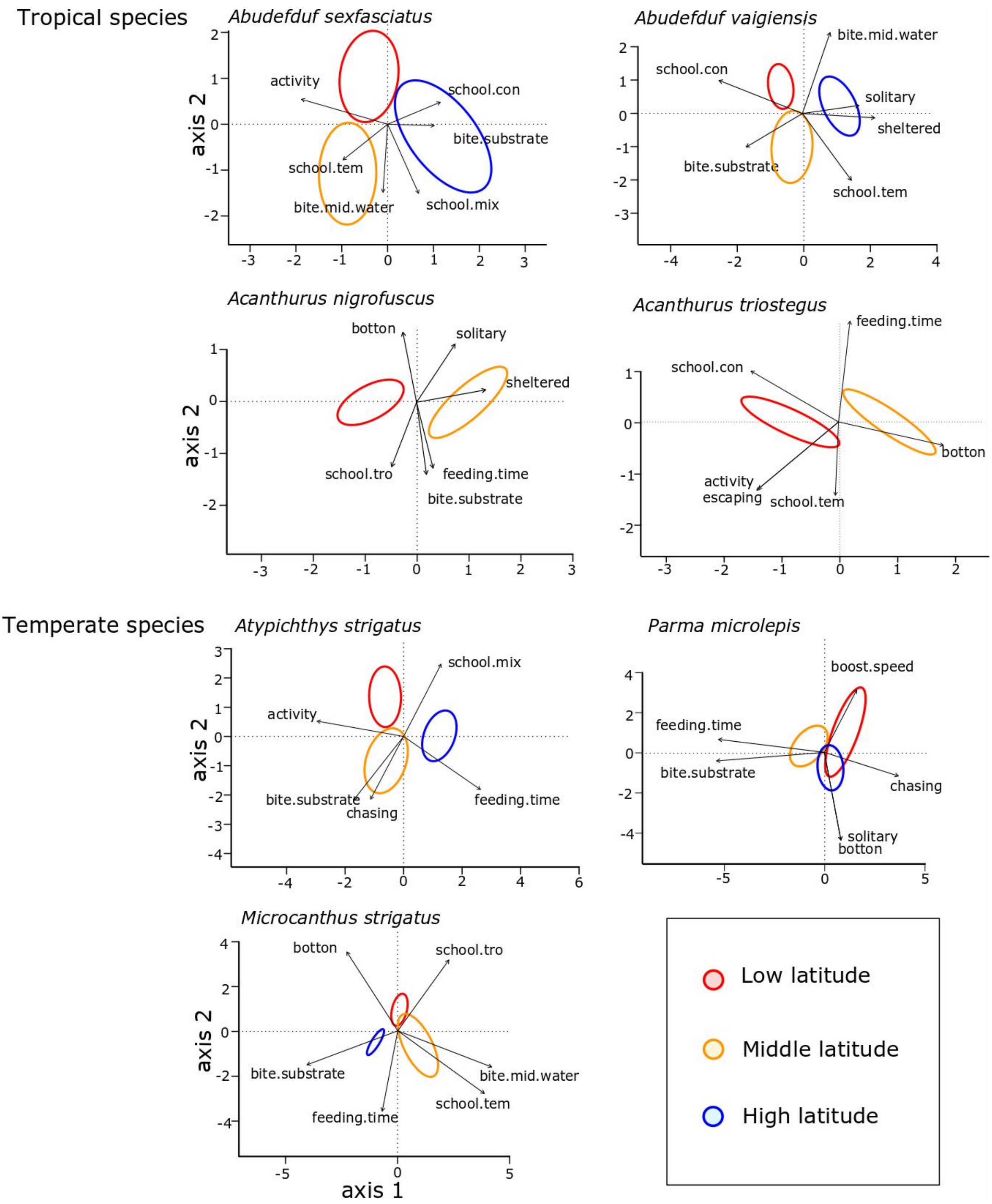

Figure S3. Redundancy analysis (RDA) showing the most influential behaviours of tropical and temperate fish species across a latitudinal gradient. Each plot represents an RDA conducted for each species separately. The vectors (black lines) show the correlation of each behaviour with each latitude and their lengths indicate the magnitude of this correlation. Behaviour abbreviations: bottom = time spent close to the substrate, school.con = schooling with individuals of the same species, school.tem = schooling with heterospecific temperate species, school.tro = schooling with heterospecific tropical species, school.mix = schooling with conspecifics and heterospecific of tropical and temperate species, boost.speed = boosted swimming (alertness), bite.substrate = # of bites on the substrate, bite.mid.water = # of bites in the water column, feeding.time = time feeding, activity = time moving.

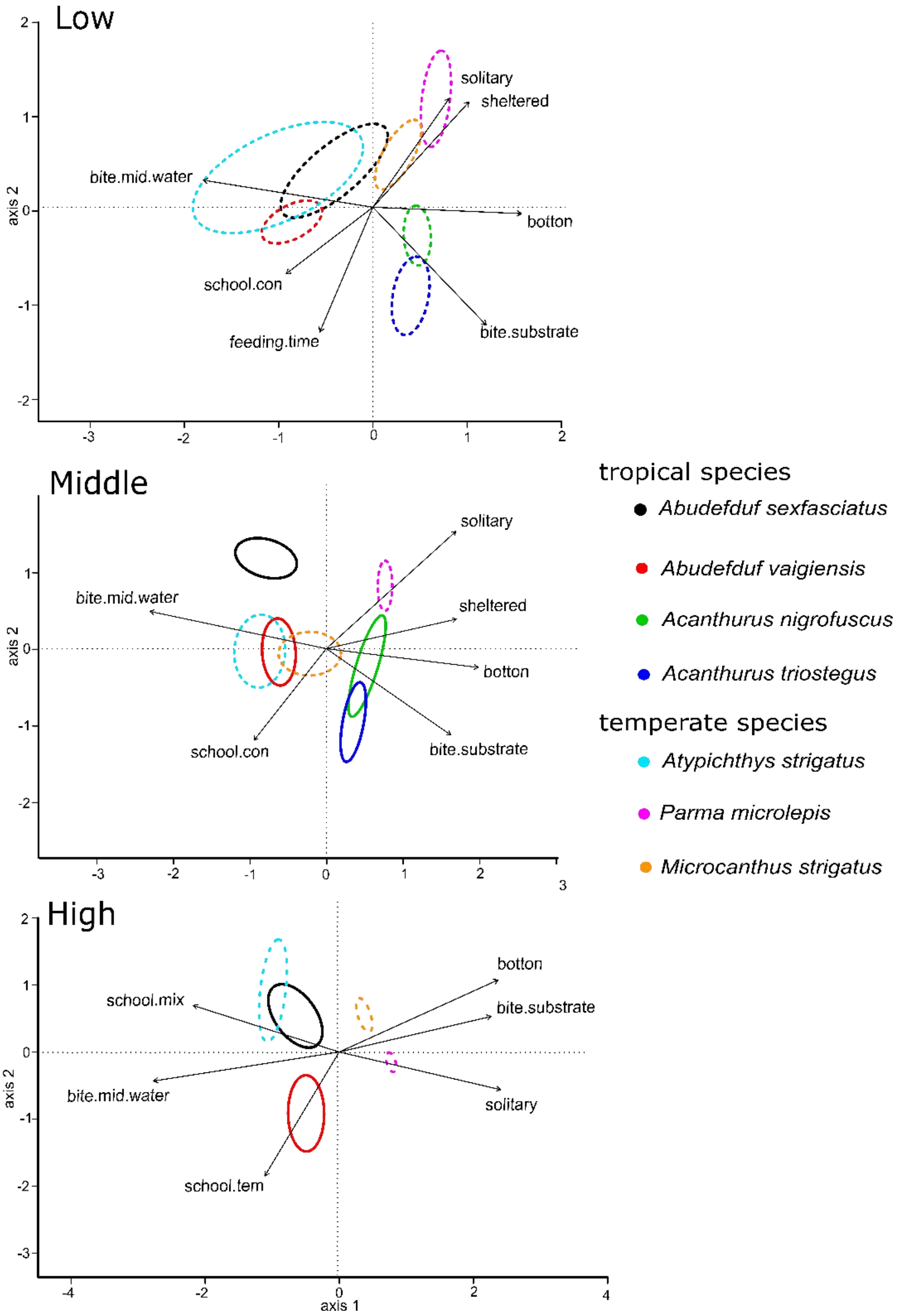

Figure S4. Redundancy analysis (RDA) showing the principal behaviours responsible for the (dis)similarities of tropical (solid circles) and temperate fish species (dashed circles) across latitudes. The vectors (black lines) show the correlation of each behaviour with each latitude and their lengths indicate the magnitude of this correlation. Behaviour abbreviations: bottom = time spent close to the substrate, school.con = schooling with individuals of the same species, school.tem = schooling with heterospecific temperate species, school.tro = schooling with heterospecific tropical species, school.mix = schooling with conspecifics and heterospecific of tropical and temperate species, boost.speed = boosted swimming (alertness), bite.substrate = # bites on the substrate, bite.mid.water = # of bites in the water column, feeding.time = time feeding, activity = time moving

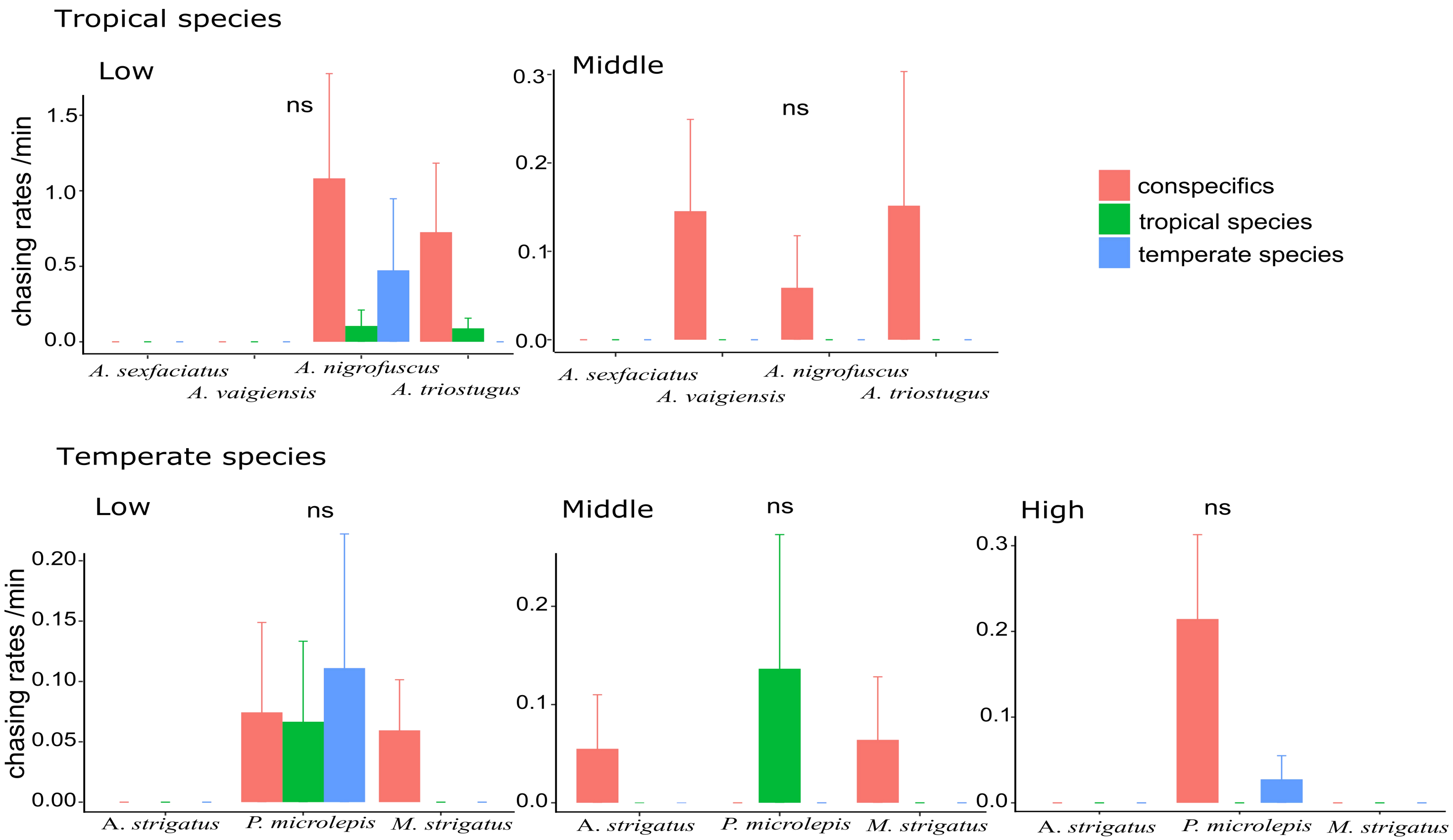

Figure S5. Aggressive behaviours based on chasing rates per minute (mean + SE) of fish species across latitudes (low, middle, high) towards conspecifics, and other tropical or temperate fish species. ns = not significant. Tropical fishes showed no chasing behaviour at high latitude.

Figure S6. Tropical vagrant fishes, *Abudefduf vaigiensis* (left photo) and *Acanthurus triostegus* (right photo) schooling with native-temperate species *Microcanthus strigatus* (stripey) at Narooma Wharf (high latitude) and Shoal Bay, Port Stephens (low latitude), respectively.

Table S1. Ethogram of the 14 behavioural variables within the 7 behavioural traits used to characterise species behavioural niche space across latitudes. State event: behaviours observed in 10-sec intervals in each period of observation; Point event: behaviours observed continuously during each observation time of each fish.

Behavioural traits	**Behavioural variables**	**Brief description**	**Type**
Water column position	Bottom vs. Midwater	individuals positioned within a distance of 0–5 times their body length from the substratum were considered on the bottom, whilst those at > 5 times their length as midwater	State event
Boldness/Shyness	Exposed vs. Sheltered or Near shelter	exposed was considered when an individual was > 5 times their body length away from the nearest shelter; sheltered was considered as when a fish was inside a crevice or under an overhanging rock and near shelter when foraging at a distance of 0-5 times their body length to the nearest shelter	State event
Alertness	Boosted swimming	abrupt body movement to any possible threat (e.g. larger fish's presence)	Point event
Feeding time	Feeding vs. Not feeding	proportion of the time that the individual was feeding	State event
	Bite rates - substrate vs.	number of bites on the substrate	Point event
	Bite rates - water column	number of bites in the water column	Point event
Schooling interactions	Conspecifics vs.	proportion of time schooling with individuals of the same species	State event
	Tropical species vs.	schooling with heterospecific tropical species	State event
	Temperate species vs.	schooling with heterospecific temperate species	State event
	Mixed species vs.	schooling with conspecifics and heterospecific tropical and temperate species	State event
	Solitary	individuals that did not occur in a school	State event
Agonistic interaction	Chasing rates	number of aggressive interactions (rapid swimming directly towards another individual)	Point event
	Escaping rates	number of times moving away from an aggressor	Point event
Activity	Active vs. Inactive	measured as fish movement, and individuals that moved >5 times their body length away from their previous position were considered active.	State event

Table S2. Loading values indicating the order of contribution of behavioural variables that are best represented by the first two RDA axes. The higher the values, the more the variable contributes to the principal component.

Behaviours (vectors)	RD1	RD2
bite rates - water column	-0.8910	0.2111
bottom position	0.7595	-0.1187
bite rates - substrate	0.6299	-0.5317
solitary	0.5977	0.5805
sheltered	0.5780	0.4172
feeding time	-0.4870	-0.3561
schooling with conspecifics	-0.3833	-0.3368
schooling mixed species	-0.4667	-0.0555
schooling with tropical species	0.0547	-0.3570
chasing rates	0.2490	-0.1935
schooling with temperate species	-0.2361	0.0339
activity (time moving)	-0.1169	-0.0975
boosted swimming (alertness)	0.1099	0.0712
escape rates	0.0916	-0.0746

Table S3. Comparison of behavioural niche breadth of tropical and temperate fishes between latitudes based on the standard ellipse area for small sample sizes (SEAc* - ‰^{2}) and Bayesian inference (SEAb - ‰^{2}). Values of the SEAb represent the probability of the ellipse area of one latitude to be significantly larger than the other. Substantial evidence for a difference between latitudes is indicated by probabilities larger than 0.60 (bold numbers). **—** = species that were not observed at high latitude sites. L = low, M = middle, and H = high latitude, respectively.

Affinity			Behavioural niche difference probability			
	Species		Low	Middle	High	Comparison of latitudes
Tropical	*A. sexfasciatus*		0.59	0.28	0.62	L=H>M
		Low		**0.90**	0.51	
		Middle			**0.90**	
	A. vaigiensis		Low	Middle	High	L<M=H
			0.51	0.67	0.69	
		Low		**0.81**	**0.86**	
		Middle			0.59	
	A. nigrofuscus		Low	Middle		L<M
			0.37	0.47	**—**	
		Low		**0.87**		
	A. triostegus		Low	Middle		L<M
			0.22	0.37	**—**	
		Low		**0.94**		
Temperate	*A. strigatus*		Low	Middle	High	L>M=H
			0.90	0.41	0.44	
		Low		**0.95**	**0.92**	
		Middle			0.52	
	P. microlepis		Low	Middle	High	L>M>H
			0.22	0.12	0.09	
		Low		**0.89**	**0.99**	
		Middle			**0.88**	
	M. strigatus		Low	Middle	High	L>M>H
			0.59	0.52	0.25	
		Low		**0.68**	**0.99**	
		Middle			**0.97**	

CHAPTER III

CORAL-REEF FISHES ARE MORE RISK-AVERSE AT THEIR POLEWARD RANGE LIMITS

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ii. permission is granted for the candidate in include the publication in the thesis; and

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ABSTRACT

As climate warms, tropical species are expanding their distribution to higher latitudes where they are confronted with unfamiliar environmental conditions, including novel predators and habitats. Predation strongly regulates ecological communities, and range-extending species that maintain an effective antipredator strategy have a higher likelihood to persist in non-native environments. Here, we test this hypothesis by comparing antipredator behaviours between range-extending coral reef fishes and native temperate fishes across a latitudinal temperature gradient. Tropical fishes became more risk-averse (increased shelter use and flight initiation distance) and decreased their feeding rates as latitude increased in their novel temperate ranges. Their shelter use and flight initiation distance were similar across seasons, suggesting that risk aversion was a more important driver of behavioural modification at higher latitudes than reduced seawater temperatures. However, their feeding and activity levels were lower in winter than in summer, suggesting a detrimental temperature effect on some vital behaviours. In contrast, native temperate fishes did not alter their behaviours across latitude. We conclude that tropical range-extending species face a trade-off between vigilance and foraging in novel temperate ecosystems, where short-term survivorship is prioritised at a cost of reduced foraging during the initial stages of range-extensions.

INTRODUCTION

A central tenet of biological invasions is that invaders create novel species interactions in recipient communities (Pearse & Altermatt 2013; Carthey & Blumstein 2017). Thus, species that have always been spatially separated are enabled to interact when their ranges overlap due to invasions, leading to novel ecological communities (Williams & Jackson 2007; Lurgi et al. 2012). Climate change has intensified this phenomenon by forcing species dispersion to regions where they did not occur historically and therefore these species need to adapt to survive under these new local conditions (Hale et al. 2016; Lee-Yaw et al. 2019). Marine animals exhibit faster range extensions than terrestrial organisms due to characteristics such as high propagule production and distant dispersal by ocean currents (Parmesan & Yohe 2003; Poloczanska et al. 2013). For example, tropical fishes are among the fastest organisms to shift their distribution to cooler latitudes, facilitated by increased ocean temperatures and strength of major ocean currents such as Australia's East Australian Current (EAC) (Booth et al. 2007, 2011). The recruitment of tropical fish species has progressively increased in temperate ecosystems around the world, for example in south-east Australia, which is a hotspot of ocean warming and tropicalisation. Yet, we do not fully understand potential mechanisms that might limit or facilitate these species to succeed in these new environments. Survivorship of tropical species is still low at higher latitudes due to detrimental minimum winter temperatures, but as the climate continues to warm permanent establishment will become inevitable (Figueira et al. 2009; Figueira & Booth 2010). Biological factors such as novel habitats, prey, predators and species interactions are also important (Sexton et al. 2009) but remain largely unstudied.

Predation is a key process regulating the structure of biological communities. Species that show adaptability in their antipredator strategies have a higher chance of survival in changing ecological environments (Orrock & Fletcher 2014). Prey species that expand their range under climate change are relieved from historically important predators, but gain novel ones in their new environments (Carthey & Blumstein 2017). For example, tropical fish species might be particularly vulnerable to a native temperate predator because of the lack of eco-evolutionary predator-prey experiences (Sih et al. 2010; Saul & Jeschke 2015). In addition to learning to recognise and respond appropriately to novel predators, range extending species have to maintain efficient escape performance in altered or suboptimal abiotic conditions (Lyon et al. 2007; Djurichkovic et al. 2019).

Temperature is a major environmental determinant of life-history processes and governs basic physiological functions and behavioural traits, including predator evasion (Szabo et al 2008; Biro et al. 2010). Temperature can affect antipredator responses through changes in swimming performance (Figueira & Booth 2010, Johansen & Jones 2011), muscle development (Hanel & Wiese 1996), contractile properties of the swimming muscles (Wakeling 2006), and neural control (Szabo et al 2008). In addition to temperature effects, local habitat structure and composition can influence success of anti-predator defences, which may be less effective in novel habitats (Lonnstedt et al. 2013, Lonnstedt et al. 2014). Fishes rely strongly on olfactory cues to perceive the presence and intensity of predation threat, but unfamiliarity with olfactory cues of novel environment may make predation risk hard to assess (McCormick & Lonnstedt 2016, Nagelkerken et al. 2019). Thus, unfamiliarity with novel temperate habitats and predators combined with the physiological effects of low temperatures can significantly alter antipredator performance of tropical fishes in their novel temperate ranges.

Effective antipredator behaviours rely on many factors related to perceived risk and costs of escaping, such as predator size relative to prey, schooling behaviour and proximity to refuge (Domenici 2010). Life stage is also an important determinant of predation risk, because young individuals are naïve and slow-moving, and hence more susceptible to predation (Sogard 1997; Day et al. 2002). Therefore, anti-predator success during early life stages is predominantly driven by their size, growth rate, and antipredator performance (Holmes & McCormick, 2010; Allan et al. 2013). Escape responses also depend on the behavioural-environmental context (Domenici 2010). Despite some differences among studies and species-specific responses (Januchowsky-Hartley et al. 2011, Nunes et al. 2019), social species are often more vigilant and confident in terms of their antipredator behaviour than solitary species (Lima & Bednekoff 1999, Benevides et al. 2018). Hence, range-extending species that school are more likely to persist during the initial stages of range extensions than solitary species (Smith et al. 2018), as they can learn (e.g. recognise unfamiliar predators) from more experienced co-schooling conspecific or native species (Hoare & Krause 2003; Paijmans et al. 2019). Habitat context, such as substrate complexity and refuge proximity, is an additional driver of antipredator behaviour. With increasing habitat complexity or decreasing distance to refuge, individuals become less vigilant and allow closer predator approaches (Nunes et al. 2015; Benevides et al. 2016). Whilst unfamiliarity with temperate climates and habitats makes early stages of coral reef fishes more vulnerable than those of temperate species, schooling with native temperate species might provide benefits to reduce their risk to temperate predators (Paijmans et al. 2020).

Risk-taking behaviour has important consequences for fitness and therefore ecological success of range-extending species (Holt & Barfield 2009; Urban et al. 2019). Although increased risk-taking can provide benefits such as more food or better habitats, it may also increase mortality risk through enhanced predator exposure (Hulthén et al. 2017). As such, many animals face a continuous trade-off between predation risk and resource acquisition (Brown et al. 2001; Rhoades & Blumstein 2007). If resources are limiting (e.g. reduced energy intake), trade-offs may occur in energy allocation towards different processes and behaviours. For example, individuals have to assess risk levels and make decisions to either spend energy fleeing from a threat or preserving energy for other physiological process (*sensu* Energy budget theory; Cooper et al. 2002). Burst swim responses from predators have a strong energetic cost, which disrupts other fitness-related behaviours such as foraging (Domenici & Blake 1997; Ramasamy et al. 2015). As such, to maintain physiological homeostasis, continuous decisions are made based on starvation-predation risk trade-offs among behavioural traits (*sensu* Economic hypothesis; Ydenberg & Dill 1986). However, climatic and biotic alterations can affect the decision-making of organisms and consequently their behavioural responses, which in turn can affect survivorship (Sih et al. 2011).

Here we investigate how tropical fishes adjust their antipredator behaviours as they extend their ranges to temperate ecosystems under climate change. These ecosystems at the leading distribution edges of tropical species represent potentially hostile environments, with novel predators and shelter habitats in addition to suboptimal temperatures. We compare various antipredator behaviours between tropical and sympatric native temperate fish species across a 730-km latitudinal temperature gradient along the SE Australian coast. To understand if altered antipredator behaviours lead to trade-offs in other behaviours, we also quantified vital behaviours such as foraging, activity levels, and shelter behaviour, all of which affect species survival and individual fitness (Sih 1992; Lind & Cresswell 2005). Phenotypic flexibility in behaviours by range extending species in response to novel predators and shelter habitats is a key determinant of their invasion success at higher latitudes, and is a strong regulator of their persistence and expansion in temperate environments.

METHODOLOGY

STUDY AREA

The study locations were selected across a latitudinal gradient along the coast of SE Australia (Fig. S1), from subtropical warmer-water locations to temperate cool-water environments. Data collection was conducted in 2017-2018 during the summer and early autumn (February-April) and post-winter (September). The study sites were categorised as ‘low’ (30° S), ‘middle’ (33° S) and ‘high’ latitudes (36° S) along the coast of New South Wales. The low latitudinal location consisted of two sites at South West Rocks and is characterised by warmer waters (~25 °C summer means, Table S1) and kelp-free shallow rocky reefs, showing the highest similarity to coral reefs. Tropical reef fishes have been present at this site for a long time, but there is no evidence of breeding populations. The high latitude location comprised one site at Narooma and three sites at Merimbula and had the coolest summer temperatures of all three locations (~21 °C). This southernmost location is representative of a fully temperate rocky reef ecosystem, and harbors much higher densities of temperate fishes and much lower densities of tropical fishes than the low latitude location. Finally, the middle latitude location comprised three sites in Sydney, representing a transition zone with intermediate temperatures (seawater ~23 °C during summer) and habitats (kelp as well as increasing tropical coral presence, Booth & Sear 2018) compared to the low and high latitude locations. This location is a hotspot of tropicalisation, which has seen increasing rates of tropical fish invasions over the last two decades (Fowler et al. 2017). The specific study sites were chosen based on known settlement areas of tropical fish on shallow rocky reefs along the coast of SE Australia from an 18-yr fish survey (Booth et al. 2007; Booth et al. 2018). From the perspective of tropical fishes, we considered the low latitude location as part of their native area, while the middle and high latitude locations are considered as range-extension areas.

STUDY SPECIES

A major challenge in studying range-extensions of coral reef fishes is that the abundance and diversity of tropical species that recruit into recipient temperate ecosystems varies monthly and annually. These species are considered tropical vagrants as they are only temporary inhabitants of temperate reefs, particularly common during summertime. As there are many pulses of recruitment during the summer, tropical fishes occur on temperate reefs in different life stages, from recruits to juveniles. However, their presence drops rapidly during autumn, whilst during winter most species die because of the cold temperatures, hindering their possibility to reach the adult phase (Figueira et al. 2009; Figueira & Booth 2010). Because of this, their abundances are lower across seasons with increasing latitude (Fig. S2, Table S2). The peak temperatures at which the abundance of the tropical species starts to decline ranges from 21.0 °C to 23.9 °C (Booth et al. 2018) and the minimum summer temperature registered in the present study was 18.9 °C in Merimbula. To achieve reasonable replication (minimum of 10 individual fish per location) we focused on the most consistentlypresent and abundant tropical species in our study area: the sergeant major *Abudefduf vaigiensis* (Pomacentridae) and two surgeonfishes (Acanthuridae) *Acanthurus nigrofuscus* (dusky surgeonfish) and *A. triostegus* (convict surgeonfish). Because the two surgeonfishes could not be found in sufficient numbers (n ≥ 5) at the high latitude location, they were not included in the analysis for that location. For native temperate fishes, we focused on species that co-occur in the same habitat and usually school with tropical vagrant fishes (Paijmans et al. 2019): the mado *Atypichthys strigatus* and the stripey *Microcanthus strigatus* (Kyphosidae).

RISK-AVERSE BEHAVIOURS IN FISHES

To evaluate whether the antipredator performance of tropical fishes is altered by the unfamiliar conditions of recipient temperate environments and/or suboptimal winter temperatures, risk-averse behaviours were quantified along the latitudinal gradient (all species) and between seasons (summer vs. winter, only *A. vaigiensis*) and compared to that of temperate species. An artificial threat-eliciting stimulus was used to mimic a potential predator attack. The stimulus was created using a cubical PVC frame connected to a 60 cm iron rod. A GoPro camera was fixed to the top of the cubical frame and positioned towards a 30 cm metal ruler, which was positioned at the most distal end of the iron rod, pointing downwards so that the bottom half of the ruler was in view of the camera's field (see inset Fig. S3; following Nagelkerken et al. 2016). Once a target fish was found the snorkeler carefully approached the fish, moving the end of the ruler towards the fish's head at a constant speed until the ruler reached the substratum, whilst the camera was recording its escape behaviour (recording at 30 frames per second). Nagelkerken et al. (2017) showed that this approach is a good proxy for escape behaviours from real predators.

Risk-averse behaviours towards a threat were evaluated as a proxy of anti-predator performance, using three behavioural proxies. Videos were watched using VCL media player 2.0.1 to quantify: (1) flight initiation distance, which is measured as the distance between the head of the fish and the tip of the ruler at which the fish flees from the approaching threat (Fig.

