Tropical fish recruitment success varies among temperate reef habitats, potentially impacting their range expansion

by

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Certificate of original authorship

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

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Date:

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General abstract

Climate change is leading to poleward range expansions of tropical fishes. But to shift poleward with warming waters, species need habitats at higher latitudes with suitable abiotic conditions, resources and communities. This thesis provides the initial empirical evidence that recruitment success of tropical reef fishes varies considerably among temperate reef habitats, encountered at forefronts of their range expansion. Global Positioning System (GPS) - tracked roaming surveys were firstly established as a preferable method for quantifying these rare and sparsely distributed range-expanding fishes, offering reliable density estimates, maximised sightings and improved efficiency compared to traditional belt transects (Chapter 2). GPS-tracked roaming surveys were then conducted in two hotspots of warming, southeastern Australia and western Japan, revealing that spatial variance in biogenic structure and wave regime between reefs may strongly organise, and even limit where tropical fishes recruit (Chapters 3 and 4). Shelter was a key limiting factor, with embayed reefs supporting greater richness, diversity and densities of new recruit and early juvenile tropical fishes than adjacent wave-exposed reefs (Chapter 3). Both habitat generalists (e.g., planktivores, herbivores and omnivores) and specialists (i.e., obligate coral feeders) were more abundant and diverse on embayed reefs. Factors structuring higher recruitment of tropical fishes on embayed reefs were the greater shelter from wave action and branching coral cover (coral-obligate habitat users only). On finer spatial scales, greater densities, diversity and species richness of tropical fish recruits associated with non-macroalgal than macroalgal reef (Chapter 4). Aquarium experiments indicated that non-macroalgal reef (no branching algae) were preferred temperate settlement habitat for tropical fish larvae. However, the abundance and composition of native predator communities impacted feeding activities of a tropical damselfish (*Abudefduf vaigiensis*; Chapter 5), suggesting that even if suitably structured reefs are available for recruiting tropical fishes, temperate predators may constrain their survival by limiting food intake. Feeding activities of *A. vaigiensis* were reduced in presence of a high predation threat, both *in situ* and in an aquarium experiment. Such predator-driven reductions in feeding were accentuated in summer, but diminished in cool winter waters, when poor metabolic performance of this warm-adapted species lowered their feeding activities independent of predation threat. This thesis shows that temperate reef structure and predator densities, and human modification of these factors, need to be considered along with dispersal factors and water temperature to accurately predict geographic responses of many tropical fishes to climate change and impacts of this redistribution on temperate marine ecosystems.

Chapter 1: General introduction

1.1 Global warming and species redistribution

Rising environmental temperatures, associated with human-emitted greenhouse gases, threaten species globally (Pereira et al. 2010; Barnosky et al. 2012). Recent climate change presents a myriad of potential challenges for species to survive (Cahill et al. 2013). For instance, marine species are threatened by climate-driven increases in sea level, storm activity and ocean acidity (Brierley and Kingsford 2009), whilst ongoing climate change is increasingly impacting terrestrial organisms by modifying precipitation and wind patterns (Walther et al. 2002). However, across all environments, extinctions may occur where warming environments destroy habitat, inhibit reproduction and/or exceed species' physiological tolerance (Thuiller et al. 2005; Somero 2010). Species may have some capacity to acclimate and/or adapt to these warmer conditions (Skelly and Freidenburg 2007; Munday et al. 2013). Thermally-driven habitat loss may also be endured to some extent by species with non-specific habitat requirements (i.e., generalists; Warren et al. 2001, but see Bridle et al. 2014). However, to avoid extinction with ongoing climate change, many terrestrial and aquatic species will need to redistribute to more thermally suitable regions (Thomas et al. 2004).

Warming air temperatures have initiated shifts of many terrestrial organisms to higher altitudes (Lenoir et al. 2008). Analogous to altitudinal shifts of terrestrial organisms, some aquatic species have moved deeper in response to warming water temperatures (Thresher et al. 2007). However, poleward redistribution of species has been the most commonly observed geographic response of species to warming environments (Parmesan and Yohe 2003; Parmesan 2006; Kelly and Goulden 2008); terrestrial and aquatic organisms have shifted their distribution poleward at a median rate of 16.9 km per decade (Chen et al. 2011). Such a sudden and substantial poleward advance of species is modifying the function and structure of many ecosystems, with great potential to impact socioeconomic activities that depend on the services they provide, including fisheries, recreation and tourism (Cheung et al. 2009; Pereira et al. 2010; Madin et al. 2012). Hence, accurate predictions of where and when species may colonise with ongoing climate change is vital for conserving threatened species and managing adverse impacts of this redistribution on valuable ecosystems.