S3). It indicates how close a prey allows a potential threat to approach before it escapes, (2) flee distance, which is measured as the distance between the position where the escape was initiated and where the escape was terminated (i.e. halted flee, or disappearance into shelter; Fig. S3), and (3) escape speed, which is measured as the velocity of the escape response. This was calculated by dividing the escape distance by the escape duration. In some cases where the fish fled towards or away from the camera, distances could not be measured (~16% of the samples). Only individuals that escaped in a direction parallel to the camera's field that is escaping either towards the left- or right-hand sides of the ruler, rather than towards or away from the camera could have their flee distance and escape distance measured. Across all species, a total of 206 individuals were tested during summer: *Abudefduf vaigiensis* (low latitude = 21, middle = 26, high = 24), *Acanthurus nigrofuscus* (low = 9, middle = 12), convict surgeonfish, *Acanthurus triostegus* (low = 14, middle = 11), *Atypichthys strigatus* (middle = 14, high = 17) and *Microcanthus strigatus* (low = 18, middle = 19, high = 21). In addition, 20 individual *A. vaigiensis* were tested over the winter season (low = 12, middle = 8). The ruler used to mimic the threat cue was also used in the videos as a scale to estimate the total body length of each fish to evaluate the anti-predator responses among different life stages. .

BEHAVIOURAL TRADE-OFFS

We evaluated whether there was a trade-off between risk-assessment behaviours and other important behaviours across a latitudinal gradient (all species) and between seasons (summer vs. winter, *A. vaigiensis*). To evaluate this, we analysed feeding behaviour (proportion of time feeding), boldness (time inside shelter), and activity levels (proportion of time active) for the same tropical and temperate fish species. The focal individuals were randomly selected from the same sites where the escape behaviours were measured. These individuals were different from the ones used to test escape behaviours to avoid any behavioural disturbances caused by the artificial fear-eliciting stimulus. The number of individual fishes sampled for the behaviours other than escape behaviour were: *Abudefduf vaigiensis* (low latitude = 22, middle = 22, high = 20), *Acanthurus nigrofuscus* (low = 19, middle = 17), convict surgeonfish, *Acanthurus triostegus* (low = 19, middle = 18), *Atypichthys strigatus* (low = 6, middle = 10, high = 8) and *Microcanthus strigatus* (low = 21, middle = 17, high = 17). Because the two surgeonfishes could not be found in sufficient numbers (n ≥ 5) at the high latitude location, they could not be included for this location.

Underwater GoPro cameras were attached to dive weights and positioned in front of a target fish at a distance of ~ 50 cm. This distance was chosen based on being able to accurately film fishes with a relatively small body size (≤ 5 cm) versus maintaining some distance to avoiding disturbing them with the presence of a camera. Each video recording was 10 min. long, but the first 3 minutes were used as acclimation time and were not analysed.

Behaviours were quantified using the software VLC media player and for each focal individual all behaviours were analysed from the same recording. To reduce the probability of pseudo-replication only one individual of each species was analysed in each video recording, especially when they were schooling with conspecifics. Because fishes were mobile, the time that they were within the view of the camera ranged between 20 sec. and 2 min. per recording. Such short observation times have been found to be sufficient to obtain a representative estimate of an individual's behaviour (Biro et al. 2010; Francini-Filho et al. 2010).

For the behavioural analyses, video recordings were subsequently divided into intervals of 10 seconds and fish were noted to be 'active' or 'inactive, 'sheltered', 'near shelter" or 'exposed' and 'feeding' or 'not feeding' at each interval, which were then transformed to proportion of time (%) spent performing the behaviours over the period of observation (events per unit time). Activity was measured as fish movements, and individuals that traversed a distance of more than five times their body length between two consecutive 10-sec intervals were considered 'active'. Sheltered was defined as when a fish was inside a crevice or under an overhanging rock, near shelter was defined as when the individual was foraging at a distance from 0–5 times their body length to the nearest shelter, while exposed was considered when an individual was > 5 times their body length away from the nearest shelter. Feeding behaviour was considered as an event where an individual was biting on the substrate or particles in the water column. Each individual fish was followed continuously whilst it was visible on the video recording and at each 10-sec interval the presence or absence of feeding was ascertained.

STATISTICAL ANALYSES

Permutational non-parametric ANOVAs (using the program PRIMER version 6; Anderson 2001; Anderson 2014) were used to test differences in risk-averse behaviours (flight initiation distance, escape distance and escape speed) and behaviours modulated by predation risk (feeding, activity, and sheltering time) between tropical vagrant and native temperate fish species across a latitudinal gradient. Analyses were run separately for tropical vs temperate species and for each behaviour. A total of three explanatory variables were tested: 1) latitude as a fixed factor with three levels 'low', 'middle' and 'high', 2) species as a random factor with three levels for the tropical fishes (3 species) and two levels for temperate native fishes (2 species), and 3) fish life stage as a random factor with two categorical levels, early-juveniles and juveniles (see study design in Fig. 1). Since the size for different life stages are different among species, the fixed size categories (mean total length) used were: *A. vaigiensis* (early-juveniles 2–4.5 cm, juveniles >4.5–7 cm), *A. nigrofuscus* (early-juveniles 5–6 cm, juveniles >6–8 cm), *A. triostegus* (early-juveniles 3–4.5 cm, juveniles 5–6 cm), *Atypichthys strigatus* (early-juveniles <4.5 cm, juveniles 4.5–11 cm), and *Microcanthus strigatus* (early-juveniles <5 cm, juveniles 5–9 cm), based on Clement (1991), Glasby & Kingsford (1994), Froese & Pauly (2016), Figueira et al. (2009), and Frédérich et al. (2012). The low number of tropical fish recruits (~ 2–3 cm TL) is likely due to data collection occurring after the period of major recruitment, resulting in observations of fish that had already settled over approximately two months.

Permutational ANOVAs were also used to evaluate seasonal (winter vs. summer) effects within latitudes (summer vs winter at middle and low latitudes) for flight initiation distance, feeding time, activity levels, and time in shelter for one tropical species (*A. vaigiensis*). For the summer vs winter comparison, risk-averse response was only evaluated using flight initiation distance. The other two escape responses could not be measured in winter because all individuals escaped towards or away from the camera, and fled outside of the view of the camera. The low number of replicates was due to the high mortality of tropical fishes during winter (cold stress), with *A. vaigiensis* the only vagrant species observed during this period at middle latitude. Where the number of permutations was low, a Monte Carlo test was used and post-hoc pooling of interaction terms was performed to enable a more powerful test of the main effect (only if their p-value was > 0.25; Winer et al. 1991). For significant effects ($p < 0.05$) pairwise tests were used to compare the respective means (Anderson 2001).

Permutational ANOVAs were also used to test whether the position from the shelter affected the proportion of time that each species spent feeding across locations. Two explanatory variables were tested: 1) latitude as a fixed factor with three levels ‘low’, ‘middle’ and ‘high’, and 2) shelter position as a random factor with three levels ‘inside shelter’, ‘near shelter’ and ‘exposed’.

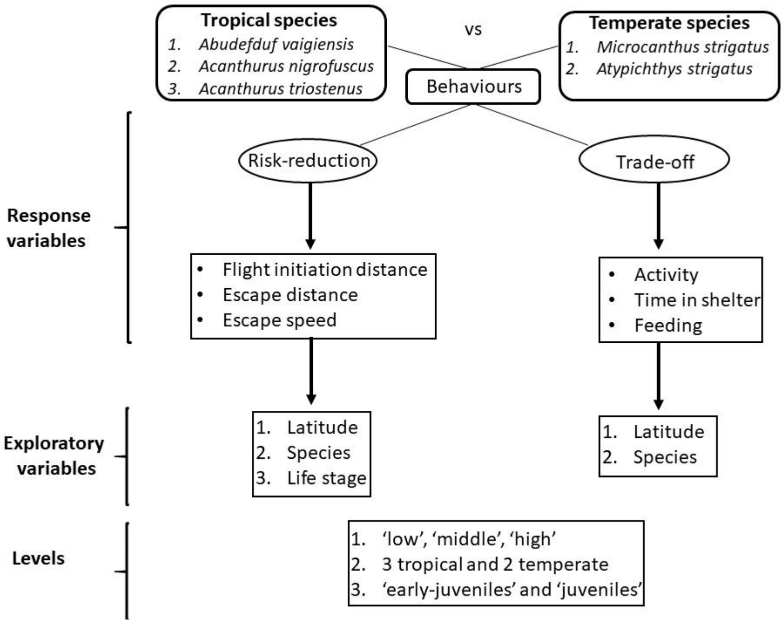

Figure 1. Diagram showing the study design. Tropical and temperate fish communities were analysed separately and for each behaviour a permutational non-parametric ANOVA was used to test for differences among latitudes, fish species, and life stage (only for antipredator behaviours).

RESULTS

IN SITU BEHAVIOURS OF TROPICAL VAGRANTS

The tropical species all showed larger flight initiation distances (i.e. higher risk aversion) with increasing latitude (Fig.2a, Table S3; 3-way ANOVA, p = 0.018), but maintained their escape speeds across latitudes under a simulated threat (Fig. S4, Table S3; p = 0.421). Escape distances (i.e. length of escape path) were similar across latitudes, except for a higher (*A. vaigiensis* early-juveniles, p = 0.012) or lower (juvenile *A. nigrofuscus*, p = 0.032) escape distance at high vs low latitude (Fig. S4, Table S3). Tropical species pooled showed reduced foraging (p = 0.013), lower activity levels (p = 0.002), and increased shelter use (p = 0.001) with increasing latitude, respectively (Figs. 2b–d, Table S4).

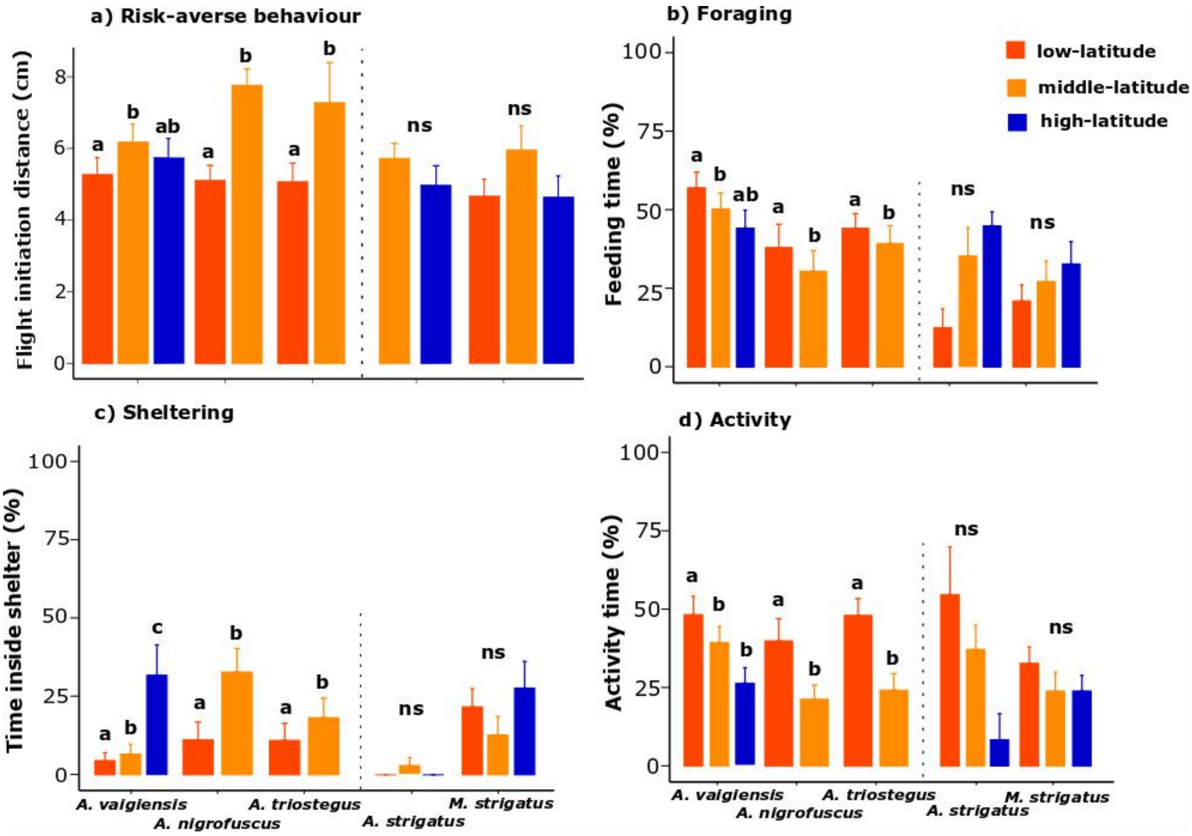

Figure 2. *In situ* behaviours (mean + SE) of tropical and temperate species as a function of latitude (low, middle, high). a) Flight initiation distance as a proxy for risk-averse behaviour towards a threat stimulus, b) proportion of the time feeding, c) proportion of the time sheltering, and d) proportion of time active. Different letters above bars indicate significant differences (see Tables S3, S4, S5, S6). ns = not significant.

Season (summer vs winter) did not affect flight initiation distance (Fig. 3a, Table S7; 2-way ANOVA, p = 0.579) or sheltering behaviour in tropical *A. vaigiensis* (Fig. 3d, 1-way ANOVA, p = 0.087), but feeding rates (Fig. 3b; p = 0.001) and activity levels (Fig. 3c; p = 0.002) were lower in winter than in summer.

IN SITU BEHAVIOURS OF NATIVE TEMPERATE FISH

Temperate species showed no difference in risk-averse behaviours (flight initiation distance, escape distance, escape speed), feeding, activity, or sheltering behaviour as a function of latitude (Fig. 2, Tables S4, S6). *M. strigatus* only showed lower escape distance at middle vs low latitude (Fig. S4, Table S4; 3-way ANOVA, p = 0.033) and *A. strigatus* lower escape speed at middle vs high latitude (Fig. S4; p = 0.050).

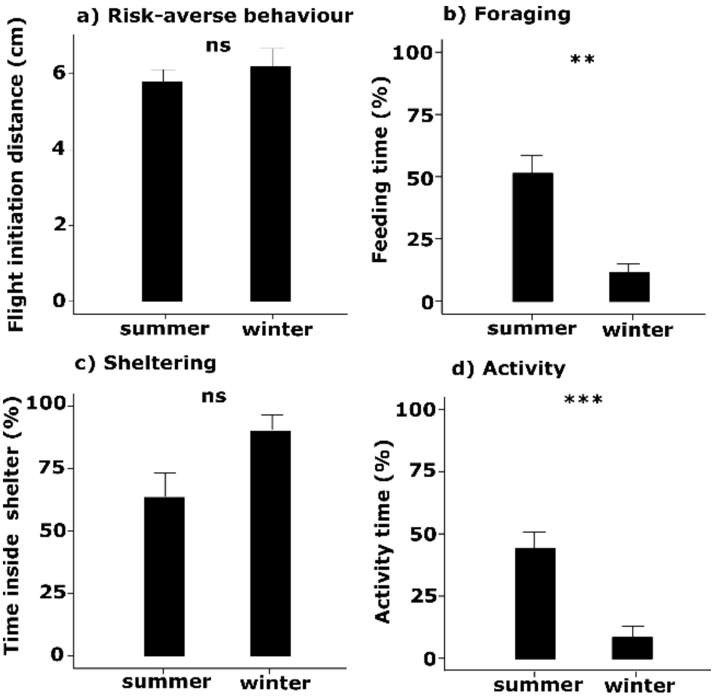

Figure 3. Behaviours (mean + SE) of a tropical range-extending fish (*Abudefduf vaigiensis*) across seasons. a) Flight initiation distance as a proxy for risk-averse behaviour towards a threat stimulus, b) proportion of the time feeding, c) proportion of the time sheltering, and d) proportion of time active. *** p < 0.001, ** p < 0.01, * p < 0.05, ns = not significant (see Table S7).

FORAGING-SHELTERING TRADE-OFFS

Irrespective of latitude, tropical and temperate species showed higher foraging activity in the vicinity of shelter than in exposed areas, with almost no feeding occurred whilst sheltering under rocky overhangs or between crevices (Fig. 4; 2-way ANOVAs, all species p ≤ 0.001, Tables S8, S9).

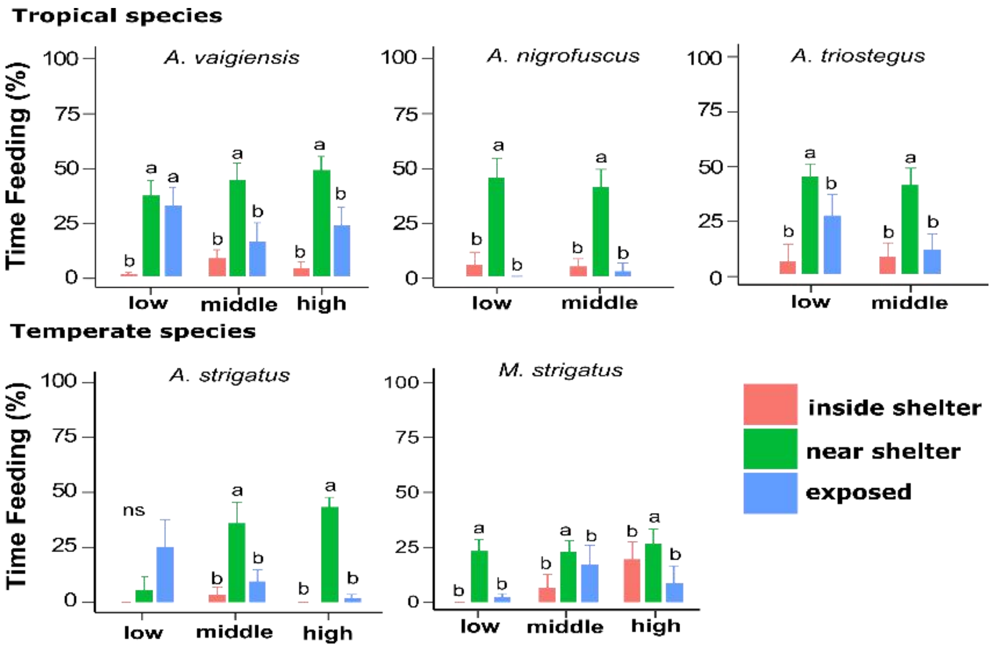

Figure 4. Proportion of time (mean + SE) that tropical (top panels) and temperate (bottom panels) fish species spent feeding when inside shelter, near shelter (distance of 0–5 body lengths from shelter) and away from shelter (exposed; distance >5 body lengths from shelter)) as a function of latitude (low, middle, high). Different letters above bars indicate significant differences within latitudes (See Table S8 and S9). ns = not significant.

DISCUSSION

We here show that tropical fishes express more risk-averse behaviours in novel environments at their temperate range edges than at their subtropical distributional range. Risk-averse behaviour is often used when prey species avoid engaging in dangerous situations and perceiving their environment as risky, or when they face unknown predators (Bell 2009). We show that in their novel temperate ranges, coral reef fishes become more risk-averse than in their native ranges by exhibiting an increased flight initiation distance and amount of time sheltering in novel temperate rocky habitats under a perceived threat. Increased risk-averse behaviours enhance the probability of successfully evading or avoiding predatory attacks (Walker et al. 2005), especially while foraging in unfamiliar habitats (Greenberg 2003) or when there is lack of a co-evolutionary prey-predator interaction (Urban et al. 2019). The conservative behaviours exhibited by tropical fishes are therefore likely due to uncertainty in an unfamiliar temperate environment (Sih 1992; Brown et al. 2013). In novel habitats, the reliability of the surrounding information on which to judge risk levels is often reduced (Sih

1992; Dall et al. 2005). Thus, exhibiting greater caution is apparently an efficient strategy to reduce predation risk whilst learning to cope with novel threats (McCormick et al. 2017). Winter temperatures did not alter the flight initiation distance or amount of time sheltering by tropical fishes at temperate latitudes. This indicates that environmental unfamiliarity rather than the physiological effects of reduced seawater temperature likely drive risk-averse behaviours displayed by tropical species in their novel temperate environments.

Shelter availability is known to influence the escape response of many animals (Quadros et al. 2019). Here, we found that feeding behaviour was affected by shelter position, however; it is also expected for escape responses in which short distances are expected in areas with high shelter and food available (Bonenfant & Kramer 1996; Dill & Houtman 1989). Additionally, shelter availability could nullify the effect of the surrounding conditions of temperate environments on the tropical fish risk-averse behaviours as found by Nagelkerken et al. (2015) study in a volcanic marine CO_2 vents where habitat composition nullifies the effect CO_2 on the escape behaviour of temperate fish community. Unfortunately, this is a limitation of our study since shelter and food availability could not be measured.

Risk-averse behaviour comes at an energetic cost for tropical range-extending fishes. We show that increased vigilance (i.e. increased flight response and sheltering behaviour) was associated with reduced feeding. This suggests that tropical fishes trade-off foraging for increased survivorship as an adaptive response to their novel environment. Animals that over-respond to a threat engage less in other fitness-related activities (Dall et al. 2001; Carthey & Banks 2014). Such trade-offs can compromise energetic intake, leading to altered energy allocation to important physiological processes such as somatic growth (Millidine et al. 2006; Kingsbury et al. 2020). Hence, irrespective of seawater temperature, risk-avoidance behaviours by range-extending species in their novel ranges likely affect energy budgets with possible ensuing effects on individual fitness.

In contrast to risk aversion, some other behaviours of range-extending tropical fishes were affected by lower seawater temperatures. We show that foraging and activity levels both decreased with increasing latitudes for tropical species. Seawater temperatures that approach or extend beyond an organism's lower tolerance limits reduce their predator defensive responses (Lyon et al. 2008; Figueira et al. 2019). Low temperatures can affect neural control, which is responsible for muscle contraction speed and development, and tail beat frequency (Batty & Blaxter 1992; Hanel & Wieser 1996). Our observation that foraging and activity levels were reduced in winter compared to summer time, supported the proposition of an additional negative cold-temperature effect on their physiology (e.g. burst swimming performance, Figueira et al. 2009; Djurichkovic et al. 2019). However, under stressful conditions some species are able to compensate the energy lost (in this case due to reduced food intake) by adjusting their time allocated to other behaviours (Lind & Cresswell 2005; Turbill & Stojanovski 2018). Although foraging and activity levels were reduced by lower seawater temperatures, reduced activity levels may be an adaptive response to counter reduced food intake. Irrespectively, we show that in addition to increased risk-averse behaviours at higher latitudes, the reduced temperatures at those latitudes negate optimal physiological performance by range-extending tropical species.

Unlike tropical fishes, temperate fishes did not show any consistent patterns of altered behaviours as a function of latitude. Hence, our prediction that native temperate fishes would maintain their antipredator responses across latitudes, because these species have always naturally occurred there, was confirmed by our findings. Temperate species are less sensitive to temperature fluctuations because they live in environments where summer and winter temperatures can often differ significantly (Tewksbury et al. 2008; Perez et al. 2016) and they are behaviourally and physiologically adapted to survive in temperate habitats (Klaiman et al. 2011; Shuter et al. 2012). Our study suggests that under current ocean warming, temperate fishes are still robust to temperature increases at their trailing edges, although this might change under future climate.

CONCLUSION

We reveal that tropical fishes can show increased risk-averse behaviours at the leading edges of their distribution ranges under ongoing climate change (i.e. increased flight initiation distance and time in shelter) leading to reduced foraging. In addition, reduced seawater temperatures lower their foraging and activity levels. In contrast, native temperate species do not show any such effects. Hence, behavioural modification by tropical fishes in their novel temperate habitats and suboptimal winter temperatures at higher latitudes are strong regulators of their current invasion success on temperate reefs. The way in which tropical fish behaviourally balance the conflicting demands between avoiding temperate predators and maintaining feeding is critical for their fitness and hence for the structuring of temperate species community under climate change.

ETHICS

All experiments were performed under animal ethics approval numbers S-2015-222A and S-2017-002 (University of Adelaide) and ETH17-1117 (University of Technology Sydney) and followed the University's animal ethics guidelines.

AUTHOR CONTRIBUTIONS

E.O.C.C, I.N., and D.J.B. conceived and designed the study, E.O.C.C. collected the data, E.O.C.C. analysed the data. All authors contributed to the writing of the article.

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SUPPLEMENTARY INFORMATION

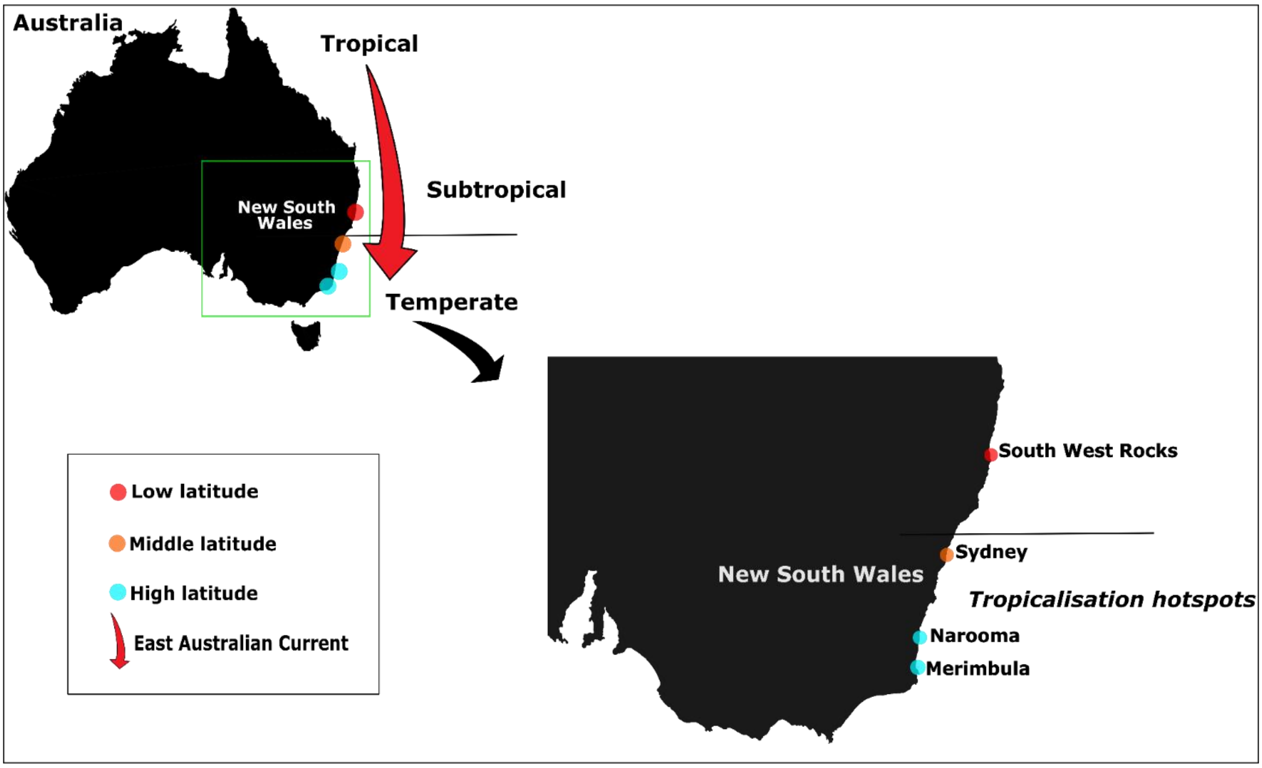

Figure S1. Map showing the study locations at three latitudes where behaviour of tropical and temperate fishes were quantified in situ along the southeast coast of Australia.

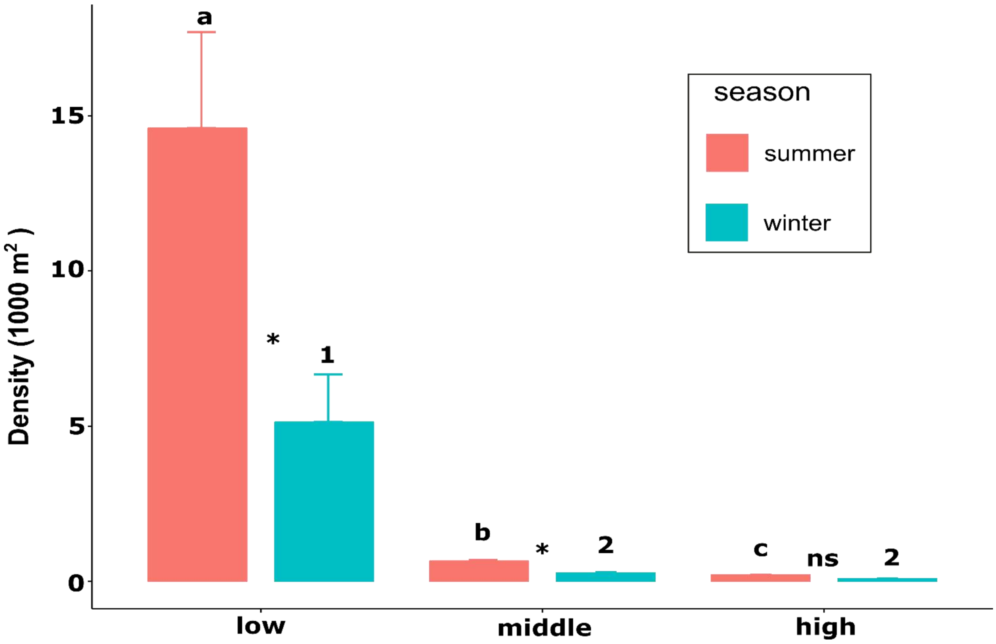

Figure S2. Mean (+ SE) density of tropical species from visual surveys (2001-2018) performed at the same sites as where the fish behaviours were recorded. Different letters and numbers above bars indicate results of an a posteriori test of differences in means among latitudes during summer and winter, respectively. * indicate difference between seasons, ns = no significant difference (see Table S2).

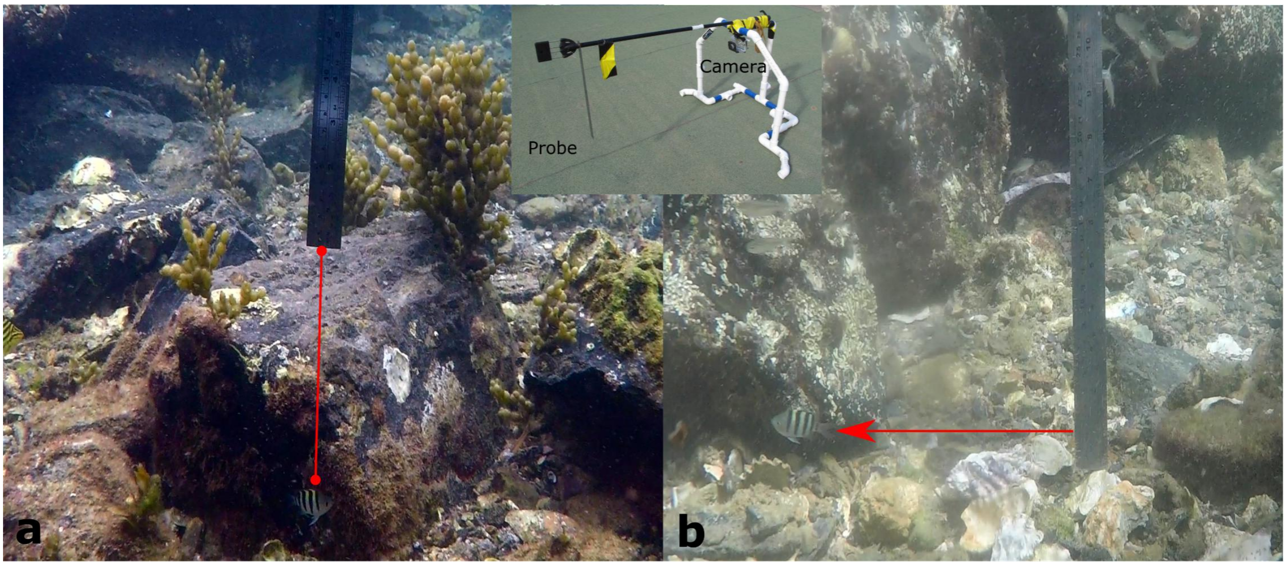

Figure S3. Underwater photographs showing how a) flight initiation distance, and b) escape distance were measured using an approaching artificial threat (metal ruler, see inset) to initiate escape behaviour.

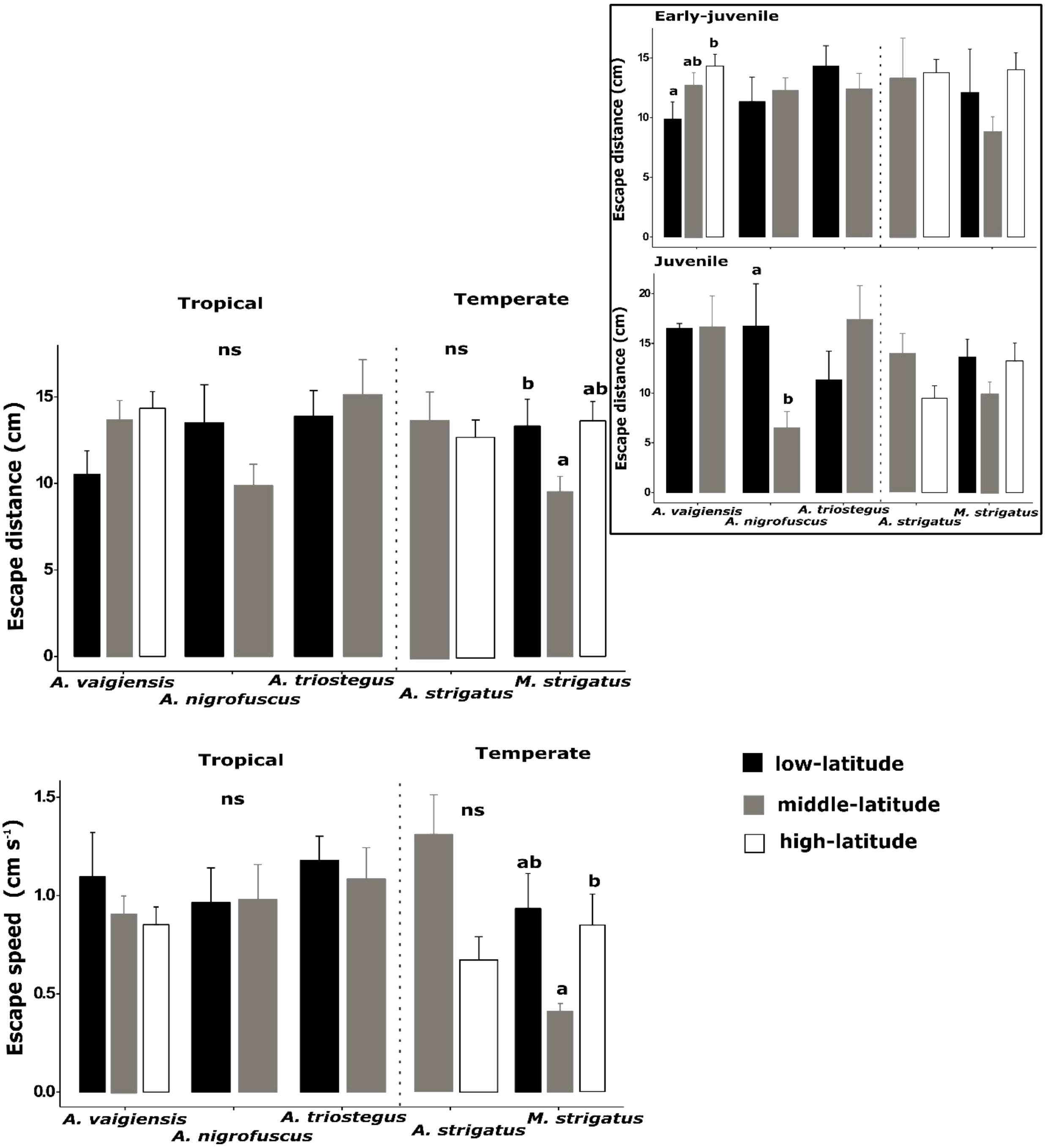

Figure S4. Escape speed and escape distance (mean + SE) measured as a proxy for risk-averse behaviours of tropical and temperate species across latitudes (low; middle; high). For escape distance, responses are also shown across life stages (early-juvenile vs juvenile). Different letters above bars indicate significant differences (see Table S2 and S3). ns = not significant.

Table S1. Mean summer and winter seawater temperatures (°C) collected using HOBO temperature recorders at the same time as the recording of fish behaviours during 2017 and 2018 (summer) and 2017 (winter).

Latitude	**Location**	**summer**		**winter**
		2017	**2018**	**2017**
low	South West Rocks	25.4	25.7	20.3
middle	Sydney	23.0	23.0	19.3
high	Narooma	21.9	21.4	17.4
	Merimbula	21.2	20.1	

Table S2. Two-way ANOVA results showing (a) the effects of latitude, season and their respective interactions on the density of tropical fish species, and (b) the pair-wise results of the significant interaction. Significant results are indicated in bold and (*).

a)

	df	**SS**	**MS**	**F-value**	**P-value**
latitude	2	24842	12421	265.42	**<0.0001***
season	1	2369	2369	50.63	**<0.0001***
latitude × season	2	1752	876	18.72	**<0.0001***
residuals	138593	6485972	47		

b) Pairwise test

Season among latitude		**diff**	**lower**	**upper**	**p-value**
low–summer vs.	**middle–summer**	13.943	12.099	15.786	**<0.0001***
high–summer vs.	**middle–summer**	-0.441	-0.569	-0.313	**<0.0001***
high–summer vs.	**low–summer**	-14.385	-16.23	-12.539	**<0.0001***
low–winter vs.	**middle–winter**	4.853	0.786	8.92	**0.008***
high–winter vs.	**middle–winter**	-0.185	-0.553	0.182	0.703
high– winter vs.	**low–winter**	-5.039	-9.118	-0.96	**0.005***

Latitude between season		**diff**	**lower**	**upper**	**p-value**
low–winter vs.	**low–summer**	-9.467	-13.93	-5.004	**<0.0001***
middle–winter vs.	**middle–summer**	-0.378	-0.529	-0.226	**<0.0001***
high–winter vs.	**high–summer**	-0.122	-0.481	0.236	0.927

Table S3. Permutational ANOVA results showing (a) the effects of latitude, species, life stage and their respective interactions on various risk-averse behaviours of the tropical fish species, and (b) the pair-wise results of the significant predictor variables. Significant results are indicated in bold and (*).

a)

Risk-averse behaviours	Predictor variables	df	SS	MS	F-value	p-value
Flight initiation distance	**latitude**	2	49.582	24.791	4.177	**0.018***
	species	2	1.771	0.885	0.122	0.908
	life stage	1	0.791	0.791	0.104	0.784
	species × life stage	2	15.305	7.653	1.289	0.274
	latitude × species (pooled)					
	latitude × life stage (pooled)					
	latitude × species x life stage (pooled)					
	Pooled	109	646.94	5.935		
Escape distance	latitude	2	7.005	3.503	0.967	0.517
	species	2	36.974	18.488	0.258	0.726
	life stage	1	1.376	1.376	0.022	0.817
	species × life stage	2	143.28	92.013	2.458	0.096
	latitude × species	2	102.75	51.374	0.558	0.635
	latitude × life stage	2	127.73	63.867	0.591	0.621
	latitude × species × life stage	2	184.03	29.149	3.157	**0.049***
Escape speed	latitude	2	0.328	0.164	0.925	0.421
	species	2	0.344	0.172	0.322	0.805
	life stage	1	0.057	0.057	0.107	0.703
	species × life stage	2	1.069	0.535	1.399	0.221
	latitude × species (pooled)					
	latitude × life stage (pooled)					
	latitude × species × life stage (pooled)					
	Pooled	5	1.561	0.312	0.818	0.462

b) Tropical species pair-wise test results

		latitude	t	p-value	Effect
Flight initiation distance		north vs. middle	2.986	**0.003***	**low<mid**
		north vs. south	0.715	0.479	low=high
		middle vs. south	0.025	0.979	mid=high
Escape distance	***A. vaigiensis*** early-juvenile	low vs. middle	1.667	0.108	low=mid
		low vs. high	2.656	**0.012**	**low<high**
		middle vs. high	1.035	0.300	mid=high
	A. nigrofuscus juveniles	**low vs. middle**	2.885	**0.032**	**low<high**

Table S4. Permutational ANOVA results showing the effects of (a) latitude, species, life stage and their respective interactions on the risk-averse behaviours of the temperate fish species, and (b) the pair-wise results of the significant predictor variables. Significant results are indicated in bold and (*).

a)

Risk-averse behaviours	Predictor variables	df	SS	MS	F-value	p-value
Flight initiation distance	latitude	2	21.711	10.855	1.922	0.156
	species	1	0.186	0.186	0.411	0.549
	life stage	1	1.033	1.033	2.259	0.193
	species × life stage	1	0.205	0.205	0.036	0.853
	latitude × species (pooled)					
	latitude × life stage (pooled)					
	latitude × species x life stage (pooled)					
	Pooled	82	463.19	5.649		
Escape distance	latitude	2	34.484	17.242	0.277	0.651
	species	1	30.947	30.947	1.825	0.427
	life stage	1	2.158	2.158	0.119	0.776
	species × life stage	1	16.671	16.671	0.615	0.439
	latitude × species	1	136.97	136.97	5.052	**0.028***
	latitude × life stage	2	37.303	18.651	0.688	0.508
	latitude × species × life stage (pooled)					
	Pooled	77	2087.7	27.113		
Escape speed	latitude	2	1.652	0.826	0.238	0.643
	species	1	1.914	1.914	6.02	0.246
	life stage	1	0.243	0.243	0.818	0.497
	species × life stage	1	0.283	0.283	0.749	0.389
	latitude × species	1	4.723	4.723	12.496	**0.001***
	latitude × life stage	2	0.441	0.22	0.583	0.558
	latitude × species × life stage (pooled)					
	Pooled	77	29.104	0.378		

b) Temperate species pair-wise test results

	species	latitude	t	p-value	Effect
Escape distance	*M. strigatus*	middle vs. high	4.304	0.15	mid=high
		middle vs. low	21.306	**0.033**	**mid<low**
		high vs. low	0.634	0.634	high=low
Escape speed	*M. strigatus*	**middle vs. high**	12.265	**0.050***	**mid<high**
		middle vs. low	3.632	0.175	mid=low
		high vs. low	0.778	0.577	high=low

Table S5. Permutational ANOVA results showing (a) the effects of latitude, species and the latitude × species interaction on the other behaviours of the tropical species and, (b) the pair-wise results of the significant predictor variable ‘latitude’. Significant results are indicated in bold and (*).

a)

Behaviours	Predictor variables	df	SS	MS	F-value	p-value
Feeding	**latitude**	2	2353.700	1176.900	64.788	**0.013***
	species	2	7675.100	3837.600	6.088	**0.004***
	latitude × species	2	36.142	18.071	0.028	0.969
Activity	**latitude**	2	9041.2	4520.6	5.709	**0.002***
	species	2	2861.6	1430.8	1.807	0.150
	latitude × species (Pooled)					
	Pooled	126	99767	791.8		
Sheltering	**latitude**	2	11277	56838.3	7.813	**0.001***
	species	2	3631.3	1815.7	2.516	0.079
	latitude × species (Pooled)					
	Pooled	138	99588	721.65		

b) Pair-wise of the other behaviours of tropical species

	latitude	t	p-value	Effect
Feeding	low vs. high	1.615	0.109	low=high
	low vs. middle	7.582	**0.009***	**low>mid**
	middle vs. high	0.779	0.444	mid=high
Activity	low vs. high	2.309	**0.017***	**low>high**
	low vs. middle	2.704	**0.006***	**low>mid**
	middle vs. high	1.470	0.136	mid=high
Sheltering	low vs. high	3.178	**0.002***	**low<high**
	low vs. middle	2.781	**0.005***	**low<mid**
	middle vs. high	2.062	**0.044***	**mid<high**

Table S6. Permutational ANOVA results showing the effects of latitude, species and their interaction on the other behaviours of the temperate species. Significant results are indicated in bold and (*).

Behaviours	Predictor variables	df	SS	MS	F-value	p-value
Feeding	latitude	2	3104.6	1552.3	2.833	0.063
	species	1	436.55	436.55	0.7969	0.376
	latitude × species (Pooled)	71	38892	547.78		
Activity	latitude	2	7115.7	3557.9	1.959	0.345
	species	1	823.21	823.21	1.324	0.256
	latitude × species	2	3631	1815.5	2.922	0.055
Sheltering	latitude	2	1034.5	517.25	0.868	0.435
	species	1	6074.2	6074.2	10.195	**0.002***
	latitude × species (Pooled)					
	Pooled	75	44685	595.8		

Table S7. Permutational ANOVA results showing the effects of (a) season (winter vs. summer), latitude (low vs. middle), life stage and their respective interactions on the risk-averse behaviours and, (b) the other vital behaviours of the most common tropical fish (*A. vaigiensis*). Significant results are indicated in bold and (*).

a)

Risk-averse behaviours	**Predictor variables**	**df**	**SS**	**MS**	**F-value**	**p-value**
Flight initiation distance	**latitude**	1	13.383	13.383	6.353	**0.039***
	season	1	0.525	0.526	1.066	0.579
	life stage	1	4.475	4.475	0.959	0.343
	latitude × season	1	4.128	4.128	0.885	0.351
	latitude × life stage	1	1.043	1.043	0.224	0.643
	season × life stage	1	0.687	0.687	0.147	0.715
	latitude × season × life stage	no test				

b)

Behaviours	**Predictor variables**	**df**	**SS**	**MS**	**F-value**	**p-value**	**Effect**
Feeding	season	1	7557.5	7557.500	13.735	**0.001***	**winter<summer**
Activity	season	1	6031.1	6031.1	10.887	**0.002***	**winter<summer**
Sheltering	season	1	3379.9	3379.9	3.249	0.087	

Table S8. Permutational ANOVA results showing the effects of (a) latitude, shelter position (inside shelter, near shelter, exposed) and their interaction on feeding time (%) of the tropical species and, (b) the pair-wise test results of the significant predictor variables. Significant results are indicated in bold and (*).

a) Tropical species

	Predictor variables	**df**	**SS**	**MS**	**F-value**	**p-value**
A. vaigiensis	**latitude**	2	1.248	0.624	0.092	0.898
	shelter position	2	230.500	115.250	41.877	**0.0001***
	latitude × shelter position	4	27.210	6.802	2.472	**0.047***
A. triostegus	latitude	1	1.987	1.987	0.964	0.427
	shelter position	2	160.670	80.336	33.807	**0.0001***
	latitude × shelter position	2	4.1217	2.0609	0.8672	0.415
A. nigrofuscus	latitude	1	1.263	1.263	1.085	0.418
	shelter position	2	179.720	89.860	56.159	**0.0001***
	latitude × shelter position	2	2.328	1.164	0.727	0.478

b) Pair-wise test of shelter position × latitude for pairs of levels of factor 'shelter position'

	latitude	**shelter position**	**t**	**p-value**
A. vaigiensis	**low**	inside shelter < near shelter	5.739	**0.0001***
		inside shelter < exposed	3.844	**0.001***
		near shelter = exposed	1.118	0.256
	middle	inside shelter < near shelter	8.226	**0.0001***
		inside shelter = exposed	2.012	0.052
		near shelter > exposed	4.121	**0.0001***
	high	inside shelter < near shelter	4.351	**0.0002***
		inside shelter = exposed	0.081	0.941*
		near shelter > exposed	4.195	**0.0003**

Pair-wise test of shelter position

	shelter position	**t**	**p-value**
A. triostegus	**inside shelter < near shelter**	9.06	**0.0001***
	inside shelter = exposed	1.862	0.072
	near shelter > exposed	5.487	**0.0001***
A. nigrofuscus	**inside shelter < near shelter**	7.141	**0.0001***
	inside shelter = exposed	1.891	0.081
	near shelter > exposed	9.512	**0.0001***

Table S9. Permutational ANOVA results showing the effects of (a) latitude, shelter position (time sheltering, near shelter, exposed) and their interaction on feeding time (%) of the temperate species and, (b) the pair-wise test results of the significant predictor variables. Significant results are indicated in bold and (*).

a) Temperate species

	Predictor variables	**df**	**SS**	**MS**	**F-value**	**p-value**
A. strigatus	latitude	2	436.91	218.46	0.126	0.804
	shelter position	2	8604.3	4302.1	15.209	**0.0001***
	latitude × shelter position	4	6888.7	1722.2	6.0884	**0.0003***
M. strigatus	latitude	1	3062	1531	2.109	0.237
	shelter position	2	8645.6	4322.8	7.421	**0.001***
	latitude × shelter position	2	2902.8	725.71	1.245	0.292

b) Pair-wise test of shelter position × latitude for pairs of levels of factor ‘shelter position’

	latitude	**shelter position**	**t**	**p-value**
A. strigatus	**low**	inside shelter = near shelter	1	0.347
		inside shelter =. exposed	1.936	0.084
		near shelter = exposed	1.389	0.19
	middle	inside shelter < near shelter	3.268	**0.004***
		inside shelter = exposed	1.057	0.302
		near shelter < exposed	2.496	**0.022***
	high	inside shelter < near shelter	13.055	**0.0001***
		inside shelter = exposed	1	0.329
		near shelter < exposed	11.086	**0.0001***

Pair-wise test of shelter position

	shelter position	**t**	**p-value**
M. strigatus	**inside shelter < near shelter**	3.421	**0.001***
	inside shelter = exposed	0.136	0.891
	near shelter > exposed	3.218	**0.001***

CHAPTER IV

NOVEL ENVIRONMENTS POSE FORAGING CHALLENGES TO RANGE-SHIFTING CORAL REEF FISHES UNDER CLIMATE CHANGE

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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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ABSTRACT

Poleward range extensions of tropical species can reshuffle temperate communities by generating competitive interactions that previously did not exist. However, novel environmental conditions and locally-adapted native temperate competitors may slow tropical invasions by reducing the ability of invaders to access local resources (food and shelter). Using a field experiment on wild marine fish in a climate warming hotspot, we test whether the competitive ability of a common tropical range-extending fish (*Abudefduf vaigiensis*) and a co-schooling temperate fish (*Microcanthus striatus*) are altered along a latitudinal temperature gradient and affected by the abundance of competitors, based on key behaviours related to feeding and competitive interference. We found that *A. vaigiensis* reduced foraging performance (i.e. slower prey perception, slower prey inspection, and decreased prey intake) in its novel temperate range. Higher abundance of temperate competitors resulted in an increased retreat behaviour by tropical fishes (i.e. withdrawal from foraging on released prey), independent of latitude. Our findings suggest that lower foraging performance of the tropical fish at their range edge is driven by the combined effect of physical (e.g. reduced seawater temperature and/or unfamiliarity with novel conditions in their novel temperate ranges) and biological factors (e.g. increased abundance of local temperate competitors). In addition, the tropical range-extending fish showed lower competitive ability than the native temperate fish whilst foraging, which may compromise their initial establishment in temperate ecosystems under climate change. Our study reveals that whilst a future increase in ocean warming is expected to alleviate foraging limitations due to reduced cold-water stress, native temperate fishes might delay the establishment of tropical fish in temperate ecosystems by limiting their access to resources.

INTRODUCTION

Understanding the mechanisms responsible for geographical range extensions of species is critical to forecast the ecological impacts on recipient communities (Gallien & Carboni 2016; Fogarty et al. 2017). Climate change is a major force driving global redistribution of species on land and in the ocean (Poloczanska et al. 2013; Pecl et al. 2017). However, the impact of range-extending species on recipient communities will strongly depend on interaction strength with local species (Masciocchi et al. 2009; Gilman et al. 2010). It is common knowledge that the structure of natural communities is shaped by biological interactions (Bolker et al. 2003; Wisz et al. 2013) and such interactions are one of the pillars maintaining ecosystem resistance and resilience. Thus, disruption of species interactions that have established over long evolutionary periods may lead to disruption of key ecosystem functions (Bascompte et al. 2006; Ives & Carpenter 2007; O'Gorman & Emmerson 2009). Yet, few studies incorporate novel ecological interactions into predictions of species range shifts and their establishment in novel ranges.

Without considering species interactions, it remains difficult to accurately forecast the impacts of range-extending species (e.g. they may be more aggressive or have higher foraging performance) on local species, and evaluate whether they are therefore likely to increase their abundances at higher latitudes to the detriment of local species under global warming (Shinen & Morgan 2009; Callaway & Ridenour 2004). Invasion theory postulates that competition is one of the main mechanisms driving successful invasion of alien species because they are usually superior competitors compared to native species (Sakai et al. 2001; Vila & Weiner 2004). Similar to alien species, the influx of range-extended species can reshuffle species dominance in temperate systems or displace native species with lower competitive performance (Nagelkerken & Simpson 2013; Milazzo et al. 2013). Although the pace of invasion by range-extending species is typically slower than that of introduced species (Sorte et al. 2010), the consequences and magnitude of their establishment might be very similar

(Kola & Lodge 2001; Sorte et al. 2010). Thus, understanding how novel competitive interactions might affect the persistence of range-extending species and their potential impacts on recipient communities is imperative.

Whilst many invasive species are superior competitors, this is not always the case (Kimbro et al. 2013; Levine et al. 2004; Parker et al. 2007). The biotic resistance theory postulates that native species sometimes exhibit higher competitive ability than invaders, reducing establishment and persistence of invaders (Levine et al. 2004; de Rivera et al. 2005; Von Holle 2005; Von Holle & Simberloff 2005; Fridley et al. 2007). Nevertheless, only few studies on marine and terrestrial range extensions have focussed on success or failure of local species to resist the establishment of novel species into their communities (Paini et al. 2008). Hence, competitive effects of invaders as well as natives are critical to understand potential changes to community structures under future climate (Vilá & Weiner 2004; Paini et al. 2008). Alternatively, species might change their behaviour through phenotypic plasticity and avoid or reduce direct conflicts and enable coexistence (Perri & Randall 1999; Wilson et al. 1999; Lambert 2002). For example, avoidance of dominant species and adjusted retreat and escape behaviours can facilitate the coexistence of some species by decreasing their risk of injuries and agonistic-related stress (Rychlik & Zwolak 2005). However, such adaptive behaviours might create trade-offs and incur costs to individual fitness (Chesson 2000; Liancourt et al. 2005). Superior native competitors might exclude newly-arriving invaders from their communities, but coexistence may occur if these new arrivals display conflict-avoidance behaviours only if it not impairs other fitness-related behaviours.

Over the last two decades, hundreds of coral reef fish species have been recruiting in temperate Australia during summer (Booth et al. 2007; Feary et al. 2013). These tropical fish species have not yet established populations at temperate latitudes because the winter temperatures there are below their thermal tolerance (Eme & Bennett 2008; Figueira & Booth 2010). However, ongoing intensification of ocean warming and strengthening of poleward ocean currents is likely to relax these abiotic thresholds in the near-future (Figueira & Booth

2010; Booth et al. 2018). Under current warming, other factors such as direct or indirect competition with temperate fish species are also of importance, and these might buffer or retard the invasion of tropical range-extending species at higher latitudes (e.g. Pigot et al. 2013). Whilst some tropical and temperate fishes seem to positively interact (Smith et al. 2018) and co-exist in their trophic niches (Kingsbury et al. 2019), competitive behaviours might still exist. Hence, understanding the competitive ability (ability to respond to the inhibitory effects of co-existing species) between tropical invader and temperate species may give insights into the competitive hierarchies that are emerging due to climate change, and the identification of potential "winners" and "losers" (e.g. Liancourt et al. 2005; Poulos & McCormick 2013) that could compromise novel communities at high latitudes.

Here we study the competitive ability of a common tropical range-extending species (*Abudefduf vaigiensis*) and a co-schooling native temperate fish (*Microcanthus strigatus)* along a latitudinal temperature gradient (6° latitude, 730 km of coastline) under current ocean warming. We assessed their competitive ability *in situ* by *quantifying their foraging performance in* terms of perceiving, inspecting, consuming, and competing for prey, from subtropical to temperate waters. To reveal whether altered foraging behaviours were related to direct or indirect competitive interactions, we also quantified aggressive interactions between the species and the abundance of all co-occurring temperate and tropical range-extending fishes across the same latitudinal gradient. Understanding whether competition might act in synchrony with abiotic conditions is crucial to predict the likelihood of tropical fish invasions in temperate environments, and their potential effects on temperate fish communities under ongoing climate change.

METHODOLOGY

STUDY AREA AND SPECIES

The study was conducted at six sites ranging from low to high latitudes along the south-eastern Australian coast (Figure S1). The lower latitude (two sites at South West Rocks) is considered as the most similar environment to the tropical fish's native range, comprised by subtropical reefs where the abundance of tropical fish species is highest among the three latitudes studied (Figure S2), and the mean seawater winter temperature (Table S1) does not surpass their lower thermal tolerance (i.e. ~18-22 ºC; Djurichkovic et al. 2019). At this latitude, the benthic environment is mostly composed of bare rocks (site 1) or a mosaic of sparse oyster reefs and rocks (site 2). The middle latitude is situated around Sydney, and included three sites which reflect tropicalisation hotspots (Booth et al. 2007): Shelly Beach, Little Manly, and Narrabeen. The benthic reef community at Shelly Beach and Little Manly was composed of a mosaic of macroalgae (e.g. kelp), turf-forming algae, bare rock and sea urchin barrens, while at Narrabeen it mainly consisted of bare rock, turf algae and sparse oyster reef. The high latitude site (Narooma) represented the coldest studied site (Table S1), and comprised the most unfamiliar environment for tropical fishes where the abundance of temperate fish species is highest among the sites (Figure S2). At this site, tropical fishes were found on shallow rocks and oyster reefs. The sites at the low and middle latitudes were chosen based on an 18-yr study of ongoing tropical fish settlement on shallow rocky reefs along the coast of south-east Australia (Booth et al. 2007; Booth et al. 2018), while the site at the high latitude has been only recently monitored (~ 3 years).

We selected one model species for each temperature affinity (tropical vs temperate): (1) the most common tropical range-extending species *Abudefduf vaigiensis (Pomacentridae)*, and (2) the common co-schooling temperate species *Microcanthus strigatus (Microcanthidae)*.

These species usually share the same space and were the most attracted to the experimental prey releases, allowing for sufficient replication within each latitude.

DATA COLLECTION AND EXPERIMENTAL DESIGN

For each fish species, we (1) observed direct competitive interactions with all surrounding species, and (2) tested their competitive ability based on foraging behaviours, as a function of latitude (ranging from warmer to cooler sea temperatures) and abundance of potential competitors. Abundance of competitors was separated into three groups: (1) abundance of conspecifics (individuals of the same species) of each studied species, (2) abundance of all native-temperate fishes, and (3) abundance of all tropical range-extending fishes. The last two groups do not include individuals of the focal species.

Various foraging behaviours were quantified *in situ* for each fish species using a maximum of 5 min. of video recording. A manipulative underwater experiment was performed to attract fish and instigate species interactions (foraging arena experiment) (Figure S3). The experiment comprised artificial release of dead prey (brine shrimp, *Artemia*). Prey was delivered through a tube of 2.5 cm in diameter and 1 m in length attached to a dive weight that was positioned on the reef substratum at approximately 50 cm from a fixed camera (GoPro) with the lens directed toward the prey's released point. This distance was chosen to best observe the tropical fish recruits that were usually < 5 cm in body size. Recruits and early-stage individuals of tropical and temperate species are relatively site-attached, minimising the chance that the same individual was repeatedly recorded across replicate recordings. To allow for independent observations, foraging arena experiments were randomly performed with a distance of at least 2 m of each other for both tropical and temperate species. The prey were constantly released through the tube via a 60-ml syringe. Each syringe contained ~1.25 g of brine shrimp (*Artemia*) mixed with ~60 ml of salt water, but only half of the syringe content was released each time. At the start of each foraging arena experiment deployment, half of the syringe content was released through the tube constantly to attract fish and concentrate them within the field of view of the camera. Once all released prey had been consumed by the fishes or had dissipated due to water currents, an additional release of prey (i.e. half of a syringe content) was performed. This procedure was repeated (~ 10 releases of ~12.5 g of brine shrimp per recoding) until the end of each 5-min recording. Recordings were performed under the wide angle setting with a resolution of 1080p at a speed of 25 frames/sec.

FISH BEHAVIOUR

The video recordings (max. 5 min) were evaluated using VLC media player 2.1.3 on a desktop computer. The following behaviours were quantified for each focal individual in each recording (Table S2): (1) prey attraction time, measured as the time (seconds) it took for the fish to swim towards the tube (i.e. prey release point) and take a bite at the prey upon their first release, (2) minimum distance to prey, measured as the shortest distance (cm) that the fish approached the prey release point during its observation time, (3) prey inspection rate, continuously counted during the observation and measured as the number of times an individual approached (distance of ≤ 5 body lengths) the prey release point, (4) bite rate, continuously counted during the observation and measured as the total number of bites taken at the released prey, (5) retreat rate, continuously counted during the observation and measured as the number of times a fish approached the prey release point within 5 body lengths but decided to abruptly return to its previous position, (6) chasing rate, continuously counted during the observation and measured as the number of times that an individual swam aggressively towards another individual, and (7) escaping rate, continuously counted during the observation and measured as the total number of times that an individual fled from an aggressor. The behaviours that were measured as continuous counts (prey inspection, bites, retreats, chasing, and escaping) were then expressed as rates per unit of time (e.g. bite rates/sec.). This was calculated by dividing the respective behavioural counts of each individual by its total observation time.

The focal individuals were randomly selected in each video, and all their behaviours were analysed from the same recording. To avoid pseudo-replication only one individual of each species was analysed per video recording, especially when they were schooling with individuals of the same species. Because fishes were mobile, the time that they were within the view of the camera ranged between 20 sec. and 5 min. Short observation times have been found to be sufficient to obtain a representative estimate of our focal behaviours (Biro et al. 2010; Francini-Filho et al. 2010).

We also quantified the abundance of all tropical and temperate fishes, and other individuals of *A. vaigiensis* and *M. strigatus* (i.e. their respective conspecific abundances) that were attracted to the prey, in intervals of 10 sec over the period of each fish observation. These replicate abundance estimates were afterwards averaged for each recording.

STATISTICAL ANALYSES

As the tropical range-extending species are more abundant at lower latitudes and the opposite is true for the temperate species, a permutational multivariate analysis of covariance (MANCOVA) was used to examine the effect of latitude (three levels of categorical and fixed factors – “low”, “middle”, “high”) on the behaviour (dependent variables: all seven behaviours) of the tropical and temperate species (species as a fixed factor – “*A. vaigiensis*” and “*M. strigatus*”) using the total abundance of temperate fishes, tropical fishes, and individuals of the same species (conspecifics) across latitudes as covariates. Interactions between the categorical factors (latitude and species) and the three covariates were removed from the final model (MANCOVA) because their initial inclusion did not show a significant effect, and maintaining them in the final model could lead to a misinterpretation of the results (Engqvist 2005; Beck & Bliwise 2014). Univariate permutational analysis of covariance (ANCOVA) was then performed for each behaviour in order to clarify the interpretation of the MANCOVAs and evaluate the individual behaviours that were responsible for any latitudinal differences as revealed by the MANCOVAs. Prior to all analyses, all behavioural data were scaled and standardised using Primer 6. *A posteriori* pairwise comparisons of the means was used to evaluate differences among latitudes, species, and species within latitude when a significant interaction was present.

For the behaviours that showed a significant effect of the covariates in the ANCOVAs, we calculated their adjusted R^2 (also known as the coefficient of determination) to evaluate the strength of their relationships for each species separately. The R^2 can indicate to what extent (expressed in %) the variance of the covariate (abundance of temperate or tropical fishes, or individuals of the same species) explains the variance of dependent variables (behaviour) (Miles 2005).

The MANCOVAs, ANCOVAs, and *a posteriori* pairwise comparisons of the means were performed using the software Primer version 6.

RESULTS

The behavioural repertoire (all seven behaviours combined) differed significantly across latitudes (Table S3, MANCOVA, F = 5.624, p = 0.0002) and between tropical (*A. vaigiensis*) and temperate (*M. strigatus*) species (MANCOVA, F = 11.889, p = 0.0002). Pairwise tests revealed that the behavioural repertoire at low latitude differed from that at middle and high latitudes for both species. The abundance of temperate fishes (MANCOVA, F = 1.981, p = 0.110), tropical fishes (F = 2.217, p = 0.092), or conspecifics (F = 0.752, p = 0.464) did not have a significant effect on the species behaviours.

TROPICAL FISH SPECIES

Six out of seven behaviours that acted as proxies for competitive performance differed as a function of latitude. Bite rates (ANCOVA, latitude: p = 0.0002), prey inspection rates (latitude × species interaction: p = 0.009) and chasing rates (latitude: p = 0.0002) were lower at middle and high latitudes than at low latitude, while prey attraction time (latitude × species interaction: p = 0.019), minimum distance to prey (latitude: p = 0.0002) and retreat rates (latitude × species interaction: p = 0.025) all increased from low to middle and high latitudes (Fig. 1, Table S4). Only two behaviours of the tropical fish were significantly related to the abundance of potential competitors: retreat rates were positively related to the total abundance of temperate fishes ($R^2 = 0.28$; ANCOVA, p = 0.0002, Fig. 2a and Table S4) but negatively related to the abundance of conspecifics ($R^2 = 0.24$; ANCOVA, p = 0.037, Fig. 2b), whilst bite rates were positively related to the abundance of conspecifics ($R^2 = 0.20$; ANCOVA, p = 0.018, Fig. 2c).

TEMPERATE FISH SPECIES

Temperate fishes differed in four out of seven competitive behaviours as a function of latitude. Bite rates (ANCOVA, latitude: p = 0.0002) and chasing rates (latitude: p = 0.0002) were higher at low latitude than middle and high latitudes, while minimum distance to prey (latitude: $p = 0.0002$) and retreat rates (latitude × species interaction: $p = 0.025$) were higher at middle than at high and low latitudes (Fig. 1, Table S4). Retreat rate was positively related to abundance of other temperate fishes ($R^2 = 0.41$; ANCOVA, $p = 0.0002$, Fig. 2a and Table S4). Only a weak negative relationship was observed between retreat rates and abundance of conspecifics ($R^2 = 0.06$, $p = 0.037$, Fig. 2b), and a weak positive relationship between bite rates and abundance of conspecifics ($R^2 = 0.09$, $p = 0.018$, Fig. 2c).

TROPICAL VS TEMPERATE FISH SPECIES

In five out of seven behaviours, the temperate fish *M. strigatus* showed a higher competitive efficiency than the tropical species *A. vaigiensis* at two or three latitudes: a shorter distance to prey (ANCOVA, $p = 0.0002$), and higher prey inspection ($p = 0.0002$), bite rate ($p = 0.0002$), escaping rate ($p = 0.0004$), and chasing rate ($p = 0.0002$), respectively (Fig. 1, Table S4).

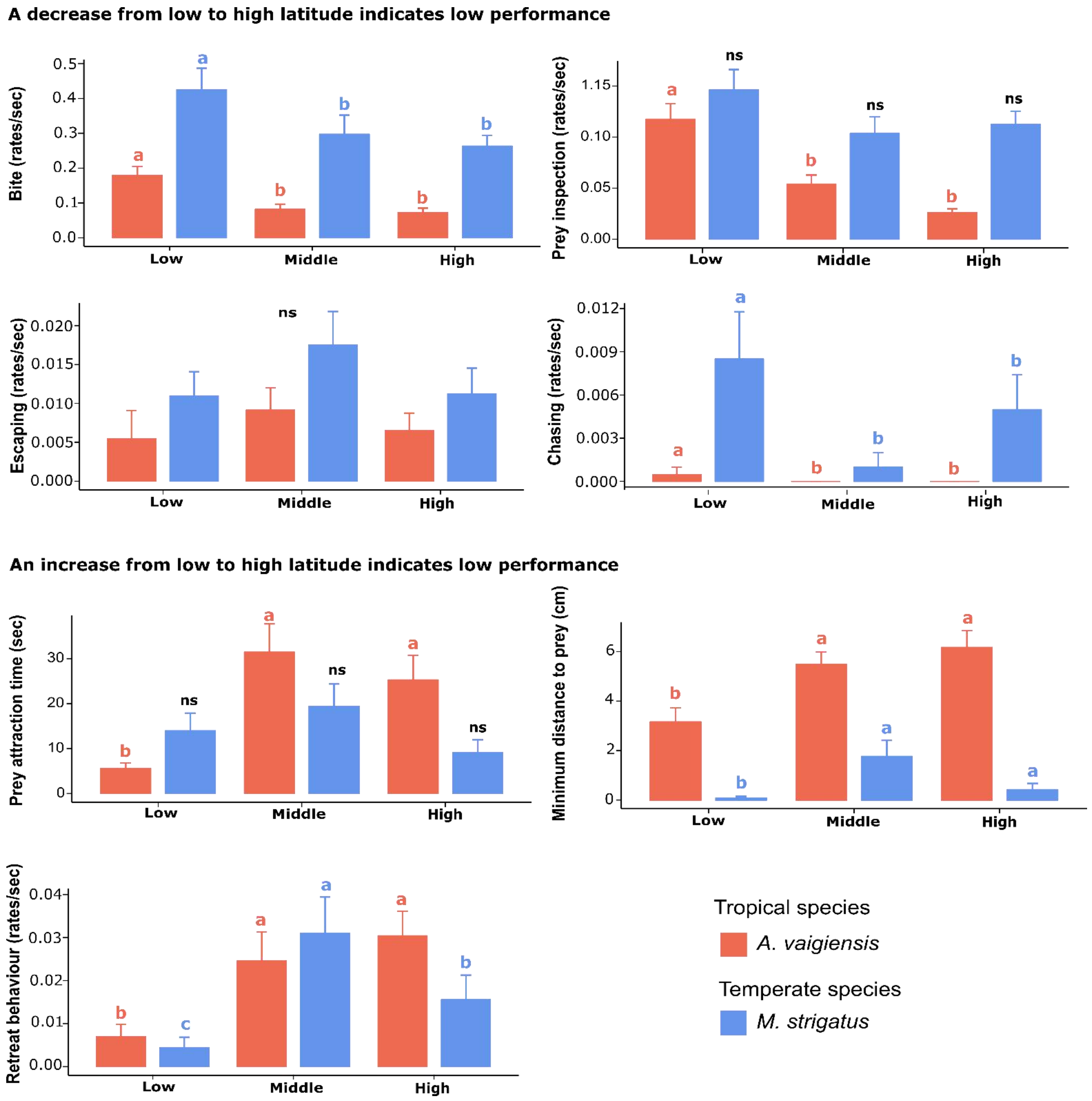

Figure 1. Behavioural proxies (mean + SE) of competitive ability in tropical and temperate fishes across a latitudinal gradient (see Figure S1) based on the foraging performance of fishes and on direct species interactions (escaping and chasing rates). The graphs are grouped into behaviours that show reduced performance when they decrease (above 4 panels) or increase (lower 3 panels) from low to high latitudes, respectively. Letters indicate significant latitudinal differences within species ($p < 0.05$; see Tables S3a, S3b). ns = no significant differences. Significant difference between the tropical and temperate fish species within latitudes are shown in Table S4.

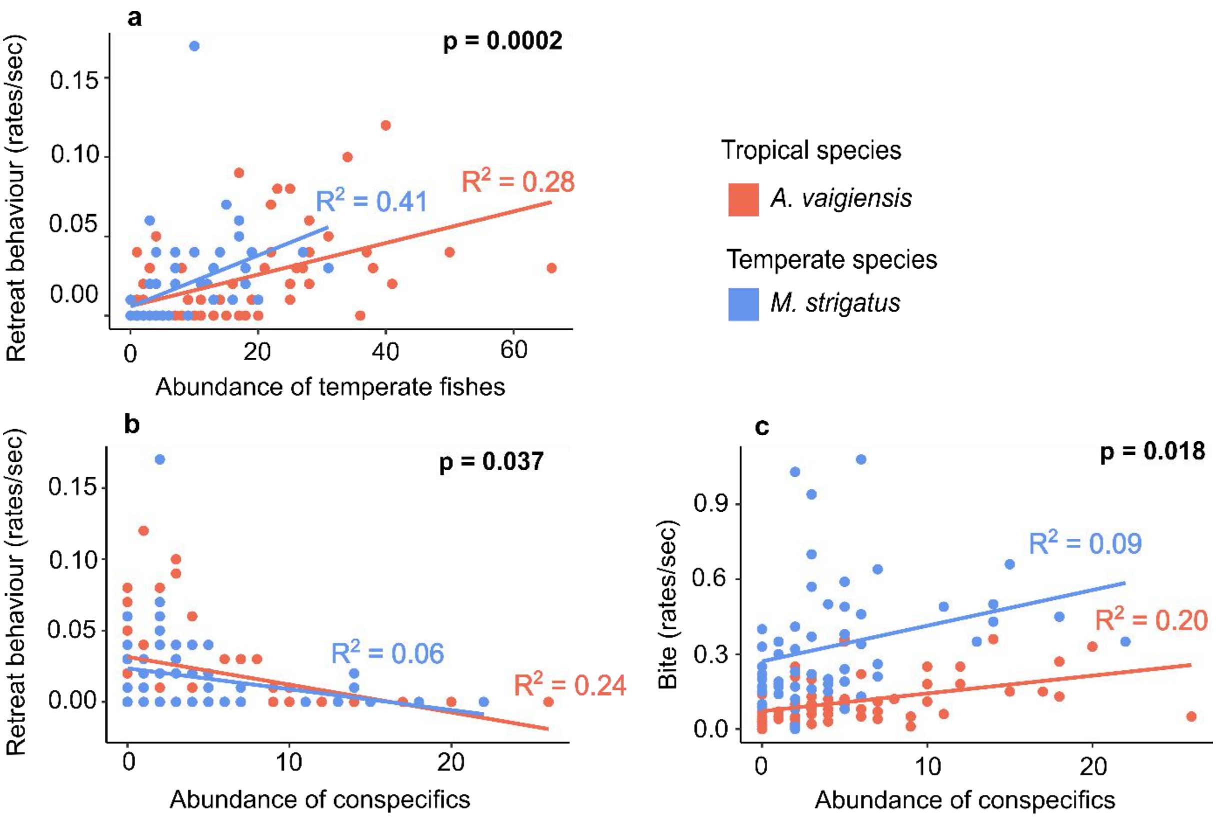

Figure 2. Relationship between behaviours (a,b: retreat rates; c: bite rates) of *A. vaigiensis* and *M. strigatus* that showed covariate significant effects in the ANCOVAs and the abundance of potential competitors (average of total number of temperate and conspecific individuals per sample). Adjusted R^2 show the proportion that the respective covariate contributed to the variability of the model. Model p-values for the covariates are shown inside each panel.

DISCUSSION

The central tenet of biological invasion theory is that alien species are often competitively stronger than non-native species and therefore experience successful invasions with substantial impacts on the communities in their novel environments (Carlton et al. 1999; Branch & Steffani 2004; Davis et al. 2003; Vila & Weiner 2004). However, we here show that the competitive performance (using various foraging behaviours as a proxy) of a common tropical range-extending fish is lower in its novel temperate range than in its native range, which may compromise its fitness in its invaded range. Reduced competitive performance of tropical fish at their high-latitude range edges was expressed through (1) increased prey attraction time, (2) increased retreat rates, (3) increased distance to prey, (4) reduced prey inspection rates, and (5) reduced bite rates, respectively, compared to their native ranges. In contrast, the magnitude of direct competitive interactions with local temperate fish (chasing and escaping behaviours) during foraging remained similar across latitudes. Such reduced foraging performance at temperate latitudes suggests that the studied tropical fish is still poorly behaviourally adapted to either low temperatures and/or unfamiliarity with a novel biological environment (e.g. prey, predators, habitat, competitors), which might increase their vulnerability to local competitors and predators (Figueira et al. 2019). Cooler-temperate waters are known to cause lower metabolic rates and foraging performance in *Abudefduf vaigiensis* and this is linked to a reduced energy allocation towards somatic growth (Kingsbury et al. 2020). Such a decline in performance by tropical range-extending fishes may be restricting their current survival and consequent permanent establishment in temperate ecosystems under current ocean warming.

Species composition at high latitudes can alter the foraging performance of tropical species in their temperate ranges. We show that individuals of *A. vaigiensis* were more efficient in approaching (decreased retreat rates) and consuming (increased bite rates) prey with increased abundances of conspecifics (irrespective of latitude), but contrastingly an increased abundance of temperate fishes increased their retreat rates. At sites with higher abundances of temperate fishes, these aggregated around the released prey and formed a physical barrier, preventing tropical fishes in approaching the prey (Fig. S3). Such physical displacement has also been observed in native and invasive terrestrial organisms (Masciocchi et al. 2009). Density-dependent competition is often observed among fishes. For example, at elevated abundance, coral-dwelling damselfishes become more aggressive and interference competition for refuge increases, leading to inferior competitors being more susceptible to predation (Holbrook & Schmitt 2002). Unexpectedly, a higher abundance of temperate fishes was not related to an increased aggression (escaping and chasing rates) between tropical and temperate species. Nevertheless, native temperate fishes were capable of indirectly competing with tropical fishes by inhibiting their access to food resources. With increasing ocean warming a higher diversity and abundance of tropical fishes it is expected in temperate systems (Fowler et al. 2017). Whilst under current warming, native temperate fishes may slow the pace of tropical invasions through competitive interference, increasing abundances of tropical fishes under future warming can counter these competitive effects through increased foraging performance when schooling with their own species.

The tropical fish had an overall lower competitive performance (six out of seven behaviours) in their novel ranges (mid and high latitudes) than the the temperate species. Inferior competitors often suffer high mortality rates by being more susceptible to predation and competition (Forrester & Steele 2000; Holbrook & Schmitt 2002; Almany 2003). Additionally, most of the tropical fishes at temperate latitudes were recruits and early-juveniles, and are therefore likely to be competitively more vulnerable to resource restriction by adult local competitors (Persson 1985; Young et al. 2003; Poulos & McCormick 2013). However, schooling with temperate fishes (including *M. strigatus*) can sometimes also facilitate the establishment of tropical fishes in temperate ecosystems by enhancing access to resources and hence increasing growth (Smith et al. 2018) and survival rates (Paijmans et al. 2020). Under current warming, temperate fishes still seem to have a competitive advantage over range-extending tropical fishes through higher competitive performance and higher abundances.

Surprisingly, the performance of the co-schooling temperate fish species was higher at warmer-low latitude than at the middle and high latitudes. Such higher foraging performance (increased bite rates and chasing rates, and reduced retreat rates) at low latitude might be explained by the fact that the natural range of *M. strigatus* covers all sites that we studied across the latitudinal gradient (Tea et al. 2019), and that they perform best at subtropical-warmer temperatures in the centre of their distributional range (Payne et al. 2016). A similar pattern was found in other temperate marine fish species in Tasman Sea (Neuheimer et al. 2011). As temperate species have a wider thermal niche than tropical species (Tewksbury et al. 2008; Perez et al. 2016), current ocean warming has positive rather than negative effects on the some of the performance traits of temperate fishes at their trailing edges.

CONCLUSION

We demonstrate that at higher latitudes (in novel temperate environments) and at elevated abundance of temperate fishes, the foraging performance of the most common range-extending tropical species is compromised. This suggests that both physical and biological factors might be acting in synchrony to restrict the establishment of tropical species in temperate ecosystems under current warming. Competitive interference for prey resources by temperate fishes might force tropical species to use less desirable resources slowing the initial stages of tropicalisation of temperate ecosystems.

ETHICS

All experiments were performed under animal ethics approval numbers S-2015-222A and S-2017-002 (University of Adelaide) and ETH17-1117 (University of Technology Sydney) and followed the University's animal ethics guidelines.

AUTHOR CONTRIBUTIONS

E.O.C.C, I.N., and D.J.B. conceived and designed the study, E.O.C.C. collected the data, E.O.C.C. analysed the data. All authors contributed to the writing of the article.

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SUPPLEMENTARY INFORMATION

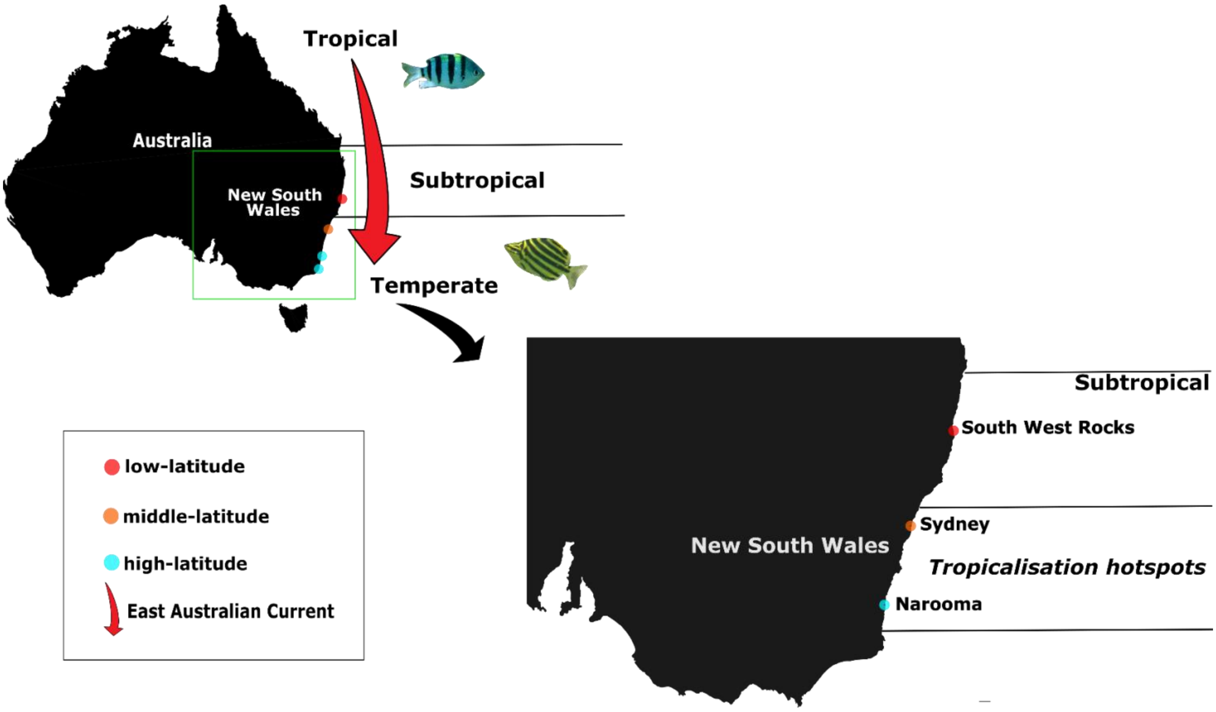

Figure S1. Map showing the sites of the *in situ* manipulative experiments and the tropical (*Abudefduf vaigiensis* - top photo) and temperate (*Microcanthus strigatus* - bottom photo) fishes studied. Red circle is the low latitude region: two sites at South West Rocks (30°52'34"S, 153°4'2"E and 30°53'0"S, 153°2'17"E). Orange circle indicates the middle latitude region: Shelly Beach (33°48'1.13"S, 151°17'31.23"E), Little Manly (33°48'23"S, 151°17'8"E) and Narrabeen (33°42'7"S, 151°18'21"E). Blue circle indicates the high latitude region: Narooma (36°12'54"S, 150°7'51"E).

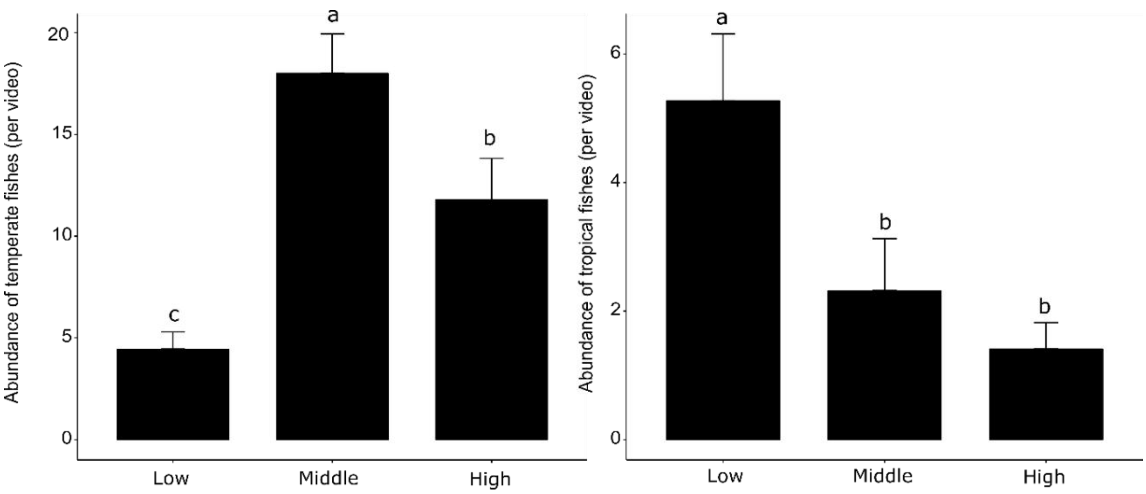

Figure S2. Abundance (mean + SE) of all tropical and temperate fishes over a latitudinal gradient quantified in the same videos in which the competitive performance of fishes was quantified. Letters indicate significant latitude differences within affinities. *** $p < 0.001$ * $p= 0.01$.

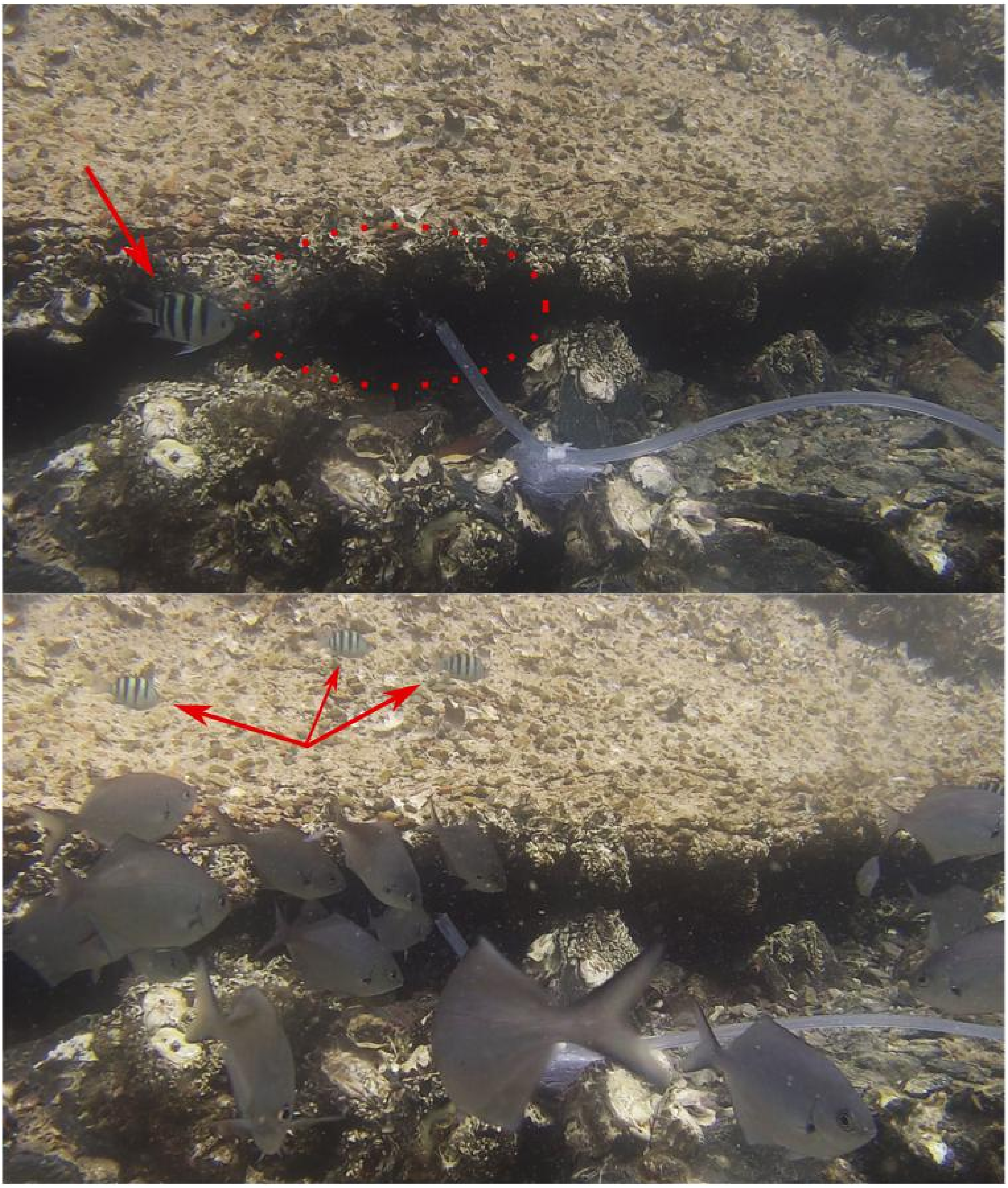

Figure S3. Manipulative underwater experiment to quantify the behaviour of, and species interactions between tropical and temperate fishes. Top panel: the tropical species *A. vaigiensis* (red arrow) attracted to and feeding on the released prey (Brine shrimp) (red circle) that are artificially released from the transparent tube by the observer. Bottom panel: consecutive attraction of temperate fishes (*Scorpis lineolata*) and their aggregation around the prey, preventing approach to the tropical fishes (red circle).

Table S1. Mean summer seawater temperatures (°C) collected using HOBO temperature recorders at the same time as the recording of fish behaviours, and the mean winter seawater temperatures (°C) based on long-term NOAA sea surface temperature data.

Latitude	**Location**	**summer**	**winter**
Low	**South West Rocks**	25.7	20.3
Middle	**Sydney**	23	19.3
High	**Narooma**	21.4	17.4

Table S2. Ethogram of the behavioural traits used as a proxy of competitive ability between tropical and temperate fish species. All behaviours were observed continuously within a recording.

	Behavioural traits	**Brief description**
Indirect competitive interaction	Bite rate	total number of bites taken at the released prey during the recording
	Prey inspection rate	total number of times that the individual got near the tube (released prey start point) at a distance of ≤ 5 their body length
	Prey attraction time	time (that each individual took to approach the prey after it was first released (swimming towards the prey)
	Minimum distance to prey	closest distance (cm) that the fish approach the tube over the entire time frame
	Retreat rate	total number of times that an individual try to approach the prey (minimum distance of ≤ 5 body lengths) but decided to abruptly turns around often to its previous position
Direct competitive interaction	Chasing rate	total number of times that an individual swam aggressively towards another individual -- conspecific, tropical or temperate heterospecific)
	Escaping rate	total number of times fled from an aggressor (conspecific, tropical or temperate heterospecific)

Table S3. Permutational Multivariate Analyses of Covariance testing the effect of the predictor variable ‘latitude’ (low, middle, high) on all behaviours (Table S2) of ‘species’ (the tropical *A. vaigiensis* and temperate *M. strigatus*) with the covariate ‘abundance’ of potential competitors excluding the interaction terms. The covariates included were: abundance of temperate fishes excluding *M. striatus*, abundance of tropical fishes excluding *A. vaigiensis*, and abundance of conspecific individuals of the study species. Significant results are indicated in bold and (*). df = degrees of freedom, SS = sum of squares, MS = mean square.

Variables	df	SS	MS	F-value	p-value
latitude	2	141.31	70.655	5.624	**0.0002***
species	1	149.34	149.34	11.889	**0.0002***
latitude × species	2	52.655	26.327	2.095	0.057
abundance temperate fishes (covariate)	1	24.897	24.897	1.981	0.110
abundance tropical fishes (covariate)	1	27.854	27.854	2.217	0.092
abundance conspecifics (covariate)	1	9.457	9.457	0.752	0.464
Res	105	1319	12.562		
Total	113	1724.5			

Pair-wise test

Latitude	**t**	**p-value**
high vs. middle	1.036	0.367
high vs. low	2.332	**0.006***
middle vs. low	2.842	**0.0006***

Table S4. Permutational univariate ANCOVA performed to help interpret the MANCOVA results by testing the effect of each behaviour across latitude, between species (*A. vaigiensis* vs *M. strigatus*) and their respective interaction, and the pair-wise results of the significant predictor variables. Significant results are indicated in bold and (*).

Bite rate

Predictor variables	df	SS	MS	F-value	p-value
Latitude	2	0.641	0.32	12.86	**0.0002***
Species	1	1.689	1.689	67.725	**0.0002***
Latitude × Species	2	0.006	0.003	0.124	0.8822
Abundance temperate fishes (covariate)	1	0.079	0.079	3.183	0.0758
Abundance tropical fishes (covariate)	1	0.006	0.006	0.257	0.6078
Abundance conspecifics (covariate)	1	0.138	0.138	5.536	**0.0184***
Res	113	2.843	0.024		
Total	122	5.404			

Latitude	**t**	**p-value**
high = middle	0.176	0.862
high < low	4.900	**0.0002***
middle < low	3.857	**0.0004***

Prey inspection rate

Predictor variables	df	SS	MS	F-value	p-value
Latitude	2	0.348	0.174	18.439	**0.0002***
Species	1	0.301	0.301	31.877	**0.0002***
Latitude × Species	2	0.093	0.046	4.951	**0.009***
Abundance temperate fishes (covariate)	1	0.001	0.001	0.177	0.664
Abundance tropical fishes (covariate)	1	0.021	0.021	2.262	0.138
Abundance conspecifics (covariate)	1	0.026	0.026	2.768	0.106
Res	114	1.077	0.009		
Total	122	1.87			

Pair-wise test (latitude × species for pair of levels of factor ‘latitude’)

Species	**Latitude**	**t**	**p-value**
A. vaigiensis	high = middle	2.362	0.023
	high < low	6.828	**0.0002***
	middle < low	3.813	**0.0004***
M. strigatus	high = middle	1.047	0.302
	high = low	1.483	0.141
	middle = low	1.984	0.053

Pair-wise test (latitude × species for pair of levels of factor ‘species’)

Latitude	**t**	**p-value**	**species**
high	8.636	**0.0002***	*A.vaigiensis < M. strigatus*
middle	2.746	**0.010***	*A.vaigiensis < M. strigatus*
low	1.294	0.207	*A.vaigiensis = M. strigatus*

Prey attraction time

Predictor variables	df	SS	MS	F-value	p-value
Latitude	2	78.177	39.088	8.2716	**0.001***
Species	1	18.547	18.547	3.9248	0.056
Latitude × Species	2	37.883	18.941	4.0082	**0.019***
Abundance temperate fishes (covariate)	1	10.84	10.84	2.2939	0.129
Abundance tropical fishes (covariate)	1	1.282	1.2827	0.27143	0.596
Abundance conspecifics (covariate)	1	15.266	15.266	3.2305	0.078
Res	113	533.99	4.7256		
Total	121	695.99			

Pair-wise test (latitude × species for pair of levels of factor 'latitude')

Species	Latitude	t	p-value
A. vaigiensis	high = middle	0.435	0.675
	high > low	4.642	**0.0002***
	middle > low	4.035	**0.0006***
M. strigatus	high = middle	1.937	0.067
	high = low	0.438	0.674
	middle = low	1.379	0.169

Pair-wise test (latitude × species for pair of levels of factor 'species')

Latitude	t	p-value	Species
high	1.161	0.260	*A.vaigiensis* = *M. strigatus*
middle	1.431	0.154	*A.vaigiensis* = *M. strigatus*
low	3.078	0.003	*A.vaigiensis* < *M. strigatus*

Minimum distance to prey

Predictor variables	df	SS	MS	F-value	p-value
Latitude	2	15.481	7.74	15.631	**0.0002***
Species	1	82.754	82.754	167.12	**0.0002***
Latitude × Species	2	2.293	1.146	2.315	0.109
Abundance temperate fishes (covariate)	1	0.014	0.014	0.030	0.864
Abundance tropical fishes (covariate)	1	1.191	1.191	2.406	0.120
Abundance conspecifics (covariate)	1	0.134	0.134	0.272	0.595
Res	106	52.489	0.495		
Total	114	154.36			

Latitude	t	p-value
high = middle	0.535	0.596
high > low	5.221	**0.0002***
middle > low	4.939	**0.0002***

Retreat rate

Predictor variables	df	SS	MS	F-value	p-value
Latitude	2	0.204	0.102	16.02	**0.0002***
Species	1	0.005	0.005	0.897	0.337
Latitude × Species	2	0.050	0.025	3.940	**0.025***
Abundance temperate fishes (covariate)	1	0.246	0.246	38.67	**0.0002***
Abundance tropical fishes (covariate)	1	0.006	0.006	1.046	0.307
Abundance conspecifics (covariate)	1	0.030	0.03	4.737	**0.037***
Res	114	0.727	0.006		
Total	122	1.272			

Pair-wise test (latitude × species for pair of levels of factor 'latitude')

Species	**Latitude**	**t**	**p-value**
A. vaigiensis	high = middle	1.323	0.184
	high > low	4.306	**0.0006***
	middle > low	2.815	**0.009***
M. strigatus	high < middle	2.269	**0.026***
	high > low	2.239	**0.032***
	middle > low	4.619	**0.0002***

Pair-wise test (latitude × species for pair of levels of factor 'species')

Latitude	**t**	**p-value**	**species**
high	2.441	**0.020***	*A.vaigiensis > M. strigatus*
middle	1.176	0.251	*A.vaigiensis = M. strigatus*
low	0.774	0.449	*A.vaigiensis = M. strigatus*

Chasing rate

Predictor variables	df	SS	MS	F-value	p-value
Latitude	2	0.001	0.006	3.902	**0.021***
Species	1	0.025	0.025	14.573	**0.0002***
Latitude × Species	2	0.009	0.004	2.558	0.074
Abundance temperate fishes (covariate)	1	0.001	0.001	0.792	0.365
Abundance tropical fishes (covariate)	1	0.003	0.003	1.886	0.157
Abundance conspecifics (covariate)	1	0.0004	0.0004	0.237	0.620
Res	114	0.199	0.001		
Total	122	0.252			

Latitude	**t**	**p-value**
high = middle	1.604	0.114
high < low	1.285	0.204
middle < low	2.712	**0.008***

Escaping rate

Predictor variables	df	SS	MS	F-value	p-value
Latitude	2	0.015	0.007	1.491	0.225
Species	1	0.057	0.057	10.864	**0.0004***
Latitude × Species	2	0.001	0.0002	0.051	0.952
Abundance temperate fishes (covariate)	1	0.012	0.012	2.357	0.130
Abundance tropical fishes (covariate)	1	0.004	0.0003	0.804	0.378
Abundance conspecifics (covariate)	1	0.0003	0.005	0.070	0.793
Res	114	0.605			
Total	122	0.696			

CHAPTER V

OCEAN ACIDIFICATION MAY SLOW THE PACE OF TROPICALISATION OF TEMPERATE FISH COMMUNITIES

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By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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ABSTRACT

Poleward range extensions by warm-adapted sea urchins are switching temperate marine ecosystems from kelp-dominated to barren-dominated systems that favour the establishment of range-extending tropical fishes. Yet, such tropicalisation may be buffered by ocean acidification. As oceans warm, they acidify, and this not only reduces urchin grazing performance but also urchin barrens that are preferred by tropical range-extending fishes. Using ecosystems experiencing natural warming and acidification, we assess the effect of ocean acidification on the poleward expansion of urchin barrens, and how this might mediate the rate of tropicalisation. Our study reveals that whilst ocean warming may facilitate tropicalisation by creating barren-dominated states, ocean acidification might buffer this extension by inhibiting the formation of barrens through reduction of urchin populations (by 87%). This buffering effect of CO_2 enrichment was observed at natural CO_2 vents that are associated with a shift from a barren-dominated to a turf-dominated state, which we found is less favourable to tropical fishes. Together, these observations suggest that ocean acidification may buffer the tropicalisation effect of ocean warming against urchin-barren formation via multiple processes (fewer urchins and barrens), and consequently slow the increasing rate of tropicalisation of temperate fish communities.

INTRODUCTION

The geographical ranges of species naturally ebb and flow through time (Parmesan 2006). Nonetheless, human-mediated environmental disturbances have intensified and allowed many species to extend their distributions to new environments (Pecl et al. 2017). The increase in global temperature has forced many warm-adapted species (e.g., sea-urchins and tropical fishes) to expand their range poleward – a process referred to as tropicalisation (Ling 2008; Feary et al. 2013). These changing species distributions can result in altered or novel biological interactions, often triggering modifications to the recipient ecosystem (Nakamura et al. 2013; Peers et al. 2014; Verges et al. 2016), such as the phase-shift from kelp-dominated to barren-dominated stage caused by the poleward extension of warm-adapted temperate sea-urchin *Centrostephanus rodgersii* (Ling et al. 2009; Johnson et al. 2005). This shift to barren states might facilitate the presence of tropical fishes on temperate reefs (native invasions) which tend to have greater associations with non-macroalgae forming habitats (Beck et al. 2017). Yet, the future ranges of tropical species and the consequent rates of tropicalisation in temperate ecosystems remain uncertain because warming is not the only global environmental driver that will alter the structure of ecological communities.

Ocean acidification and global warming are known to directly alter the structure of marine habitats (Nagelkerken & Connell 2015; Wernberg et al. 2016; Connell et al. 2018), and the resources that species depend on to survive (Nagelkerken et al. 2017; Sunday et al. 2017). Warming drives loss of kelp forests directly (e.g. through heatwaves, Wernberg et al. 2016) and indirectly by intensifying herbivory (e.g. range extensions of warm-adapted sea urchins: Ling et al. 2008 and tropical herbivorous fishes: Verges et al. 2016). Yet, loss of kelp may also be driven by ocean acidification that triggers the superior competition of algal turfs that benefit from CO_2 (Connell et al. 2013, 2018). Whilst habitat-forming organisms, such as kelps and seagrasses, can benefit directly from increased CO_2 (Russell et al. 2013; Palacios & Zimmerman 2007; Hepburn et al. 2011;

Linares et al. 2015), shifts towards turf-forming algae are likely to be more common because warming and acidification combine to reduce the performance of habitat-creating species, but increase turf performance (e.g. kelp systems: Russell et al. 2009; Connell & Russell 2010; coral systems: Diaz-Pulido et al. 2011; Johnson et al. 2017). Yet, it is important to highlight that the majority of community-level studies have focused on the single, direct and negative effects of abiotic change, ignoring the fact that ocean acidification and warming can combine in synergistic and antagonistic ways (Kroeker et al. 2017). In some cases, for example, change in one 'stressor' may act as a resource to boost abundances (CO_2 can enhance algal productivity: Connell et al. 2013, or fish abundances: Nagelkerken et al. 2017), or it may act as a stressor to suppress abundances (temperature can negatively affect secondary producers, Goldenberg et al. 2017).

Tests of the simultaneous effect of ocean acidification and warming are often easier to achieve through laboratory than field experiments (e.g. Wernberg et al. 2012). However, the biological outcomes of laboratory experiments may not match those of field experiments (Kroeker et al. 2011), because of the mediating influence of ecological interactions (Goldenberg et al. 2018) that buffer change (Connell & Ghedini 2015). In addition, almost all experimental studies involve the response of organisms to abrupt changes ignoring the fact that climate conditions are gradually changing and the rates of the organism responses may differ from abrupt to gradual changes that occur in nature (Widdicombe et al. 2008). Although it is not possible to study the gradual effect of ocean acidification at CO_2 vents, recently many studies have highlighted the benefit of natural CO_2 vents to evaluate the effect of future CO_2 conditions *in situ* on organisms naturally adapted and exposed long-term to reduced pH levels. Observations from natural systems, therefore, may complement and even improve laboratory experiment findings because they increase the predictive value of the effects of future climate (Hofmann et al. 2011; Connell et al. 2013).

There has been considerable focus on how global warming enhances the poleward movement of warm-adapted species (Parmesan & Yohe 2003; Hoegh-Guldberg & Bruno 2010), but there is almost nothing known on how ocean acidification might accelerate or buffer these range-extensions, despite the fact that both stressors will increase in strength in the near future (Bopp et al. 2013). One key issue for marine systems is the divergent forecasts of ocean warming and ocean acidification on the foraging effects of ecosystem engineers such as warm-adapted sea urchins, particularly the consequences of their range expansion to cooler latitudes. Whilst warming is considered a primary driver of the expansion of their barrens at cooler latitudes by increasing urchin abundances leading to overgrazed kelp forests (Ling et al. 2015), ocean acidification might inhibit the creation of barrens by reducing urchin fitness and abundance, allowing the increase of non-calcified organisms. Although some sea-urchin species may be able to adapt to ocean acidification (Calosi et al. 2013), such phase-shift may still occur where the CO_2-driven boost to primary productivity overwhelms the capacity of urchins to compensate through herbivory (Connell et al. 2018).

To investigate how these opposing effects might influence the rate of tropicalisation, we assessed whether ocean acidification might not only buffer the effects of ocean warming (i.e. inhibit urchin barrens) but also mediate the rate of tropicalisation (i.e. accelerate or inhibit recruitment of tropical fishes). Because it was not possible to investigate these two stressors simultaneously *in situ* and in an orthogonal way, we present a new approach to this vexing challenge using two different natural laboratories connected by a strong biological link to study ocean warming (tropicalisation hotspots; Booth et al. 2007) and ocean acidification (natural CO_2 vents; Nagelkerken et al. 2016), both containing the range-expanding sea-urchin (*Centrostephanus rodgersii*) as an important habitat engineer. Whilst warming hotspots represent ongoing warming, natural CO_2 vents represent pH conditions forecast for the end of the century (under various RCP greenhouse gas emission scenarios). Nevertheless, our findings are important to anticipate how the effects of warming on tropicalisation (i.e. at the leading edges of warm-adapted species distributions where species track their native thermal niches) might be transformed by acidification in the near future.

Here, we first observed whether moderate ocean acidification (~ RCP 4.5–6.0 and SSP2-4.5-SSP4-6.0) might reduce the densities of sea urchins and the extent of barrens (at CO_2 vents), both of which would otherwise increase under ocean warming. We then propose a novel phase-shift from barren to turf habitat when the effects of acidification are included (Fig. 1). Finally, we consider how these shifts may also change the rate of establishment of range-extending tropical fishes; i.e., we observe whether tropicalisation of fishes is facilitated by urchin barrens and turf habitats. Understanding the rate of barren formation and their effect on invading tropical reef fishes has direct implications for understanding tropicalisation of temperate ecosystems in general.

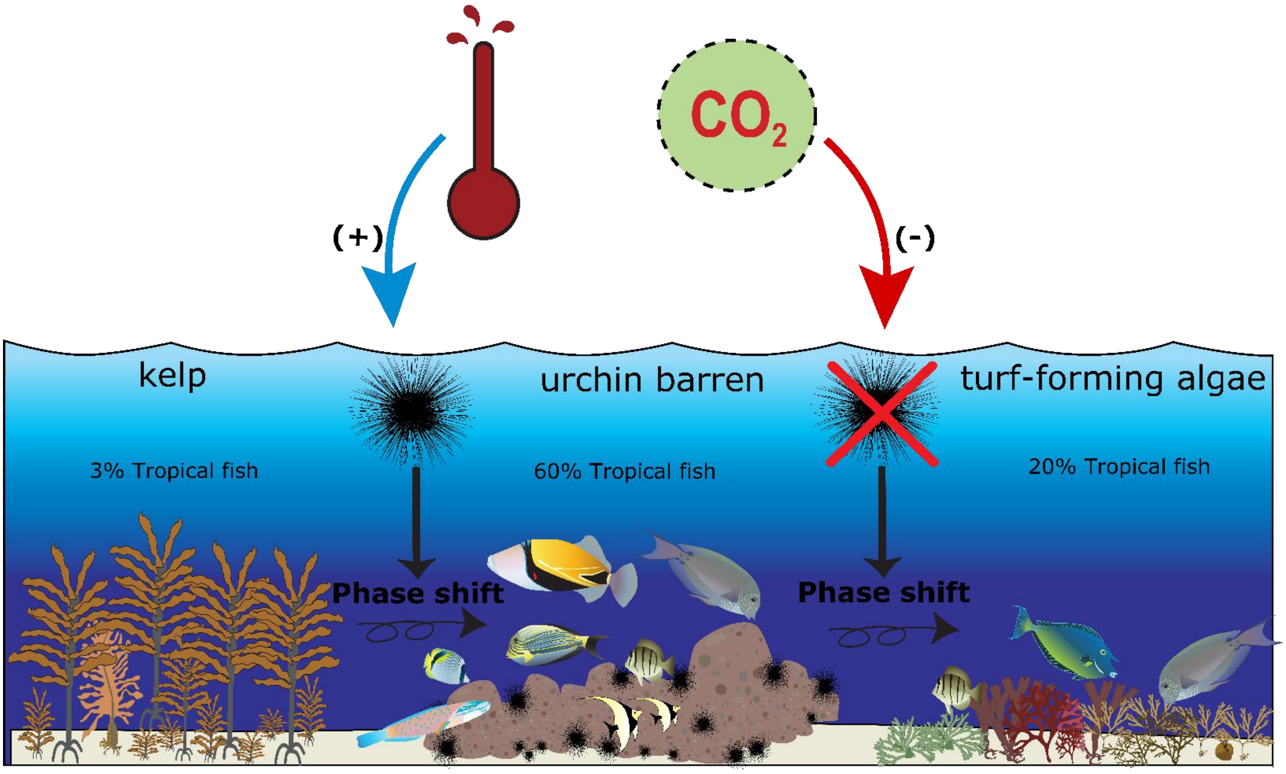

Figure 1. A conceptual diagram depicting the potential direct, indirect, negative (-) and positive (+) effects of ocean warming and ocean acidification on sea urchin-induced habitat phase shifts and the cascading effects on species richness of range-extending tropical fishes in temperate ecosystems (% values represents the relative fish species richness per habitat). Elevated temperature enables the range expansion of sea urchins, which enable a phase shift from natural kelp forests to rocky barrens. Ocean acidification, however, decreases range-extending urchin densities (via negative physiological effects), and enables a phase shift from barren to turf-dominated habitats (via CO_2 enrichment). In conclusion, the invasion of tropical fishes in temperate waters may be slowed down by ocean acidification.

METHODOLOGY

STUDY AREAS

We combined observations from two subtidal volcanic CO_2 vents (New Zealand) and three tropicalisation hotspots (south-eastern Australia) (Fig. S1). We used these areas as an "early warning" system to assess the combined consequences of ocean acidification and ocean warming at tropicalisation hotspots across temperate coastal ecosystems. Three main rocky-reef habitat types were distinguished (Connell & Irving 2008): kelp forests (dominated by *Ecklonia radiata*), turf-forming algae (<10 cm in height; defined in Connell et al. 2018) and sea urchin barrens (dominated by crustose coralline algae). These barrens are created by the native temperate species (*Evechinus chloroticus*) and warm-adapted sea urchin *Centrostephanus rodgersii*. *Centrostephanus rodgersii* creates widespread barren habitat across ~50% of the shallow reefs in SE Australia, which amounts to several thousand hectares (Connell & Irving 2008). This species has been largely restricted to the coast of New South Wales including Sydney, but from ~50 years ago the range of this species has extended southwards to northern Tasmania (Johnson et al. 2005) and to northern New Zealand (Pecorino et al. 2012).

Although the two stressors were separately evaluated, in areas with distinct environmental features, the two studied regions can be compared because: (1) both are located in shallow temperate rocky reef ecosystems; (2) they have similar bathymetric zones (shallow reefs ranging from ~1 to 6 m); (3) the major benthic components and vegetation are similar (described above); and (4) the two key ecosystem engineers (sea urchins) occur in both regions. Such similarities indicate that these systems might be used to draw meaningful conclusions at the leading edges of species distributions about the synergistic effect of ocean warming and acidification on the tropicalisation of temperate systems.

NATURAL CO_2 VENTS

Volcanic CO_2 vents are naturally enriched in CO_2 where the levels of ocean pH correspond to predicted future levels of ocean acidification, enabling the investigation of the prolonged effect of future CO_2 concentrations on marine communities *in situ* (Hall-Spencer et al. 2008; Brinkman & Smith 2015). The vents studied (~6–8 m depth) were located on the north-eastern coast of an active volcanic island (Bay of Plenty, White Island, New Zealand; 37°31.013’ S, 177°11.649’ E) where CO_2 bubbles are released from the rocky reef substrate in a total area of ~580 m^2. A total of four sites were sampled: two adjacent control areas located approximately 25 m from the vents, with pH levels similar to normal conditions (means across years: 8.05–8.08), and two sites with locally reduced seawater pH (means across years: 7.82–7.88), with values close to Representative Concentration Pathway projections of 4.5 and 6.0 and Shared Socioeconomic Pathways of SPP2-4.5 and SPP4-6.0 for the year 2100 (Bopp et al. 2013; O’Neill et al. 2016). The SSP2-4.5 scenario is relatively comparable to the RCP4.5, while the SSP4-6.0 is similar to the RCP6.0 scenario (O’Neill et al. 2016). The southern vent had pH values that reflected an approximate RCP 4.5 or SSP2-4.5 scenarios with a reduction of 0.19 pH units compared to the control site, while the northern vent showed a pH reduction of 0.24 units which is close to an RCP 6.0 or SSP4-6.0 scenarios (Table S1). The pH levels at the vents were relatively stable over time and are not confounded by other physico-chemical variables (Table S2). These pH reductions represent moderate end-of-century predictions rather than a more extreme RCP 8.5 scenario reflective of no greenhouse gas mitigation measures (Hughes et al. 2017).

At CO_2 vent sites, the benthic community is primarily composed of turfs where CO_2 concentrations are elevated, whereas outside this CO_2 influence kelp and barrens form mosaics with turfs (Connell et al. 2018). The fish community is composed of a few roving species, which are unlikely to be continuously exposed to the low pH levels at the vents due to their high mobility, but a large community (comprising >90% of the total fish density) of territorial and site-attached species composed mainly of triplefins and blennies. At the CO_2 vents, we defined “fish assemblage” as species with well-defined and small home range and low mobility that are within the CO_2 plume and are directly affected by elevated CO_2. By using only species that match these criteria (low mobility and small home range), such as triplefins and blennies, we are able to draw stronger conclusions about the effects of habitat modification triggered by CO_2 on a fish community. Previous studies showed that seawater temperature does not differ among the four sites and the pH values show only a small variation at any given site over the day (Nagelkerken & Connell 2015, Connell et al. 2018).

TROPICALISATION HOTSPOTS

Over the last two decades, Sydney’s coastal areas (New South Wales, Australia) have experienced arrivals of an increasing diversity and density of vagrant tropical fishes that annually recruit there throughout the summer (~100 species) (Booth et al. 2007). There has been a gradual increase in the abundance of overwintering survivors due to increasing coastal seawater temperatures (Booth et al. 2018). All these factors in combination with the gradual strengthening of warmer currents (e.g. East Australia Current) moving down from tropical regions to high latitudes (Ridgeway 2007; Hobday & Pecl 2014) make the Sydney coast a tropicalisation hotspot (Figueira & Booth 2010; Feary et al. 2013). We selected the same sites where vagrant tropical fish assemblages have been regularly monitored for nearly 18 years (Sydney: Cabbage Tree Bay, Fairy Bower and Little Manly). These reefs are dominated by a mosaic of the three main types of habitats (kelp, turf, barrens) in addition to patches of oyster reefs which were also used in this study because of its importance as a habitat provider for many organisms (McLeod et al. 2019) including some tropical fishes that were observed using this habitat as a refuge. Oyster reefs were once a common habitat of temperate coastal waters in NSW but after severe overharvesting only small patches persist in the intertidal zone (Gillies et al. 2018).

STUDY DESIGN

FISH DENSITY AND DIVERSITY

The abundance and diversity of local (temperate) and vagrant (tropical) fishes were estimated in south-eastern Australia (2017–2018), and local species in New Zealand (between February and April, in years 2017 and 2018). Visual surveys estimated the density of fish within sampling units that were randomly distributed among patches of the most common habitats identified for each region (see *Study areas* above).

The specific method used to quantify fish assemblages was designed to best represent the local assemblage and the size and shape of habitats. At the vents in New Zealand, only some species (e.g. triplefins, blennies and scorpionfish) were considered because these species are site-attached and the consequences of long-term exposure to elevated CO_2 at vents could be properly investigated. The site-attached fish assemblage studied was identified to species and visually quantified in replicate stationary circular census. Due to the small fish body sizes, the counts were made in small cylindrical survey areas of 1 m in diameter. Fishes were counted inside the cylinder for approximately 1 minute. This approach produces the best density estimates for small fishes (≤10 cm) (methodology adapted from Minte-Vera et al. 2008). Individual fish body size was also estimated between two categories (<5 and >10 cm total length). At each of the two control sites a total of ~15 quadrats were surveyed per habitat (kelp, turf, and barrens). At the vents, the benthic cover is dominated by turf habitat and therefore 27 quadrats were surveyed for this habitat at the vent sites (11 at the southern vent and 16 at the northern vent).

In the Sydney area, belt transects were used to quantify the temperate and tropical fish assemblages in each main benthic habitat type identified in this region. About 15–30 transects were surveyed per habitat (kelp, turf, barren and oyster banks). The method consisted of a diver swimming along a transect of 10 m length, identifying and counting all fishes including their respective body length (size categories of <5, 5–10, 10–20, 20–30, >30 cm total length) within 2 m of each side of the transect tape (40 m^2 area per transect). All benthic and pelagic fish species were included. First, the larger fishes were counted and then for the same transect an intensive search for small and cryptic species was performed between and underneath kelp leaves, rocks and inside crevices (methodology adapted from Fulton et al. 2016). The difference in the census area and shape between the two regions (Australia vs New Zealand) corresponds to the length and shape of the habitats. Larger census areas in Sydney were used because of the larger and longer patches of habitats than those in New Zealand.

For both study regions, differences in the fish assemblage among habitats were evaluated at the individual species as well as functional levels. Fishes were split into major functional groups according to their diet and feeding habits: (1) planktivores; (2) omnivores; (3) invertivores; (4) herbivores; and (5) carnivores (fish and invertebrate feeders). Additionally, because the herbivorous fish community is not a homogeneous group we subdivided them into: (6) solely epilithic algae matrix (EAM) feeders (roving-grazing herbivores, territorial-grazing herbivores and herbivores/detritivores); (7) solely browsing herbivores (macroalgae feeders); (8) combined browsing and grazing herbivores (EAM and macroalgae feeders); and (9) kelp feeders. These categories follow Choat & Clement (1992), Clements & Choat (1997), Ciccarelli et al. (2007), and Zarco-Perello et al. (2017). All diet information and functional characteristics were collected from FishBase (Froese & Pauly 2016). As the benthic fish species in New Zealand were all are part of the same functional group (i.e. invertivores – following FishBase), functional group analysis was not performed for the New Zealand study area.

CO_2 EFFECTS ON SEA URCHIN POPULATIONS

In New Zealand, sea urchin densities were quantified inside circular quadrats of 2 m in diameter at the same patches of habitats where the fishes were surveyed. A total of 15 circular quadrats were performed in turf habitats at the vents and each of the three habitats at controls. A maximum of 10 sea urchins within each habitat were randomly selected and their body sizes (longest diameter) were measured using callipers. In total, the body size of ~400 native sea urchins and 30 warm-adapted sea urchins (due to their lower abundance in comparison with the natives) was measured. Finally, after each survey we measured the largest and smallest dimensions of 15 patches of barrens at control sites had their largest and smallest dimensions measured of each barren at control sites was measured in order to calculate the area (m^2) of each barren and correlate sea-urchin abundances to barren size. At the end of each survey, seawater samples were collected directly above the substrate of each circular transect to measure seawater pH. A diagram summarising the methodology is shown in Fig. S2.

STATISTICAL ANALYSIS

A canonical analysis of principal coordinates (CAP) was used to evaluate the relationship between habitat type, and taxonomic and functional fish assemblages. The decision to use a constrained (CAP) over an unconstrained analysis was because constrained data is normally considered as the most appropriate multivariate analysis, especially when there is an *a priori* assumption of how explanatory variables (in this case habitats) determine response variable values (in this case species abundance) measured in the same set of objects (e.g. samples or sites). In addition, constrained ordination analysis uncovers patterns that are masked in unconstrained multivariate analyses (e.g. nMDS ordination), allowing us to better visualize specific differences between habitat types (Anderson & Willis 2003; Paliy & Shankar 2016).

As the tropical and temperate fishes do not share the same taxonomic composition, comparisons between these two different communities was performed based on species functionality (Hemingson & Bellwood 2018). Hence, comparing the function played by vagrant tropical and temperate species might reveal their potential to compete and/or share the same resources. To reduce the contribution of disproportionately abundant species on the analysis, the data were square-root transformed. Dissimilarities in the taxonomic and functional abundance of fish assemblages (tropical, temperate and CO_2 vents fish assemblages) were calculated using one-way Analysis of Similarities (ANOSIM), and ANOVAs were then used to test for univariate differences in species richness, density and biomass of fish between the factors of origin (tropical vs temperate) and habitat (kelp-dominated vs barren-dominated vs turf-dominated vs oyster-dominated vs CO_2 vents), using habitat as a fixed factor. Biomass of each community was obtained by converting fish counts to biomass using Length–Weight relationships from FishBase (Froese & Pauly, 2006). Estimates were calculated by multiplying the weight from the midpoint of each size category by the number of fish per size category, and them summing size categories (McClanahan & Kuanda-Arara, 1996). A similarity percentage analyses (SIMPER) was used to evaluate which species and functional groups mostly contributed to dissimilarities among habitat types. Ordination and similarity analyses were performed using the PRIMER 6 software. Student–Newman–Keuls (SNK) multiple comparisons of means were performed as *post-hoc* tests for all ANOVAs and pairwise comparisons of the mean were used in the ANOSIMs (Zar 1999; Anderson 2001).

To test the relationships between sea urchin density and pH, between barren size and pH, urchin density, and urchin body, size simple linear regression analyses were used. Finally, differences in sea urchin size across habitats were tested using a one-way ANOVA. Regression and ANOVA analyses were conducted using R software version 3.4.1.

RESULTS

TROPICAL AND TEMPERATE FISH COMMUNITY COMPOSITION ACROSS HABITAT

Species richness (Fig. 2a; one-way ANOVA, $F = 28.88$; $p < 0.0001$), density (Fig. 2b; $F = 18.68$; $p < 0.0001$) and biomass (Fig. 2c; $F = 19.55$; $p < 0.0001$) of tropical fishes was highest on sea urchin barrens, lowest in kelp forests, and intermediate on oyster beds and algal turf. Likewise, native temperate fishes showed highest species richness (Fig. 2d; one-way ANOVA, $F = 14.61$; $p < 0.0001$), total density (Fig. 2e; $F = 11.61$; $p < 0.0001$) and biomass on sea urchin barrens (Fig. 2f; $F = 5.842$; $p < 0.001$). However, the three other habitats showed similar richness, densities, and biomass. At the CO_2 vents, native temperate fish species richness, total density and biomass were not significantly different among habitats (Fig. 2h, i, j), except for a higher biomass at the vent with highest pCO_2 values (Fig. S3).

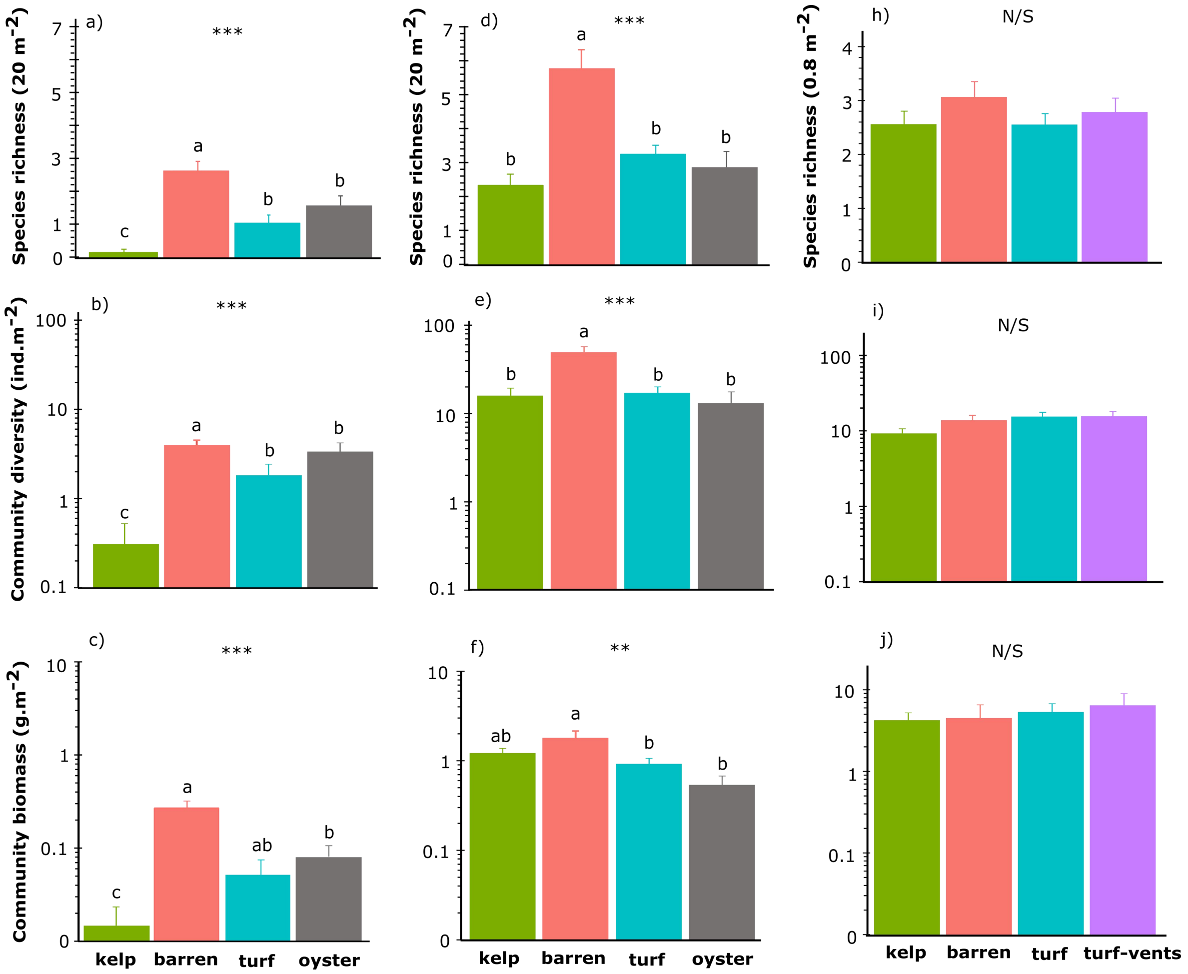

Figure 2. Species richness per transect (top panels), density (middle panels) and biomass (bottom panels) of fish assemblages across different coastal habitats (mean + SE) showing urchin-barrens as a key habitat for tropical and temperate fish assemblages while kelp-habitat is avoided by tropical fishes. a-b-c) range-extending tropical fish communities of south-eastern Australia; d-e-f) local temperate fish communities of south-eastern Australia; h-i-j) temperate fish community at CO_2 vents (turf-vents) and three control habitats at White Island, New Zealand. *** $p < 0.001$, ** $p < 0.01$, N/S = not significant (tested using ANOVA); different letters above bars indicate significant differences among habitats (post hoc tests). At the vents the benthic cover is dominated by turf algae, therefore it was considered as the only vent habitat. The y-axes for the density and biomass graphs were all log-scaled for consistency.

The fish community composition differed significantly among habitats for tropical (Fig. S3; ANOSIM, Global R = 0.36; p = 0.0002) and native temperate (Fig. S3; ANOSIM, Global R = 0.29; p = 0.0002) fishes in south-eastern Australia, and for local species at CO_2 vents in New Zealand (Fig. S3; ANOSIM, Global R = 0.06; p = 0.042). For both tropical and temperate fish assemblages, pairwise tests revealed that all habitats significantly differed from each other in Australia, while for the fish community at the CO_2 vents, kelp forests were the most dissimilar habitat (Table S3a). The tropical fishes that contributed most to the dissimilarities among habitats were the common species sergeant major *Abudefduf vaigiensis* (most abundant on oyster and urchin-barren habitats) and dusky surgeonfish *Acanthurus nigrofuscus* (most abundant on urchin barrens) contributing to approximately half of the dissimilarities (Table S4). For the temperate fish community, mado *Atypichthys strigatus* (kelp forests) and hulafish *Trachinops taeniatus* (urchin barrens) together were responsible for ~ 41–60% of the dissimilarity among habitats (Table S5). Finally, at the CO_2 vents community, ~ 56–66% of the dissimilarity among habitats was attributed to the common triplefin (*Forsterygion lapillum*) (Table S6).

FUNCTIONAL COMPOSITION OF TROPICAL AND TEMPERATE FISH COMMUNITIES ACROSS HABITAT

The trophic functional composition of the tropical fish community (Table S3b; ANOSIM, Global R = 0.28, p = 0.0002) clearly differed among the four habitats in Australia, except for turf and oyster habitats. For the temperate fish community, however, barrens was the only habitat that significantly differed from the other habitats (Table S3b; Global R = 0.25, p = 0.0002). Most of the functional groups of tropical fishes were associated with barrens, except for planktivores, which were also highly associated with oyster reefs (Fig. 3, Table S7). For the temperate fish species in Australia, roving grazing herbivores, territorial grazing herbivores, both browsing/grazing herbivores, and planktivores were most associated with barrens, and they were the functional groups that overlapped in habitat use for tropical and temperate fish assemblages (Fig. 3, Table S7). Only temperate functional groups, particularly omnivores, kelp feeders, browsing herbivores, and herbivorous/detritivores were associated with kelp habitats. Turf and oyster-dominated habitats were associated with few functional groups: temperate invertivores, and temperate carnivores, respectively.

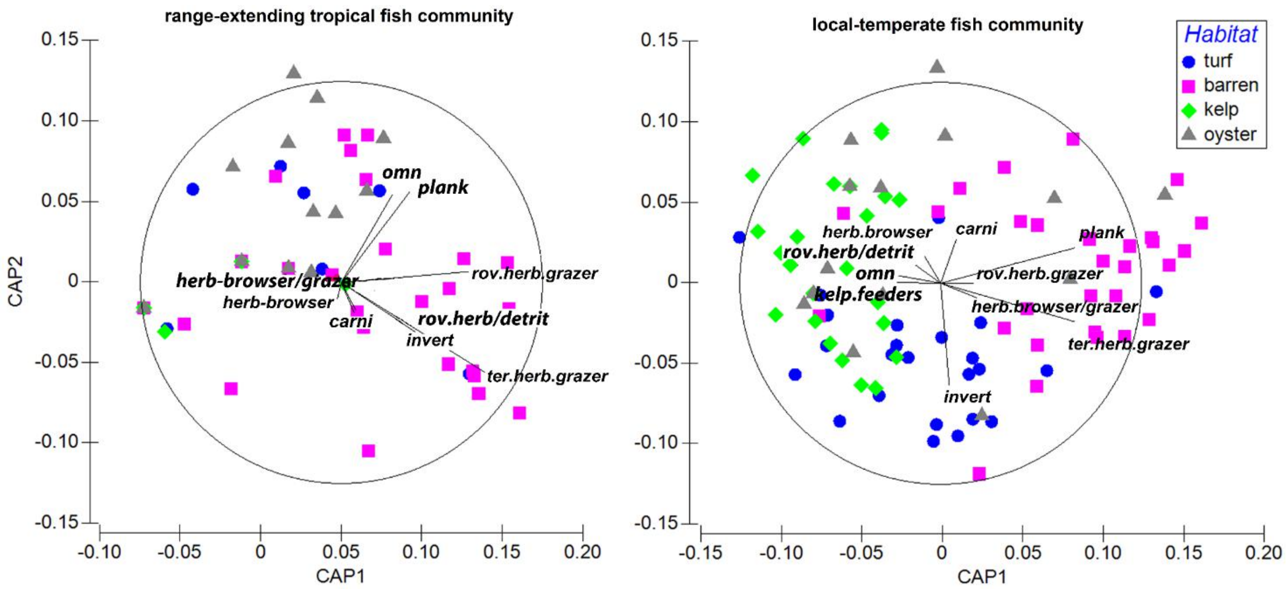

Figure 3. Canonical analysis of principal coordinates (CAP) ordination based on Bray-Curtis distance showing the correlation between trophic functional groups of range-extending tropical and local-temperate fish assemblages with temperate reef habitats of south-eastern Australia and the overlap between tropical and temperate grazing herbivorous fishes in sea-urchin barrens. The vectors (black lines) show the correlation of each functional group with each habitat and their lengths indicate the magnitude of this correlation. Functional group abbreviation: omn = omnivores, plank = planktivores, rov.herb-grazer = roving grazing herbivores, rov.herb/detrit = roving herbivores detritivores, invert = invertivores, ter.herb-grazer = territorial grazing herbivores, carn = carnivores, herb-browser = browsing herbivores and herb-browser/grazer = browsing and grazing herbivores.

RESPONSE OF SEA URCHIN POPULATIONS TO ELEVATED CO_2

Both the temperate native (Fig. S4; one-way ANOVA, $p = 0.001$) and warm-adapted (Fig. S4; one-way ANOVA, $p = 0.021$) sea urchins occurred in greater density at control sites compared to elevated CO_2 vent sites. Although the low R^2 indicates high unexplained variability by the regression line (probably caused by the higher number of zeros, especially for the warm-adapted sea urchins), densities of both sea urchin species still showed a significant decline with reduced pH (Figs. 4a, b; linear regression – native sea urchins: $R^2 = 0.22$, $p = 0.0001$, and warm-adapted sea urchins: $R^2 = 0.08$, $p = 0.019$). The warm-adapted sea urchin showed higher sensitivity than the native species to reduced pH with densities at pH < 8.0 being zero, and they were only observed at pH levels ranging between 8.09 and 8.30. Native urchins were found down to pH levels of 7.2, albeit at very low densities.

Heavy metal, trace element, and sulphur concentrations in seawater sampled at the study sites did not differ between controls and vents across years (Table S2). Therefore, these abiotic factors are deemed unrelated to altered sea urchin densities and barren sizes between controls and vents. Only pH and $p\mathrm{CO}_2$ differed significantly between vents and controls.

At the control sites in New Zealand, barren size was positively related to sea urchin density (Fig. 4c; both species combined: $R^2 = 0.86$, p-value = 0.0001) and pH (Fig. 4d; $R^2 = 0.37$, p-value = 0.036), but not to urchin body size (Fig. S5; both species combined: $R^2 = 0.30$, p-value = 0.101). Native urchin species were significantly larger at vents and barrens than at kelp and turf habitats (Fig. S6; one-way ANOVA; p = 0.0001), while body size of the warm-adapted urchin species did not differ among habitats (one-way ANOVA; p = 0.461).

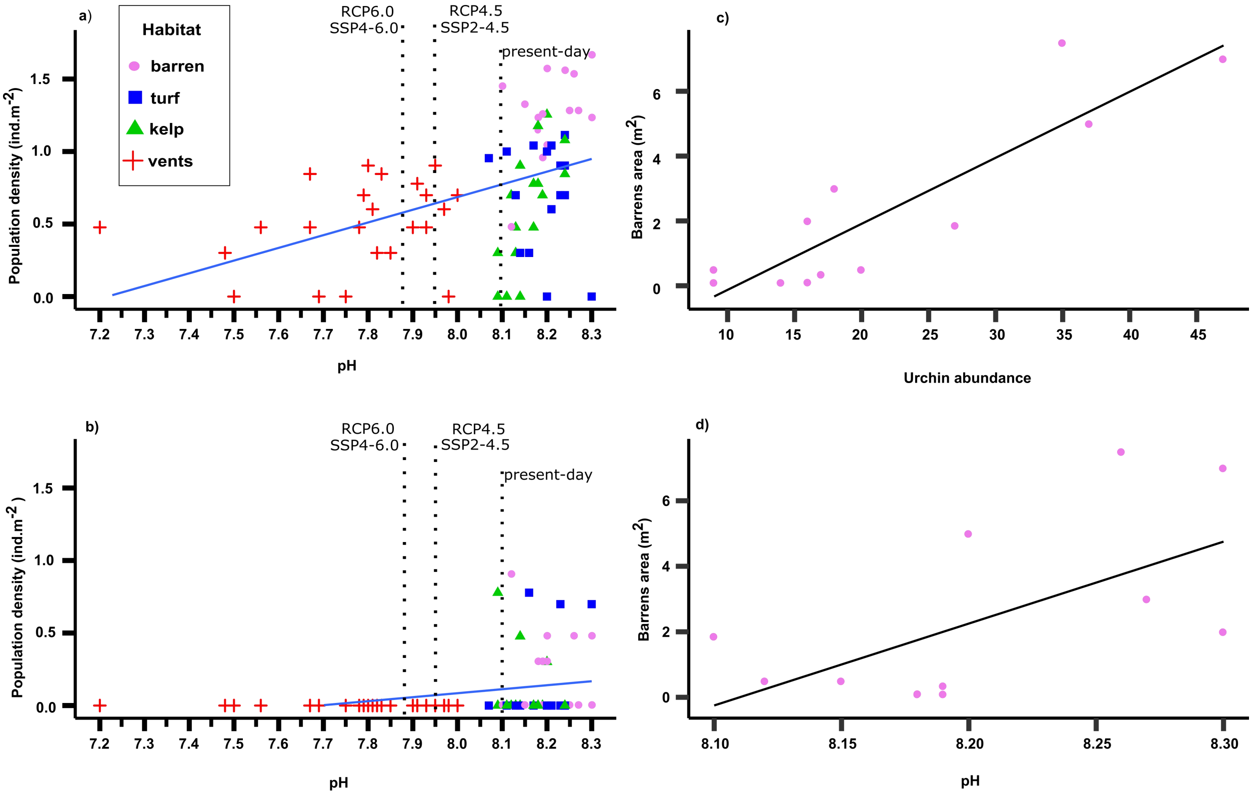

Figure 4. Linear regressions showing the relationship between seawater pH and sea-urchin densities for: a) native temperate sea urchin (*Evechinus chloroticus*; $R^2 = 0.22$, $p = 0.0001$), and b) warm-adapted sea urchin (*Centrostephanus rodgersii*; $R^2 = 0.08$, $p = 0.019$), respectively, across a pH gradient at CO_2 vents and controls (New Zealand), and the relationship between c) total sea-urchin density and barren size ($R^2 = 0.86$, p-value = 0.0001), and d) pH and sea-urchin barren size ($R^2 = 0.37$, p-value = 0.036). Sea urchin density data on the y-axes of graphs a) and b) were $\log_{10}(x+1)$ transformed. Vertical dashed lines indicate the global average of present-day and future seawater pH for the 21st century according to Representative Concentration Pathway scenarios by Bopp et al. (2013) and the latest climate model (Shared Socioeconomic Pathways) by O’Neill et al. (2016).

DISCUSSION

Our study demonstrates that ocean acidification may buffer the negative effects of ocean warming by inhibiting range-extending urchins so that their abundances are sparser than those required to form barren-dominated habitats in temperate ecosystems. We also reveal that these two divergent global forces play opposing effects on the rate of tropicalisation. Ocean warming facilitates the range expansion and recruitment of tropical vagrant fishes by mediating a phase-shift (through urchins) from a kelp-dominated to a barren-dominated state (resulting in a 20-fold increase in densities and biomass, and a 3.5-fold increase in species richness of tropical vagrant fishes at their leading edges). Ocean acidification acts as a stressor on urchins so that their sparser densities are insufficient to form barrens, but also facilitates the emergence of turf-dominated habitats that are directly boosted by CO_2 nutrient enrichment. This individual effect of elevated CO_2 on reduced sea-urchins density and barrens, and regime shifts towards turf-dominated habitats has also been observed at other natural CO_2 vents (Hall-Spencer et al. 2008; Kroeker et al. 2013; Enochs et al. 2015). Considering the sole effect of urchin overgrazing, a reversal from barrens to kelp habitat is unlikely to occur due to a hysteresis effect in which the pathway of ecosystem recovery differs from the pathway of degradation (Suding & Hobbs 2009; Fig. S7). This hysteresis appears strong under future climate in which physiological performance and abundance of urchins appear reduced by ocean pH so that shallow temperate ecosystems are less likely to return to their previous natural state of kelp domination. Where warming, acidification, and urchin grazing combine, a switch from kelp to turf-dominated habitats would reduce the recruitment of tropical fishes and consequently retard the rate of tropicalisation of temperate fish assemblages (see conceptual diagram in Fig. 1 and Fig. S6). Yet, current models about warming alone suggest accelerated tropicalisation as urchin barrens expand in distribution and extent.

The acidification effects we present suggest that the strength of future tropicalisation is still unknown. Many tropical fishes are extending their ranges to higher latitudes under warming to stay within their preferred thermal niche (Perry et al. 2005). Whilst at their leading edges these species can escape the detrimental effects of warming, they are less likely to escape the effects of increasing CO_2 concentrations through range extensions. By studying CO_2 vents, we can disentangle the effects that future acidification might have on the establishment of tropical species at their leading edges of their distribution. The mechanisms we reveal for each of these stressors in natural environments appear to have strong potential to interact antagonistically and create very different future ecosystems than when considered alone.

TROPICAL AND TEMPERATE FISH COMMUNITY ACROSS HABITAT

Our findings suggest that temperate urchin barrens sustain the highest biomass and a more diverse and abundant tropical fish community than structurally more complex habitats. As such, barrens are a key habitat for tropical fish to establish viable populations on temperate reefs. These findings are consistent with previous observations showing that most tropical species preferred non-macroalgal rocky habitats (Beck et al. 2017). Urchin barrens are hard substrata usually covered only with a thin layer of filamentous algae, which is a principal food source for grazing herbivores and, for example, explains why the tropical herbivorous dusky surgeonfish (*Acanthurus nigrofuscus*) was strongly associated with this habitat (Steneck 1988, Purcell & Bellwood 1993). Although the most abundant tropical species *Abudefduf vaigiensis* was relatively more abundant in oyster-dominated habitats, it also had high abundances in urchin barren-dominated habitats, which may be explained by the fact that (1) *Abudefduf vaigiensis* usually forages in the water column and in areas with intense water movement which may coincide with the same areas where oyster reefs and urchin barrens are found and, (2) oysters and urchins also create hard-substrate habitats that provide refuge for many temperate and tropical fishes that prefer habitats free of algae (Curley et al. 2002, Coen et al. 1999, Lenihan et al. 2001). As such, declines in oyster reefs mediated by climate change (Jackson et al. 2001, Thomas et al. 2018) and overfishing in Australia (Alleway & Connell 2015) may further reduce the establishment of the most common vagrant tropical fish in temperate ecosystems.

Various temperate fish species (24% of total temperate species) were observed inhabiting and/or foraging in kelp-dominated habitats, suggesting that kelp forests are a key habitat for the maintenance of temperate reef fish diversity and their population abundances. Besides overgrazing by urchins, additional collapse of kelp forests driven by climatic disturbances (e.g. marine heatwaves, ocean acidification, and range extensions of tropical herbivorous fishes; Verges et al.

2016; Wernberg et al. 2016; Connell et al. 2018) may further disrupt the structure of temperate fish communities by opening up more suitable habitat for range-extending coral reef fishes. Temperate fishes were similarly associated with turf and kelp-dominated habitats. In contrast, vagrant tropical fishes, almost completely avoided kelp habitats, while some species were associated with turf habitats. This suggests that: (1) although tropical fishes are highly associated with barrens (due to increasing warming), a regime shift to turf-dominated habitats (with increasing CO_2) will not completely inhibit the establishment of tropical fishes in temperate ecosystems and only slow the pace of tropicalisation, and (2) a regime shift from present-day kelp domination to turf-dominated systems (with increasing warming and acidification combined; Wernberg et al. 2016; Filbee-Dexter and Wernberg 2018; O'Brien & Scheibling 2018) is more likely to have a greater positive effect on vagrant tropical fishes than resident temperate fishes, facilitating the creation of novel community structures under future climate.

FUNCTIONAL COMPOSITION ACROSS HABITAT

We predicted that the expansion of urchin barrens would facilitate the overlap in habitat use between functional groups of tropical invaders and temperate fish assemblages. We found that the tropical and temperate trophic functional group that overlapped most in habitat use (on urchin barrens) was that of the grazing herbivorous fishes. The increasing density of grazing herbivorous fishes on temperate reefs may intensify the grazing pressure on kelp forests, hindering their capacity to recover once they have turned into barrens (Verges et al. 2014; 2016). Alternatively, such overlap in habitat use is expected to increase niche competition, which can lead to niche displacement depending on which species has a higher competitive ability (Bulleri et al. 2016). To a lesser extent planktivores also overlapped in habitat use. However, unlike grazing herbivores, tropical and temperate planktivores are usually observed schooling together, allowing tropical species to increase their survivorship in temperate environments (Smith et al. 2018). Thus, by adopting this social behaviour, tropical and temperate planktivorous fishes might share the same habitat and coexist in temperate ecosystems under climate change (Kingsbury et al. 2019; Kingsbury et al. 2020).

SEA URCHIN PERFORMANCE UNDER ELEVATED CO_2

Whilst some laboratory studies have found that sea urchins might adapt to long-term exposure of ocean acidification (Foo et al. 2012; Kelly et al. 2013), species living at natural CO_2 vents showed little evidence of adaptation potential to ocean acidification (Uthicke et al. 2019). We showed declines in the density of both native and warm-adapted temperate sea urchins and size of their barrens in natural ecosystems subjected long-term to elevated CO_2. Our results suggest that the reduction in sea urchins densities and the decrease in urchin feeding rates under elevated CO_2 (Connell et al. 2018) may suppress the formation of urchin barrens under future ocean acidification as anticipated for species with a reduced scope for adaptation.

Although the effects of ocean acidification on sea urchins varies with species identity (Somero 2010) and laboratory designs, experimental field and laboratory suggest that our findings might be quite general as sea urchins tend to be considered particularly vulnerable to lowered pH as observed through a reduced performance (e.g. grazing rates, growth, reproduction) and reduced density (Siikavuopio et al. 2007; Connell et al. 2018; Dworjanyn & Byrne 2018). This is likely due to a limited extracellular acid-base regulatory ability (i.e. homeostatic regulation of the pH of the body's extracellular fluid), especially when exposed long-term (e.g. Miles et al. 2007; Spicer et al. 2011). Indeed, reciprocal experiments conducted at the same vents where the present study was performed (New Zealand) showed that feeding rates and densities of the native urchins (*Evechinus chloroticus*) decline when translocated from control to elevated CO_2 conditions at vents (Connell et al. 2018).

We did not find a relationship between urchin body size and barren formation, probably because of the low sample sizes or the low abundances of *C. rodgersii*, which is considered to be the main sea urchin species that can enable alternative states of shallow reef communities in Australasia (Ling et al. 2015). The increase in algal production at elevated CO_2 levels provides more food at vents, which might explain the larger-sized native sea urchins at the vents compared to other habitats in temperate (this study) as well as tropical regions (Uthicke et al. 2016). Thus, future CO_2 conditions and the decreasing density and rates of urchin herbivory combined with ocean warming might accelerate the expansion of turf algae cover (O'Brien & Scheibling 2018). In contrast, other habitats that are sensitive to one or the combination of these stressors, such as barrens (this study) and kelp (Wernberg et al. 2010, Simonson et al. 2015), might be rapidly overgrown by turf-forming algae which will reduce the density and diversity of range-extending tropical fishes, modifying the trajectory of tropicalisation of temperate systems. Despite transgenerational acclimation to reduced pH has been observed in the laboratory for some sea urchins (Ross et al. 2016; Wong et al. 2018; Clark et al. 2019), the boosted productivity of turfs by CO_2 enrichment increases the probability of turf-domination where urchin grazing rates are unable to compensate (Ghedini et al. 2015).

The limited evidence for transgenerational adaptation to climate change in fish showed mixed outcomes and is likely to be species-specific (Munday et al. 2019). Whilst some studies have found evidence of physiological (growth: Miller et al. 2012) and behavioural (antipredator behaviour: Allan et al. 2014) acclimation through phenotypic plasticity and adaptation, others found little evidence of potential adaptation of fish behaviour to elevated temperature and CO_2 (Welch et al. 2014; Rummer & Munday 2017). The eutrophication effect of elevated CO_2 will prompt habitat modifications through the promotion of turf algae expansion in temperate systems and its effects are improbable to be altered under longer-term exposure. Transgenerational alteration of tropical fish habitat choice in novel temperate habitat composition (turf-dominated habitat) is therefore unlikely to occur.

CONCLUSION

Whilst ocean warming facilitates tropicalisation by creating barren-dominated states, ocean acidification might buffer this extension by inhibiting barren-dominated states. Acidification inhibits the formation of preferred barren-habitat of tropical fish that are created by urchins. We conclude that the pace of ongoing tropicalisation due to climate change may be slowed by ocean acidification through its indirect (inhibiting sea-urchin abundances) and direct effects (promoting the expansion of non-barren habitats). Whilst ocean warming is currently driving tropicalisation, future ocean acidification may facilitate natural buffering processes that can dampen tropicalisation.

ETHICS

All experiments were performed under animal ethics approval numbers S-2015-222A and S-2017-002, and according to the University's animal ethics guidelines.

AUTHOR CONTRIBUTIONS

E.O.C.C, I.N., D.J.B. and S.D.C. conceived and designed the study, E.O.C.C. and C.M.F. collected the data, E.O.C.C. analysed the data. All authors contributed to the writing of the article.

DATA AVAILABILITY

The data that support the findings of this study are available from the lead contact Ivan Nagelkerken (ivan.nagelkerken@adelaide.edu.au).

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SUPPLEMENTARY INFORMATION

Figure S1. Map showing the three tropicalisation hotspots in Sydney (Australia) where tropical and temperate fish communities were surveyed and the CO$_2$ vents at White Island - New Zealand where the effects of elevated CO$_2$ on fish communities and sea-urchins were investigated.

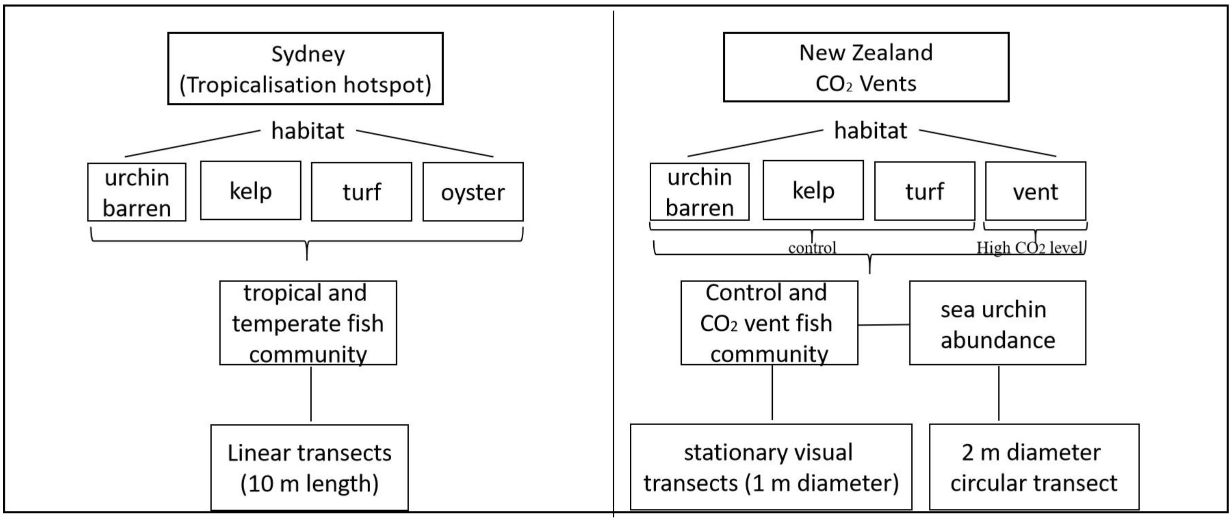

Figure S2. Diagram summarising the methodology used to quantify the fish assemblages and sea urchin densities in the most common coastal habitats in Sydney (Australia) and New Zealand.

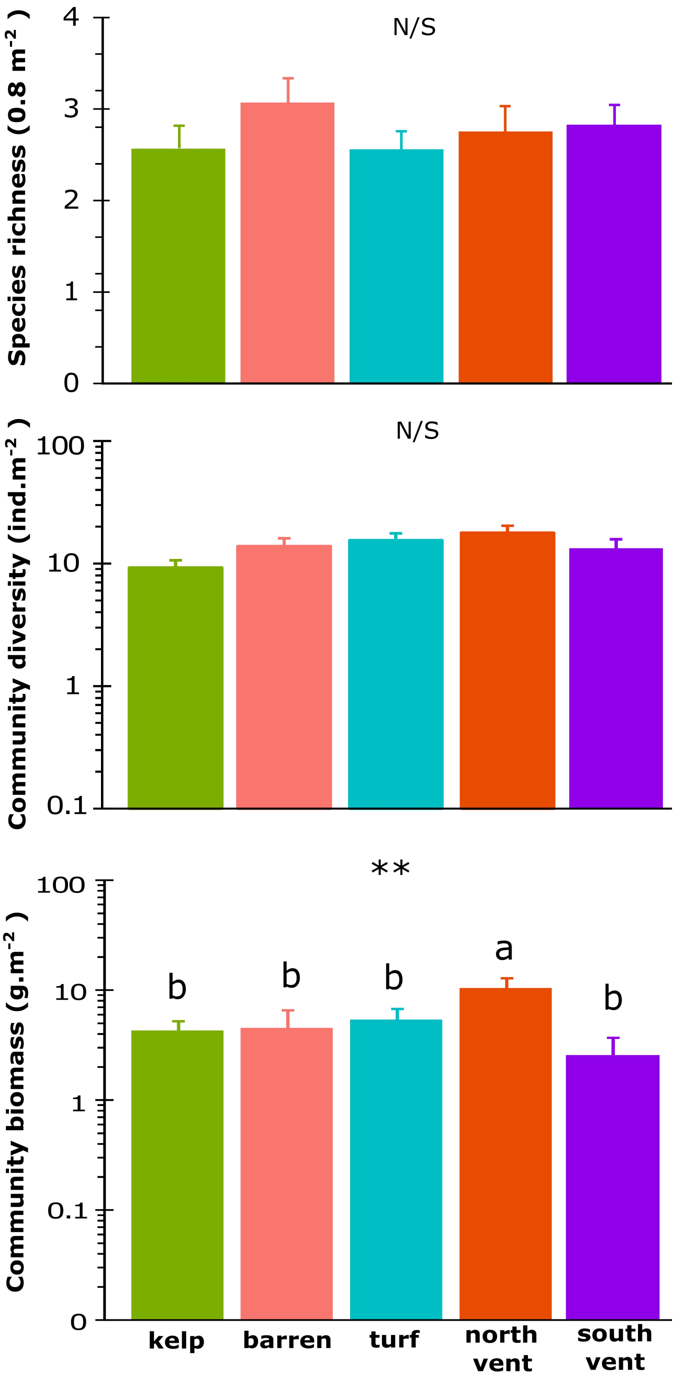

Figure S3. Species richness per transect (top panels), density (middle panels) and biomass (bottom panels) of the temperate fish community in turf habitat at the two CO_2 vent sites (north and south vents) and three control habitats (mean + SE) at White Island, New Zealand. The southern vent had pCO_2 values close to an RCP 4.5 and SSP2-4.5 scenario, while the northern vent had pCO_2 values close to an RCP 6.0 and SSP4.6.0 scenarios (Table S1).

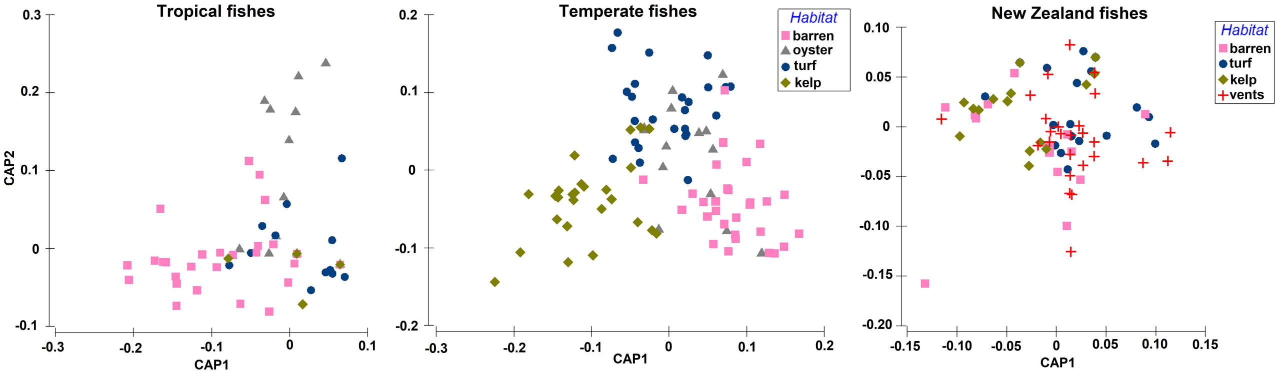

Figure S3. Canonical analysis of principal (CAP) coordination of fish community structure associated with each habitat, based on square-root transformed species abundance data using Bray-Curtis distance. Left panel: SE Australian tropical fish community; Middle panel: SE Australian local-temperate fish community; Right panel: New Zealand control (3 habitats) and CO_2 vent fish community.

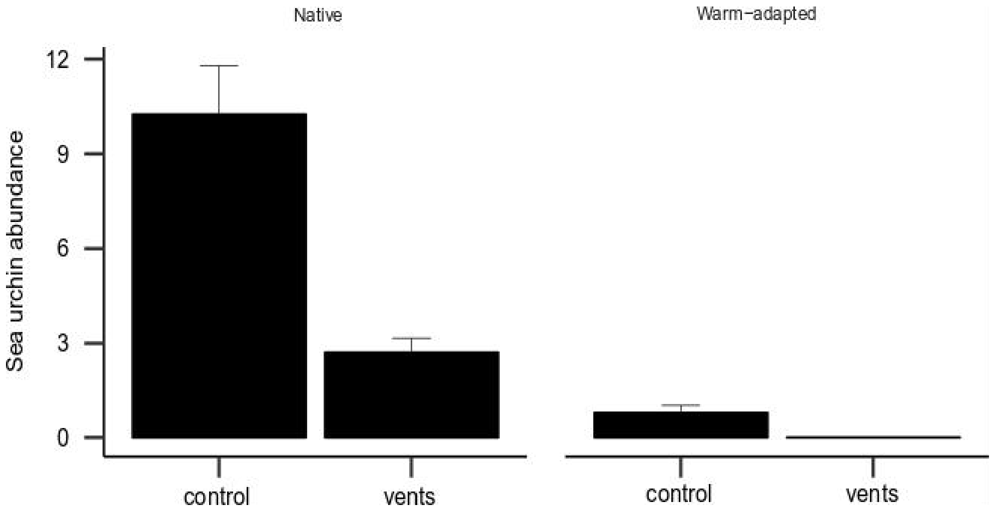

Figure S4. Mean (+ SE) abundance (per 3.14 m^2) of native (*Evechinus chloroticus*) and warm-adapted (*Centrostephanus rodgersii*) sea urchins at control and vent sites at New Zealand.

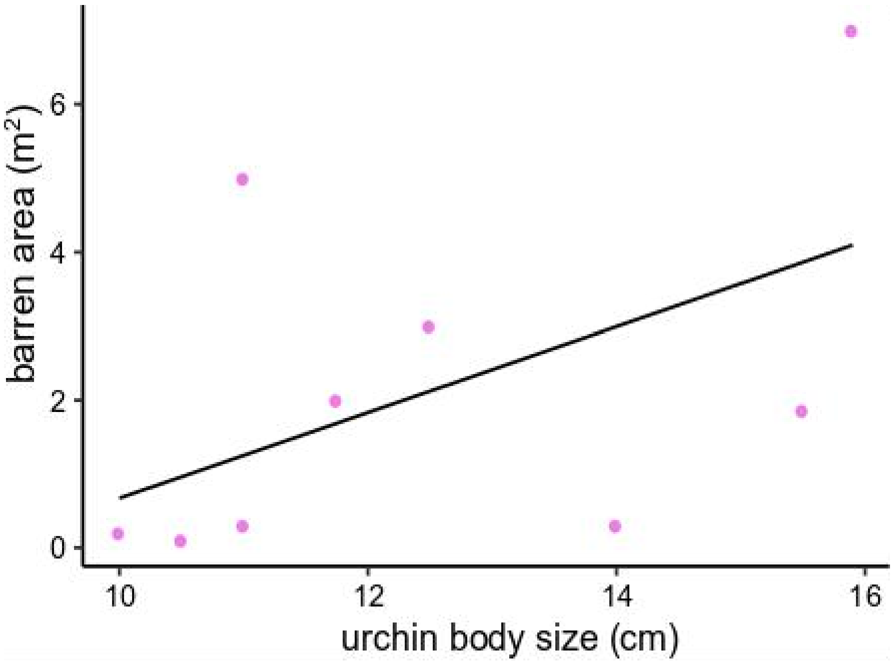

Figure S5. Linear regression showing the relationship between the mean combined native and warm-adapted sea urchin body size on barren size at New Zealand ($R^2 = 0.30$, p-value = 0.101).

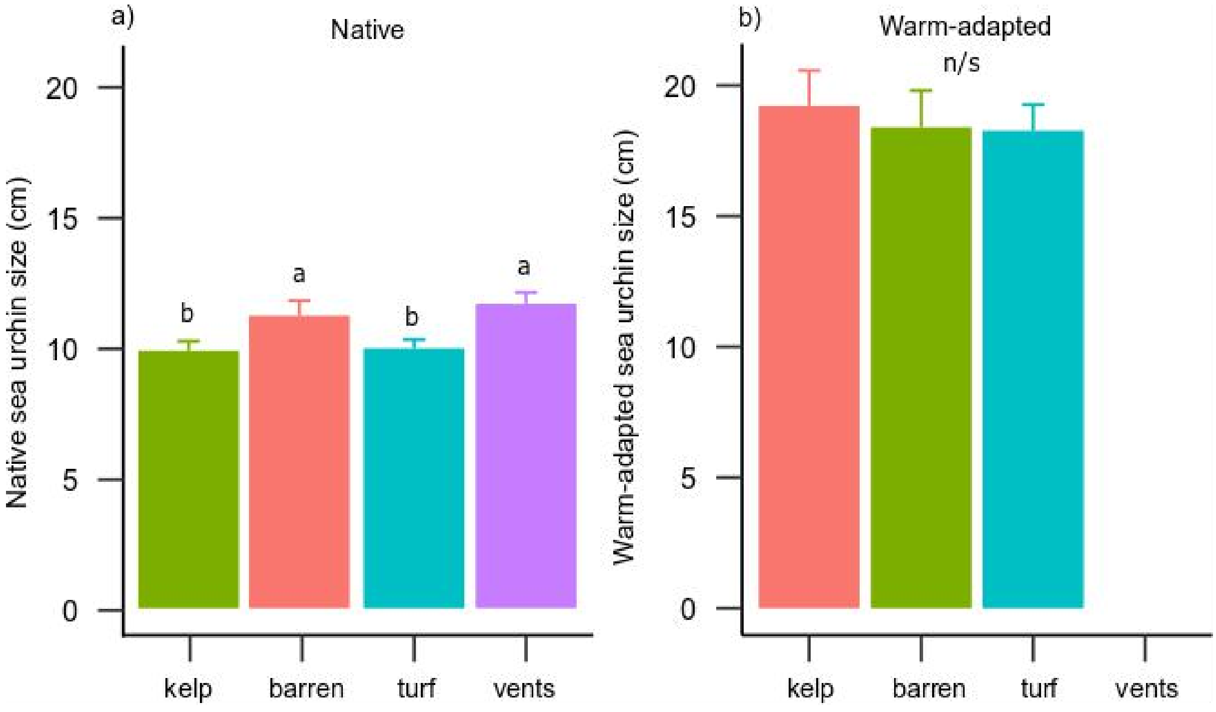

Figure S6. Mean (+ SE) test sizes of native (*Evechinus chloroticus*) and warm-adapted (*Centrostephanus rodgersii*) sea urchins in different habitats at control and vents sites at New Zealand. Different letters above bars indicate significant differences ($p < 0.05$); n/s = not significant.

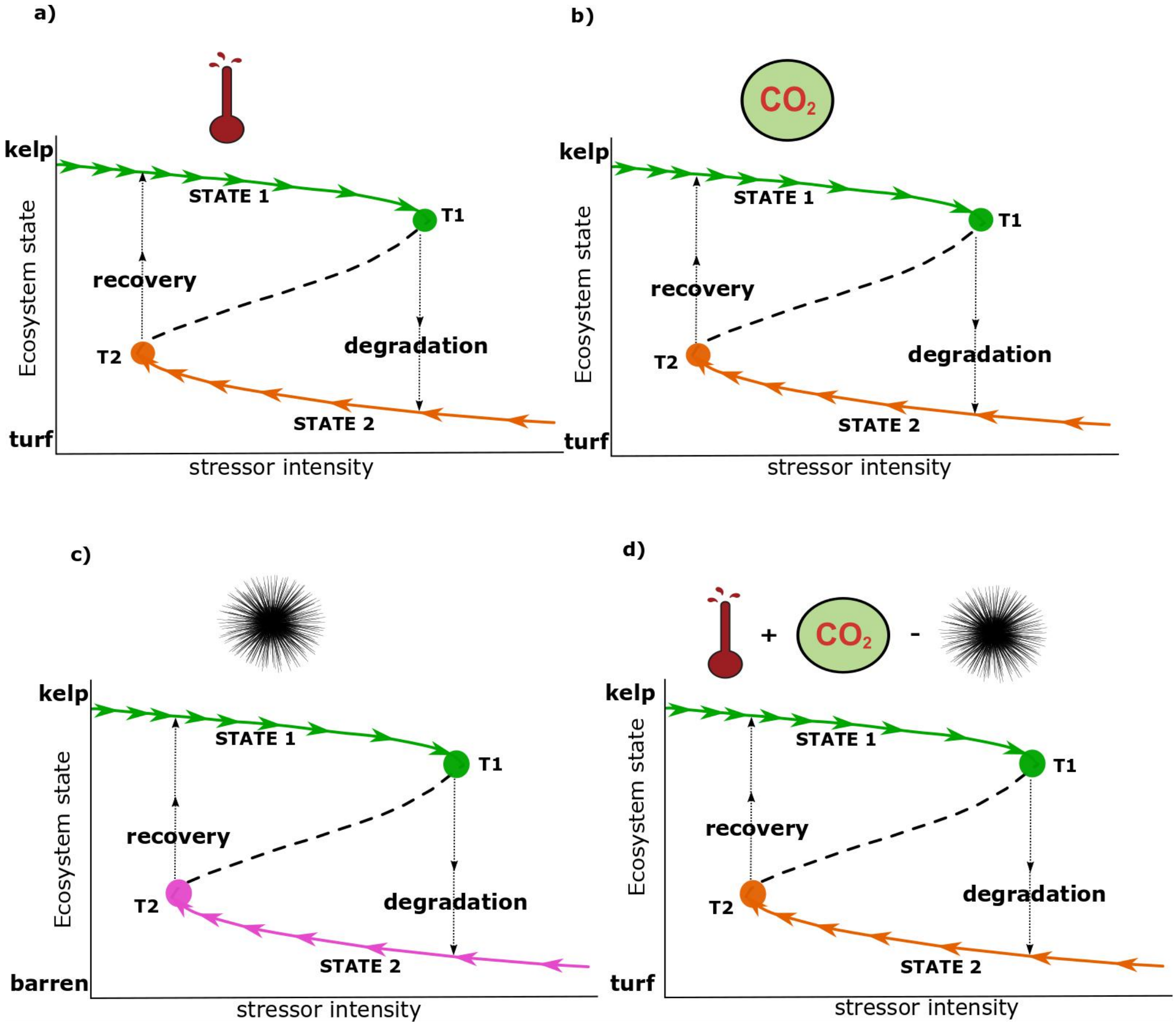

Figure S7. Regime shifts from kelp forests (green solid lines) to alternative turf and barren-dominated states (orange and pink solid lines) and the occurrence of hysteresis under different climate change scenarios: a) ocean warming (Wernberg et al. 2013; 2016), b) ocean acidification (Connell et al. 2013), c) urchin overgrazing (Ling 2008; Johnson et al. 2011), and d) all three stressors combined (present study). When the stressors are strong enough, and ecosystem state 1 passes beyond the tipping point (T1), and a discontinuous critical transition occurs from an unstable equilibrium (dashed line) to the alternative stable state 2 (degradation) (downward black arrow). However, if stressor levels are then reduced, a hysteresis occurs because the opposing forces fail to push the ecosystem to return to its original state. The recovery to state 1 is only possible if the magnitude of the stressors is reduced to a much lower level (T2) (upward black arrows) than that of the tipping point during the degradation. Adapted from Scheffer 2009 and Jax 2016.

Table S1. Representative Concentration Pathway 4.5 and 6.0 scenarios and their respective pH reductions for the 21st century (Bopp et al. 2013), compared to pH reductions at the two CO_2-vents at White Island – New Zealand. The pH reductions were calculated as the difference between the respective control and vents, and averaged across years (n = 3; 2017-2019).

	Present study	**Bopp et al. (2013)**
	pH reduction	**pH reduction per RCP**
South vent	-0.19 ± 0.005	-0.15 ± 0.001 (RCP 4.5)
North vent	-0.24 ± 0.005	-0.22 ± 0.002 (RCP 6.0)

Table S2. Physico-chemical measurements and concentrations of dissolved trace elements in seawater from control and CO_2-vents at White Island -New Zealand during 2017-2019. TA = total alkalinity.

							p-values	
	year	**month**	**control**	**N**	**vent**	**N**	**treatment**	**site**
pH_{NBS} (units)	2017	Feb.	8.08±0.01	12	7.82±0.04	20	**0.032**	0.396
	2018	Feb.	8.03±0.02	12	7.84±0.04	12	**0.011**	0.808
	2019	Jan.	8.05±0.01	30	7.88±0.03	28	**0.033**	0.328
$p\mathrm{CO}_2$ (ppm)	2017	Feb.	503±9	12	1049±122	20	**0.032**	0.39
	2018	Feb.	628±29	12	1066±112	12	**0.006**	0.927
	2019	Jan.	565±13	30	966±102	28	**0.024**	0.69
TA (μ mol kg^{-1})	2017	Feb.	2263±5	6	2255±5	5	0.532	0.08
Temp. (°C)	2017	Feb.	20.1±0.1	12	20.1±0.1	19	0.955	**0.026**
	2018	Feb.	23.2±0.1	12	23.2±0.1	10	0.804	0.663
	2019	Jan.	21.2±0.03	4	21.2±0.04	4	0.629	0.078
Salinity	2017	Feb.	36±0	2	36±0	5		
	2018	Feb.	31.0±0.1	16	31.0±0.1	16	0.671	0.865
	2019	Jan.	33.4±0.3	30	33.2±0.2	28	0.915	0.189
S (ppm)	2018	Feb.	982±52	10	1043±29	10	0.553	0.111
	2019	Jan.	954±13	7	908±14	15	0.101	0.766
Mg	2018	Feb.	919±48	10	1020±30	10	0.150	0.594
	2019	Jan.	1067±13	7	1079±13	15	0.471	0.213
K (ppm)	2018	Feb.	294±19	10	262±11	10	0.076	0.863
	2019	Jan.	335±4	7	336±5	15	0.642	0.289
Ca (ppm)	2018	Feb.	349±19	10	392±26	10	0.391	0.225
	2019	Jan.	358±5	7	367±11	15	0.391	0.85
Sr (ppm)	2018	Feb.	6.6±0.3	10	7.0±0.2	10	0.431	0.201
	2019	Jan.	7.4±0.1	7	8.1±0.1	15	0.11	0.167
Rb (ppm)	2018	Feb.	010±0.00	10	0.10±0.00	10	0.381	0.185
	2019	Jan.	0.11±0.00	7	0.12±0.00	15	0.089	0.261
Mn (ppm)	2018	Feb.	0.004±0.002	10	0.004±0.002	10	0.971	0.264
	2019	Jan.	0.012±0.003	7	0.023±0.007	15	0.519	0.401
Fe (ppm)	2018	Feb.	0.17±0.11	10	0.11±0.09	10	0.732	0.418
	2019	Jan.	0.41±0.14	7	1.19±0.71	15	0.632	0.314
Cu (ppm)	2018	Feb.	<0.0004	10	<0.0004	10	ns	ns
	2019	Jan.	0.17±0.05	7	0.24±0.04	15	0.649	0.36
Zn (ppm)	2018	Feb.	<0.0006	10	<0.0006	10	ns	ns
	2019	Jan.	0.11±0.02	7	0.18±0.05	15	0.472	0.41
Cd (ppm)	2018	Feb.	<0.000008	10	<0.000008	10	ns	ns
	2019	Jan.	<0.000004	7	<0.000004	15	ns	ns
Ba (ppm)	2018	Feb.	<0.006	10	<0.0004	10	ns	ns
	2019	Jan.	0.04±0.01	7	0.07±0.01	15	0.362	0.133

Table S3. ANOSIM results for pairwise comparison of species community composition for both tropical, native temperate and CO_2 vents (a), and functional assemblage composition for tropical and temperate fishes (b), using the Bray-Curtis similarity coefficient. Significant pairwise comparisons are shown in bold.

a)

	Taxonomic assemblage- Tropical species	Taxonomic assemblage- Temperate species	Taxonomic assemblage - New Zealand species	
Groups	p-value	p-value	Groups	p-value
Global R	0.358	0.285	Global R	0.058
oyster, turf	**0.001**	**0.001**	turf, barren	**0.043**
oyster, barren	**0.016**	**0.0002**	turf, kelp	**0.018**
oyster, kelp	**0.0002**	**0.015**	turf, vents	0.870
turf, barren	**0.001**	**0.0002**	barren, kelp	**0.028**
turf, kelp	**0.0002**	**0.006**	barren, vents	0.178
barren, kelp	**0.0002**	**0.0002**	kelp, vents	**0.026**

b)

	Trophic functional assemblage Tropical species		Trophic functional assemblage Temperate species	
Groups	R Statistic	p-value	R Statistic	p-value
Global R		0.289		0.247
oyster, turf	0.091	**0.053**	0.1	0.065
oyster, barren	0.132	**0.024**	0.384	**0.0002**
oyster, kelp	0.553	**0.0002**	0.081	0.117
turf, barren	0.193	**0.0002**	0.303	**0.0002**
turf, kelp	0.158	**0.0004**	0.03	0.11
barren, kelp	0.548	**0.0002**	0.452	**0.0002**

Table S4. Results of similarity percentage (SIMPER) analysis among four habitats (oyster, turf, barren and kelp) and the average dissimilarity between the habitats for the tropical fish community at Sydney (south-eastern Australia).

Oyster habitat versus Turf habitat - Average dissimilarity = 92.47

Species	Average abundance		Contribution%
	Oyster	Turf	
Abudefduf vaigiensis	2.79	1.44	37.34
Acanthurus nigrofuscus	0.36	0.36	19.11
Acanthurus triostegus	0.86	0	13.36
Acanthurus dussumieri	0.07	0.36	10.89
Chaetodon auriga	0.21	0.08	6.45
Abudefduf sexfasciatus	0.14	0	2.62
Acanthurus olivaceus	0	0.08	2.36

Oyster habitat versus Barren habitat - Average dissimilarity = 89.86

Species	Average abundance		Contribution%
	Oyster	Barren	
Abudefduf vaigiensis	2.79	1.21	27.67
Acanthurus nigrofuscus	0.36	1.62	21.72
Acanthurus triostegus	0.86	0.10	9.15
Acanthurus dussumieri	0.07	0.45	6.65
Stegastes gascoynei	0.00	0.41	5.34
Abudefduf sexfasciatus	0.14	0.69	5.33
Mecaenichthys immaculatus	0.00	0.21	4.97
Chaetodon auriga	0.21	0.00	3.06
Pomacentrus coelestis	0.07	0.14	3.01
Naso unicornis	0.00	0.10	2.15
Labroides dimidiatus	0.00	0.17	1.92

Turf habitat versus Barren habitat - Average dissimilarity = 90.62

Species	Average abundance		Contribution%
	Turf	Barren	
Acanthurus nigrofuscus	0.36	1.62	26.60
Abudefduf vaigiensis	1.44	1.21	19.58
Acanthurus dussumieri	0.36	0.45	12.02
Stegastes gascoynei	0.04	0.41	7.04
Mecaenichthys immaculatus	0.00	0.21	7.01
Abudefduf sexfasciatus	0.00	0.69	4.23
Pomacentrus coelestis	0.00	0.14	2.97
Naso unicornis	0.00	0.10	2.95
Labroides dimidiatus	0.00	0.17	2.34
Pomacentrus bankanensis	0.04	0.07	1.94
Thalassoma lunare	0.00	0.07	1.92
Chaetodon citrinellus	0.00	0.10	1.72

Oyster habitat versus Kelp habitat - Average dissimilarity = 89.65

	Average abundance		
Species	**Oyster**	**Kelp**	**Contribution%**
Abudefduf vaigiensis	2.79	0.00	37.68
Acanthurus nigrofuscus	0.36	0.12	22.67
Acanthurus triostegus	0.86	0.00	18.12
Chaetodon auriga	0.21	0.00	7.01
Acanthurus dussumieri	0.07	0.19	4.42
Abudefduf sexfasciatus	0.14	0.00	3.56

Turf habitat versus Kelp habitat - Average dissimilarity = 98.46

	Average abundance		
Species	**Turf**	**Kelp**	**Contribution%**
Acanthurus dussumieri	0.36	0.19	29.33
Acanthurus nigrofuscus	0.36	0.12	25.54
Abudefduf vaigiensis	1.44	0.00	18.53
Acanthurus olivaceos	0.08	0.00	6.35
Chaetodon auringa	0.08	0.00	5.51
Pomacentrus bankanensis	0.04	0.00	5.26

Barren habitat versus Kelp habitat - Average dissimilarity = 89.82

	Average abundance		
Species	**Barren**	**Kelp**	**Contribution%**
Acanthurus nigrofuscus	1.62	0.12	30.77
Abudefduf vaigiensis	1.21	0.00	12.39
Acanthurus dussumieri	0.45	0.19	11.23
Mecaenichthys immaculatus	0.21	0.00	10.06
Stegastes gascoynei	0.41	0.00	8.00
Abudefduf sexfasciatus	0.69	0.00	4.45
Naso unicornis	0.10	0.00	3.90
Pomacentrus coelestis	0.14	0.00	3.77
Fistularia commersonni	0.07	0.04	3.02
Labroides dimidiatus	0.17	0.00	2.66

Table S5. Results of similarity percentage (SIMPER) analysis among four habitats (oyster, turf, barren and kelp) and the average dissimilarity between the habitats for the temperate-local fish community at Sydney (south-eastern Australia).

Oyster habitat versus Turf habitat - Average dissimilarity = 86.03

Species	Average abundance		Contribution%
	Oyster	Turf	
Atypichthys strigatus	2.57	7.00	29.41
Trachinops taeniatus	4.36	1.08	11.63
Parupeneus spilurus	1.64	1.88	11.22
Microcanthus strigatus	1.21	1.24	10.18
Pempheris affinis	1.43	2.60	8.81
Notolabrus gymnogenis	0.57	1.52	6.40
Acanthopagrus australis	0.50	0.28	3.62
Brachaluteres jacksonianus	0.14	0.52	3.52
Ophthalmolepis lineolata	0.00	0.20	2.20
Pictilabrus laticlavius	0.21	0.32	2.16
Aplodactylus lophodon	0.14	0.32	2.15

Oyster habitat versus Barren habitat - Average dissimilarity = 89.36

Species	Average abundance		Contribution%
	Oyster	Barren	
Trachinops taeniatus	4.36	28.00	42.33
Atypichthys strigatus	2.57	8.69	14.84
Parupeneus spilurus	1.64	2.17	7.47
Pempheris affinis	1.43	2.52	5.66
Microcanthus strigatus	1.21	0.48	4.11
Acanthopagrus australis	0.50	1.07	3.98
Girella tricuspidata	0.07	1.34	3.62
Prionurus microlepidotus	0.07	0.76	3.10
Parma unifasciata	0.07	1.03	2.68
Notolabrus gymnogenis	0.57	0.52	2.18
Scorpis lineolata	0.14	0.59	2.05

Turf habitat versus Barren habitat - Average dissimilarity = 86.01			
	Average abundance		
Species	**Turf**	**Barren**	**Contribution%**
Trachinops taeniatus	1.08	28.00	38.73
Atypichthys strigatus	7.00	8.69	17.86
Parupeneus spilurus	1.88	2.17	7.72
Pempheris affinis	2.60	2.52	6.15
Microcanthus strigatus	1.24	0.48	3.54
Notolabrus gymnogenis	1.52	0.52	3.22
Girella tricuspidata	0.12	1.34	3.22
Acanthopagrus australis	0.28	1.07	2.97
Prionurus microlepidotus	0.08	0.76	2.53
Parma unifasciata	0.20	1.03	2.36
Scorpis lineolata	0.08	0.59	1.65
Brachaluteres jacksonianus	0.52	0.03	1.50

Oyster habitat versus Kelp habitat - Average dissimilarity = 89.65			
	Average abundance		
Species	**Oyster**	**Kelp**	**Contribution%**
Atypichthys strigatus	2.57	10.46	31.39
Trachinops taeniatus	4.36	1.27	10.94
Microcanthus strigatus	1.21	1.00	9.17
Notolabrus gymnogenis	0.57	0.77	6.22
Parupeneus spilurus	1.64	0.31	6.20
Pempheris affinis	1.43	0.19	5.45
Acanthopagrus australis	0.50	0.38	4.75
Meuschenia trachylepis	0.00	0.58	4.47
Aplodactylus lophodon	0.14	0.54	3.78
Olisthops cyanomelas	0.00	0.58	3.07
Pseudolabrus guentheri	0.07	0.46	2.64
Brachaluteres jacksonianus	0.14	0.12	2.14

Turf habitat versus Kelp habitat - Average dissimilarity = 82.49

Species	Average abundance		Contribution%
	Turf	Kelp	
Atypichthys strigatus	7.00	10.46	39.14
Parupeneus spilurus	1.88	0.31	8.73
Microcanthus strigatus	1.24	1.00	6.66
Notolabrus gymnogenis	1.52	0.77	6.13
Pempheris affinis	2.60	0.19	5.68
Trachinops taeniatus	1.08	1.27	5.40
Aplodactylus lophodon	0.32	0.54	3.10
Meuschenia trachylepis	0.04	0.58	3.09
Brachaluteres jacksonianus	0.52	0.12	3.00
Pseudolabrus guentheri	0.20	0.46	2.57
Olisthops cyanomelas	0.04	0.58	2.56
Acanthopagrus australis	0.28	0.38	2.53

Barren habitat versus Kelp habitat - Average dissimilarity = 89.82

Species	Average abundance		Contribution%
	Barren	Kelp	
Trachinops taeniatus	28.00	1.27	37.83
Atypichthys strigatus	8.69	10.46	22.46
Parupeneus spilurus	2.17	0.31	5.50
Pempheris affinis	2.52	0.19	3.50
Girella tricuspidata	1.34	0.12	3.27
Acanthopagrus australis	1.07	0.38	3.22
Prionurus microlepidotus	0.76	0.04	2.62
Parma unifasciata	1.03	0.04	2.39
Notolabrus gymnogenis	0.52	0.77	2.31
Microcanthus strigatus	0.48	1.00	2.27
Aplodactylus lophodon	0.38	0.54	1.75
Meuschenia trachylepis	0.00	0.58	1.72
Scorpis lineolata	0.59	0.15	1.67

Table S6. Results of similarity percentage (SIMPER) analysis among four habitats (turf, barren, kelp and vents) and the average dissimilarity between the habitats for the temperate fish community at White Island (New Zealand).

Turf habitat versus Barren habitat - Average dissimilarity = 53.38

	Average abundance		
Species	**Turf**	**Barren**	**Contribution%**
Forsterygion lapillum	12.00	9.33	62.61
Notoclinops yaldwyni	0.89	1.73	11.33
Notoclinops segmentatus	0.61	0.87	7.63
Parablennius laticlavius	0.78	0.53	7.15
Forsterygion maryannae	0.00	0.80	4.19

Turf habitat versus Kelp habitat - Average dissimilarity = 48.87

	Average abundance		
Species	**Turf**	**Kelp**	**Contribution%**
Forsterygion lapillum	12.00	6.31	62.69
Notoclinops yaldwyni	0.89	1.25	11.71
Notoclinops segmentatus	0.61	0.56	8.20
Parablennius laticlavius	0.78	0.06	7.54

Barren habitat versus Kelp habitat - Average dissimilarity = 57.49

	Average abundance		
Species	**Turf**	**Barren**	**Contribution%**
Forsterygion lapillum	9.33	6.31	56.46
Notoclinops yaldwyni	1.73	1.25	12.5
Notoclinops segmentatus	0.87	0.56	8.81
Forsterygion maryannae	0.8	0.81	8.59
Parablennius laticlavius	0.53	0.06	4.36

Turf habitat versus Vent habitat - Average dissimilarity = 45.79

	Average abundance		
Species	**Turf**	**Vents**	**Contribution%**
Forsterygion lapillum	12.00	13.15	66.20
Notoclinops yaldwyni	0.89	1.19	9.58
Parablennius laticlavius	0.78	0.67	8.35
Notoclinops segmentatus	0.61	0.67	7.02

Barren habitat versus Vent habitat - Average dissimilarity = 54.66

	Average abundance		
Species	**Barren**	**Vents**	**Contribution%**
Forsterygion lapillum	9.33	13.15	61.30
Notoclinops yaldwyni	1.73	1.19	10.64
Notoclinops segmentatus	0.87	0.67	7.19
Parablennius laticlavius	0.53	0.67	6.16
Forsterygion maryannae	0.80	0.44	5.35

Kelp habitat versus Vent habitat - Average dissimilarity = 53.80			
	Average abundance		
Species	**Barren**	**Kelp**	**Contribution%**
Forsterygion lapillum	6.31	13.15	62.23
Notoclinops yaldwyni	1.25	1.19	10.66
Notoclinops segmentatus	0.56	0.67	7.08
Forsterygion maryannae	0.81	0.44	6.73
Parablennius laticlavius	0.06	0.67	5.19

Table S7. Results of similarity percentage (SIMPER) analysis among four habitats (oyster, turf, barren and kelp) and the average dissimilarity between the habitats for the local-temperate and tropical fish functional groups at Sydney (south-eastern Australia).

Oyster habitat versus Turf habitat - Average dissimilarity = 66.96

Origin	Functional group	Average Abundance		Contribution%
		Oyster	Turf	
Temperate	Omnivorous	1.3	2.32	22.99
Temperate	Invertivorous	1.21	1.9	15.61
Temperate	Planktivorous	1.11	0.81	15.47
Tropical	Planktivorous	1.18	0.44	13.78
Tropical	Grazer herbivorous	0.78	0.54	9.39
Temperate	Carnivorous	0.37	0.2	5.02
Temperate	Territorial grazer herbivorous	0.2	0.37	5.01
Tropical	Omnivorous	0.34	0.12	3.91

Oyster habitat versus Barren habitat - Average dissimilarity = 71.08

Origin	Functional group	Average Abundance		Contribution%
		Oyster	Barren	
Temperate	Planktivorous	1.11	4.66	27.83
Temperate	Omnivorous	1.3	2.24	12.55
Tropical	Planktivorous	1.18	0.75	9.04
Temperate	Invertivorous	1.21	1.28	8.45
Tropical	Territorial grazer herbivorous	0	0.93	7.21
Temperate	Grazer herbivorous	0.78	1.21	7.1
Temperate	Territorial grazer herbivorous	0.2	1.09	6.85
Temperate	Carnivorous	0.37	0.4	4.87
Temperate	Browser/Grazer Herbivorous	0.07	0.65	4.4
Temperate	Grazer herbivorous	0.07	0.38	3.28

Turf habitat versus Barren habitat - Average dissimilarity = 68.44

Origin	Functional group	Average Abundance		Contribution%
		Turf	Barren	
Temperate	Planktivorous	0.81	4.66	28.19
Temperate	Omnivorous	2.32	2.24	14.2
Temperate	Invertivorous	1.9	1.28	10.47
Tropical	Territorial grazer herbivorous	0.11	0.93	7.24
Tropical	Grazer herbivorous	0.54	1.21	6.95
Tropical	Planktivorous	0.44	0.75	6.23
Temperate	Territorial grazer herbivorous	0.37	1.09	6.2
Temperate	Browser/Grazer herbivorous	0.1	0.65	4.52
Temperate	Carnivorous	0.2	0.4	4.23
Temperate	Grazer herbivorous	0.06	0.38	3.28

Oyster habitat versus Kelp habitat - Average dissimilarity = 70.52

Origin	Functional group	Average Abundance Oyster	Average Abundance Kelp	Contribution%
Temperate	Omnivorous	1.3	2.66	24.98
Temperate	Planktivorous	1.11	0.5	14.71
Tropical	Planktivorous	1.18	0	13.12
Temperate	Invertivorous	1.21	1.32	12.15
Tropical	Grazer herbivorous	0.78	0.14	9.47
Temperate	Carnivorous	0.37	0.38	6.5
Temperate	Browser herbivorous	0.14	0.39	5.22
Temperate	Kelp feeder	0	0.34	3.89

Turf habitat versus Kelp habitat - Average dissimilarity = 61.23

Origin	Functional group	Average Abundance Turf	Average Abundance Kelp	Contribution%
Temperate	Omnivorous	2.32	2.66	31.05
Temperate	Invertivorous	1.9	1.32	16.23
Temperate	Planktivorous	0.81	0.5	10.45
Tropical	Grazer herbivorous	0.54	0.14	7.74
Temperate	Browser herbivorous	0.25	0.39	6.3
Temperate	Carnivorous	0.2	0.38	5.96
Temperate	Territorial grazer herbivorous	0.37	0.04	4.83
Tropical	Planktivorous	0.44	0	4.8
Temperate	Kelp feeder	0.04	0.34	4.55

Barren habitat versus Kelp habitat - Average dissimilarity = 61.23

Origin	Functional group	Average Abundance Barren	Average Abundance Kelp	Contribution%
Temperate	Planktivorous	4.66	0.5	27.4
Temperate	Omnivorous	2.24	2.66	15.52
Temperate	Invertivorous	1.28	1.32	8.02
Tropical	Grazer herbivorous	1.21	0.14	8.01
Tropical	Territorial grazer herbivorous	0.93	0	7.09
Temperate	Territorial grazer herbivorous	1.09	0.04	7.02
Temperate	Carnivorous	0.4	0.38	4.8
Tropical	Planktivorous	0.75	0	4.39
Temperate	Browser/Grazer herbivorous	0.65	0.09	4.34
Temperate	Browser herbivorous	0.3	0.39	3.39
Temperate	Grazer herbivorous	0.38	0.04	3.12

CHAPTER VI

GENERAL DISCUSSION

GENERAL DISCUSSION

My thesis advances ecological theory related to the mechanisms (1) that underlie the potential establishment of tropical range-extending species in novel temperate environments, and (2) facilitate the emergence of novel temperate communities under ocean warming. Predicting species persistence in novel ranges and the future biodiversity of invaded systems requires a broad understanding of their ecological responses, and ability to adapt their behaviour or physiology to new boundaries of thermal niches under global anthropogenic climate change (Chapple et al. 2012; Kingsbury et al. 2020; Wolfe et al. 2020). Generally, species behaviour is directly shaped by the surrounding environment in which they are embedded (Bryant 1989), and as the environment changes, species need to be able to modify the behavioural repertoire (plasticity) to ensure population maintenance (Wong & Candolin 2015). Thus, investigating species behavioural repertoire and plasticity is crucial because it might represent a pathway to adaptation that determines whether a species persists or disappears in a local environment (Lister 2013; Lister 2014). By focusing on the behavioural response of native temperate species and reef-associated marine fishes that are rapidly expanding their distribution poleward under pressing ocean warming, I show how the emergence of novel communities in temperate ecosystems might occur in the near future. My findings help to improve range shift predictions and the potential persistence and overall ecological impacts of tropical fish species populations on temperate communities.

The holistic understanding of behavioural changes is key not only to determine the ability of tropical range-extending species to cope with the newly invaded habitat but also how local species will resist the newcomers. It also provides insights under which circumstances behavioural plasticity can lead to segregation between species ecological niches and influence novel biotic interactions. This is likely to determine the fate of tropical species revealing who might succeed, and the emergence of new communities in temperate ecosystems. In general, I found that behavioural plasticity and segregation of tropical and temperate fish around their overlapping distributional edges could facilitate their coexistence (Chapter 2). Some behavioural traits are modified, triggering alterations in interactions strengths that are essential for species persistence, such as predator avoidance (chapter 3) and competition (chapter 4). When combined with another global stressor (ocean acidification) which inhibits the persistence of suitable temperate habitat for tropical fishes, establishment of tropical fishes in temperate invaded ranges might be buffered under ocean warming (chapter 5).

Modelling studies that forecast the pace of marine range-extending species have mainly accounted for climate and species dispersal ability traits as the principal drivers of species geographical expansion (Luiz et al. 2013; McHenry et al. 2019). Yet, these models should be interpreted with caution because while species can disperse to other environments, they may not persist in the new environmental conditions (Angert et al. 2011; Figueira & Booth 2010; Figueira et al. 2019). When species arrive in novel environments, biological (e.g. schooling behaviour) and functional traits (ecological generality) become the main mechanisms facilitating the initial establishment of range-extending species (Luiz et al. 2012; Feary et al. 2013, Monaco et al. 2020), which are often neglected in range-extending models. Biological and functional traits, generally expressed by species behaviour and interactions, are the main drivers leading to adaptation and enhancing species survivorship at invaded ranges (Cahill et al. 2013; Ockendon et al. 2014; Sunday et al. 2015). Currently, only a few studies have evaluated the behavioural performance of tropical range-extending species, but they only rely on single behaviours (e.g. feeding, swimming performance, habitat use, social behaviour) (Beck et al. 2016; Beck et al. 2017; Smith et al. 2018; Paijmans et al. 2019), ignoring that species show complex adaptive behaviours that reflect an important ecological niche (Gouraguine et al. 2019). In addition, most of these behavioural studies were performed using aquarium experiments. This thesis, therefore, may complement and improve laboratory experiment findings because *in situ* behavioural observations increase ecological realism.. Besides, studies testing proxies of biological interactions between tropical range-extending and temperate fishes remain largely in their infancy (Kingsbury et al. 2019; Smith et al. 2018; Figueira et al. 2019). This thesis addresses this gap and may potentially help modellers to create more accurate predictions by including species behaviour and interactions across a latitudinal gradient. I show how alterations in tropical fishes behavioural repertoire can influence the outcome of biological interactions in novel communities, and therefore how it can be an important mechanism driving the tropicalisation of temperate ecosystems.

Specifically, this thesis shows that behavioural plasticity (ability to change their behavioural niche breadth) and behavioural segregation (low degree of behaviour overlap) with local species at temperate latitudes might allow tropical fishes to exploit novel environmental-biotic conditions and avoid or reduce competition with temperate species, increasing the establishment likelihood on temperate reefs (Chapter 2). I also revealed that the antipredator strategy of tropical fishes at higher latitudes (increasing flight initiation distance and time in shelter) was associated with reduced food consumption, likely resulting in lower energy intake and thus compromising their survival on temperate reefs (Chapter 3). Similarly, the reduced ability to perceive, access, consume and compete for prey at temperate invaded ranges, can disadvantage tropical fishes competitively, which in turn would affect their coexistence with local temperate species (Chapter 4). Such alteration in food acquisition is in response to reduced activity at low temperatures. Additionally, even though tropical fishes utilised a temperate habitat (sea-urchin barrens) which would facilitate their successful migration to higher latitudes and potentially compete with local species, ocean acidification might inhibit the formation of this suitable habitat, reducing their successful recruitment and the appearance of novel communities (Chapter 5).

By using a technique that allowed me to reduce the multi-variate space of species behaviours into a bi-dimensional space, I was able to identify whether species display behavioural plasticity or rigidity when facing novel environments as well as the potential of temperate species to resist these tropical invasions (Chapter 2). Since species display multiple behaviours that are interconnected to form their behavioural repertoire, I show based on the species behaviour niche space, that the behaviour repertoire (14 behaviours used) of tropical range-extending species increased (i.e. becoming more generalistic) at their temperate invaded ranges, giving them the necessary advantage to cope with novel environmental challenges. In contrast, temperate species exhibited an increased behavioural niche space in the opposite direction (becoming more generalistic in lower-latitude regions). The expansion of the ecological niche depends on the variability of the responses among individuals. For example, the increased variability in behavioural responses among individuals of tropical fishes at high latitudes means that individuals are responding differently to the new environment, predators and competitors which may, in turn, affect population growth and community dynamics at their new ranges (Phillips & Suarez 2012). Different organisms have shown behavioural flexibility as a mechanism of adaptation to environmental changes, assuring survival under human-altered conditions (Sih et al. 2011; Tuomainen & Candolin 2011; Candolin & Wong 2012; Sih 2013). Because not all behavioural adaptations are beneficial, some of the behavioural plasticity exhibited by tropical fishes could, in theory, be maladaptive (e.g. increased time in refuge) (Robertson et al. 2013; Martín et al. 2003; Hugie 2004). Yet, I found that the behavioural plasticity displayed by both temperate and tropical species can be adaptive and play a vital role in increasing their success as the environment changes. The ability of tropical range-shift species to be flexible in their behavioural niche, as revealed in this thesis, demonstrates the increased likelihood of these species to maintaining a viable population as they enter temperate communities. Which in turn could have cascading effects on ecological and evolutionary processes, altering population dynamics (Sih et al. 2011; Tuomainen & Candolin 2011) at temperate communities.

Through the same technique used to investigate species behavioural plasticity, I was also able to evaluate the ecological niche overlap between tropical and temperate species. The influx of tropical species into temperate reefs can lead to competition with local species, especially when they share similar niches (Alexander et al. 2015; Alexander et al. 2016). By evaluating the overlap of behavioural niches between tropical and temperate species, I could obtain strong insights on the strength of potential resource competition experienced by tropical and local species and their likelihood to coexist in temperate ecosystems. I revealed that the selected tropical fishes do not appear to be negatively interacting with temperate fishes. First, I demonstrate that there is behavioural segregation among these species across their distributional ranges where they co-occur, indicating that they may differ in resource use (see also Kingsbury et al. 2020). Second, aggressive behaviour was almost absent between tropical and temperate fishes, with the highest rates of aggressiveness observed between conspecifics (individuals of the same species). Although we do not have evidence of resource limitation, such behavioural niche segregation can prevent competition and enable both affinities to successfully coexist in temperate latitudes. This segregation is also likely to occur due to the flexibility in their behaviour use along the latitudinal gradient such as co-schooling behaviour (Smith et al. 2018). The findings presented in this thesis corroborates with a recent study which reveals that tropical range-shifting species did not overlap in trophic niche space with local temperate species (Kingsbury et al. 2020). Under future climate change, the number of species extending to higher latitudes is predicted to increase, and niche segregation might be crucial to allow the coexistence among species (Hutchinson 1959; Bulleri et al. 2015). However, under future warming when tropical fishes are able to reach adulthood in temperate ecosystems, the strength and extent of current niche segregation might be altered.

Whilst the behavioural plasticity and segregation might benefit tropical fishes in temperate ecosystems, the behavioural trade-off that they face, favouring increased vigilance and time sheltering over foraging activity, might compromise their survival in the short term (Chapter 3). Although the decrease in boldness at first glance appears to be an appropriate choice to avoid unknown predators (Walker et al. 2005), such alterations in the antipredator behaviour or risk avoidance might be maladaptive (Millidine et al. 2006; Kingsbury et al. 2020), and for now restrict the establishment of tropical fish in temperate zones. Additionally, as winter temperatures did not alter the flight initiation distance and time sheltering by tropical fishes at temperate latitudes, the environmental unfamiliarity rather than the physiological effects of reduced seawater temperature is likely to be the principal driver of risk-averse behaviours displayed by tropical fishes. Generally, animals that over-respond to a threat and engage less in other fitness-related activities (Dall et al. 2001; Carthey & Banks 2014) can compromise energetic intake, leading to altered energy allocation to important physiological processes such as somatic growth (Millidine et al. 2006; Kingsbury et al. 2020). Maintaining energetic budget stable is crucial for the functionality of physiological process (Cooper et al. 2002), especially for species that are facing changes in their surrounding environment such as for the tropical fishes at temperate areas which have their metabolism compromised by the low temperature (Figueira & Booth 2010; Booth et al. 2018) and at the same time need to efficiently escape from unknown predators. Hence, irrespective of seawater temperature, risk-avoidance behaviours by range-extending species in their novel ranges is likely to affect energy budgets with possible ensuing effects on individual fitness. Therefore, tropical range-extending fishes that can efficiently balance the conflict demands of feeding and predator avoidance have greater chances to succeed in temperate waters.

I further revealed that tropical fish are less effective in food acquisition behaviours in novel temperate environments than in subtropical latitudes and with an increased abundance of potential temperate competitors (Chapter 4). By being less efficient in perceiving, approaching and consuming prey, in combination with feeding interference by temperate fishes, tropical range-extending species compromise their fitness and survival at temperate waters. Yet, very little attention has been given to the question of whether tropical range-extending and native species may compete and, if yes, how this competition may buffer or facilitate the invasion into climate warming hotspots (Louthan et al. 2015). In the biological invasion literature, successful invasive species are in most of the cases linked to higher performance and competitive ability than local species (Parker et al. 2013; Wallingford et al. 2010). But, when the local species are superior competitors, biotic resistance can occur (Masciocchi et al. 2010; Kimbro et al. 2013). Here, I show that due to the lower foraging and competitive performance of tropical species in novel temperate environments (e.g. low temperatures), native temperate fish might outcompete tropical ones, reducing their chances to establish in novel temperate ranges. However, as water temperatures continue to rise, I expected that tropical fishes may improve their foraging and competitive performance at temperate waters and maybe outcompete local species.

For coral reef-associated marine organisms, the availability of suitable habitats (non-macroalgae forming habitats; Beck et al. 2017) at temperate latitudes may also strongly limit their initial colonisation under ocean warming. I discovered that ocean warming can indirectly facilitate the colonisation of tropical fishes via habitat modification from kelp-forests to sea-urchin barren dominated habitats. However, as the ocean warms it also acidifies and the formation of urchin-barrens might be reduced due to the known (e.g. decreasing foraging activity) effects of ocean acidification on urchins' fitness (Siikavuopio et al. 2007; Connell et al. 2018) which in turns will have a negative consequence on tropicalisation rates. As I hypothesised, ocean acidification may buffer the negative effects of ocean warming by inhibiting sea urchin abundances and the consequent formation of barren habitats in temperate ecosystems. Whilst ocean warming facilitates the recruitment of tropical fishes by increasing the availability of their preferred habitat (urchin barrens), ocean acidification acts as a stressor on sea urchins, diminishing barren creation and allowing the emergence of less favourable turf-forming habitats. This shows that when combined, climatic stressors tend to have a very different effect on marine biota than when only a single stressor is considered (Byrne et al. 2013) and studies forecasting the establishment of tropical species need to take this into account.

FUTURE DIRECTIONS

In my thesis, I studied a set of behaviours that play a key role in the fitness and survivorship of the most abundant tropical range-shifting fishes in temperate invaded ranges. Two comparative approaches were used to provide different insights into potential determinants of invasiveness (van Kleunen et al. 2010): (1) comparing species behaviour responses between species populations at warmer and cooler parts of distributional ranges, and 2) comparing the behavioural responses between tropical invaders and native temperate fishes at the same latitudes. The investigation was based on observational data collection and manipulative experiments *in situ* improving the predictive value on the mechanisms that influence future colonisation (Holway & Suarwz 1999; Phillips & Suarez 2012) and impacts of tropical fishes on temperate communities (Wallingford et al. 2020). However, to further advance the field of tropicalisation research many unknowns still need to be addressed. Some suggestion to improve the predictions of tropical range-shifting species may include:

(1) More complex laboratory experiments using mesocosm setups and including multiple species, different habitat formation and a wide variety of species interactions. Such experiments would add complexity layers normally not present in simple laboratory experiments (Goldenberg et al. 2017; 2018). I also suggest that these experiments should run for a long-term period (minimum 6 months) allowing the investigation of species adaptive and evolutionary responses that short-term experiments are unable to observe, driving researchers to draw incomplete or unrealistic predictions on species ability to persist under stressing climatic conditions. In addition, the majority of the studies have been focusing on the initial life stage of range-extending species and we still do not known how mature animals may behave. Such long-term studies will then allow understanding of the mechanisms that influence the establishment of range-shifting species across all life stages.

(2) Studies involving ecological interactions, similar to this study, but using positive interactions such as mutualism (e.g. Paijmans et al. 2019) and understudied negative interactions (parasitism) combined with abiotic conditions (warming and acidification) should be prioritized. The outcomes of range-extension or contraction depends on the strength of biotic vs. abiotic conditions and the balance among these forces (Siren & Morelli 2019). Despite the increasing evidence of the mechanisms that may drive the successful (or failure) establishment of tropical fishes in temperate

ecosystems, how biological factors and species interactions act in synergy or antagonism with climatic conditions remains understudied.

(3) Combining behavioural and physiological data sets should also be considered due to their intimate connection. Despite behaviour being the first response of an organism to altered environments, behavioural changes are generally driven by the species' underlying physiology (Huey et al. 2012). Additionally, organisms change their behaviour to maintain their physiological requirements (Kearney et al. 2009; Sunday et al. 2014) and fitness. By integrating these two processes, biologists can better predict which range-shifting species (Wingfield et al. 2015) may present a stronger ability to colonise temperate environments under pressing climatic disturbances. I would suggest for example link boldness variation with endocrine stress response (Atwell et al. 2012) which could disentangle whether reduced boldness displayed by tropical fishes is related to the physiological stress posed by the low temperature or unfamiliarity with the novel temperate habitat. In addition, whether reduced food intake exhibited by tropical fishes at temperate reefs is affecting their physiological stability.

(4) I investigated tropical vs. temperate fish behavioural responses and interactions over a latitudinal gradient, but my warmest (average summer temperature ~ 23 ºC) and coolest (average summer temperature ~ 20 ºC) studied regions comprised a subtropical (South West Rocks) and temperate areas (Merimbula), respectively, where tropical and temperate species occur together. The subtropical area used in the present thesis lacks the principal forming habitat of tropical regions (coral reefs) and does not encompass the warmest area of tropical fishes range (trailing edge). In this case, additional investigations should be replicated in areas where each affinity does not share the same space. Studying tropical fishes in native and warm coral reef habitats (average summer temperature ~ 29 ºC), further north of South West Rocks (30 °S), would be useful as this would provide a baseline data on how these species behaviourally perform and interact with other tropical species in their natural environments.

(5) The integration of multiple stressors should be attempted in future range shift studies. In this thesis, I showed the possible role of ocean acidification on the range-shifting rates and future establishment of tropical fishes into temperate invaded ranges under ocean warming through habitat modification. Yet, we still need to investigate how the behavioural plasticity and interactions between tropical and temperate fishes would be altered under ocean warming and acidification combined. I also suggest considering the addition of local stressors such as pollution and overfishing to global stressors into the range-shifting predictions, by using areas exposed to different levels of pollution and fishing (e.g. marine protected areas vs. open fishing areas). Such an approach might provide a more realistic prediction of which human activities may facilitate or restrict colonisation of tropical fishes in temperate communities since all these stressors are well known to have a profound impact on the structure of natural temperate reef ecosystems (Steneck et al. 2002).

GENERAL CONCLUSION

This thesis provides an in-depth look at range shifts and highlights how species behavioural plasticity is an important mechanism determining both species performance and interactions. It also provides strong evidence of the impact that range-extending species may pose to native species and communities. The results found here will help to anticipate suitable management and conservation actions, such as managing the colonisation of harmful species and limiting the catch of harmless range-shifters to allow new fish populations to flourish in temperate regions. Additionally, the previous literature has poorly addressed the interactive effects of behaviour, species interactions, and climatic conditions on range-extending species establishment. Thus, my research shows the importance of this interactive approach for the future of marine range shift research. I also revealed that tropical and temperate local species behaviour plasticity, generalism, and segregation may further mediate the success of invasion by tropical fishes into temperate environments under climate change and allow generalist temperate fish species to persist under this invasion.

By assessing antipredator performance, I demonstrated that temperate fish maintained their antipredator responses from temperate to subtropical regions, but tropical fishes were more risk-averse in higher temperate latitudes. Increased risk-averse response might be beneficial to avoid unknown predators, increasing the chances of survival on the short-term. However, this compromises their survivorship in the long-term, due to reduced foraging activity. This behavioural trade-off can be an adaptive response deployed by naïve range-extending species during the initial stage of the range-extension process. Possibly in the later range-extension stages, tropical fishes may have better adapted to novel temperate habitats and predators. Likewise, I found that tropical fish are inferior competitors for food in temperate ecosystems compared to temperate species, which in turn may delay their colonisation of temperate ecosystems. Future warmer temperate waters is likely to accelerate the successful establishment of tropical species by increasing the extension of habitats that favour their recruitment. However, ocean acidification is likely to retard this process by countering the formation of suitable urchin barren habitats. In summary, I demonstrate the ability of generalist tropical fishes to colonise and coexist with native fishes in temperate invaded ranges under the initial stages of climate change range shifts.

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