1.2 Current shortfalls when predicting species' geographic response to climate change

The capacity of ecologists to reliably predict the rate of climate-associated species range shifts is currently limited by an incomplete understanding of factors that control species' distribution. Certainly, the dispersal potential and thermal tolerance of a species are both important factors that will likely influence whether, and the extent to which species shift poleward with climate change (Parmesan et al. 1999; Keith et al. 2011; Sorte 2013; Pinsky et al. 2013). Consequently, when predicting the future distribution of land animals and plants, it may be important to consider both the direction and strength of prevailing wind patterns, due to their strong influence on species dispersal (e.g., seeds and larvae) and the thermal suitability of local climates (Burrows et al. 2014). In a similar sense, ocean currents may strongly control advection of marine larvae and local water temperatures, having a major bearing on the latitudinal breadth of many marine species' ranges (Gaylord and Gaines 2000; Keith et al. 2011; Sorte 2013; Pinsky et al. 2013). Yet, where species' physiological, energetic and demographic responses to climate and propagule transport are solely considered (i.e., species' climate envelope, *sensu* Buckley et al. 2010), predicted responses of species to climate change often deviate considerably from those observed, especially on fine-spatial scales (Pearson and Dawson 2003; Guisan and Thuiller 2005; Hijmans and Graham 2006). This inconsistency between the observed and predicted geographic response of species to climate change (using such a mechanistic approach) exposes the potentially high influence of non-climatic environmental factors on species occupying their full thermal niche (Gaston 2009).

To colonise higher latitudes, not only do species need to be transported to regions where they can physiologically tolerate local environmental temperatures, but they must also access habitats that support their survival. These habitats must provide colonising individuals necessary resources, including food, shelter and living space (Olyarnik et al. 2009). To survive within a new range, colonising organisms must also tolerate changes in abiotic conditions in these habitats, such as salinity, turbidity, sunlight and pH (Warren et al. 2001; Wenger et al. 2011; Bennie et al. 2013; Grenouillet and Comte 2014). They also need to succeed in interactions with resident predators, competitors, pathogens and mutualists (Davis et al. 1998a; Hochberg and Ives 1999; Schweiger et al. 2008; Angert et al. 2011; Angert et al. 2013; Urban et al. 2013). Hence, spatiotemporal variance in the distribution of habitats, which contain a suite of resident species and a range of physical conditions and resources that may differ (sometimes considerably) from those within the natal range of a species, may ultimately organise where and when species can colonise (HilleRisLambers et al. 2013). However, currently there is a paucity of studies exploring how both climate and non-climatic factors may interact to organise species' range limits, substantially limiting our ability to accurately anticipate species' responses to climate change. This knowledge gap was recently identified within several literature reviews, including Gaston (2009), Sexton et al. (2009), Angert et al. (2013), HilleRisLambers et al. (2013) and Bates et al. (2014).

1.3 Habitat limitations to poleward redistribution of reef-associated marine species

Due to the high dispersal capacity and strong thermal dependence of many marine invertebrates and fishes, these organisms may rapidly range-shift poleward in response to warming sea surface temperatures (Pinsky et al. 2013; Burrows et al. 2014). For example, a recent meta-analysis revealed that marine organisms, including seaweeds, invertebrates and fishes, have shifted poleward an order of magnitude faster on average than terrestrial organisms (Sorte et al. 2010). This rapid redistribution has modified herbivory (Ling 2008), competition (Arrontes 2002), disease (Ford and Smolowitz 2007) and predation (Zeidberg and Robison 2007) within receiving marine ecosystems, threatening their structure and function (e.g., Johnson et al. 2011). However, despite the increasingly common occurrence of marine organisms in new ranges, and emerging impacts caused by redistributing species, roles of reef habitats in organising the redistribution of marine organisms are still largely unresolved (Bates et al. 2014).

Logically, reef-associated species may be constrained from colonising regions where reefs, positioned at suitable depths, are scarce or absent. For instance, a lack of offshore shallow water reefs is expected to limit poleward shifts of corals along the Western Australian coastline despite frequent poleward advection of coral larvae and rising water temperatures in this region (Bates et al. 2014). Where ecological constraints of a species are known within their historic range, we may also predict with some confidence how reef habitats may impact their colonisation where shifting species encounter habitats that are similar at higher latitudes. For example, based on an historic understanding of factors influencing the distribution of intertidal fauna, Helmuth et al. (2006) hypothesised how local abiotic stressors, sparse resources and harmful native fauna may impact the survival of range expanding organisms during their various life stages within a new range. However, in many cases, species are shifting to regions where they encounter foreign sets of physical stressors, resources and fauna (Gilman et al. 2010). Under such novel circumstances, outcomes of interactions between shifting species and these habitats may be difficult to predict purely based on an understanding of the ecology of the range expander within their source range (Williams and Jackson 2007). For example, within its source range, survival of the barnacle *Tetraclita rubescens* is largely impacted by predatory whelks (Sanford and Swezey 2008). But in its newly expanded range, *T. rubescens* is largely resistant to attacks by whelks native to the region, as their shell is too thick for these native predators to rupture (Sanford and Swezey 2008). To reliably understand how novel reef communities impact species' colonisation, empirical studies are required at the edge of species' ranges (Wernberg et al. 2012a) - where these shifting species encounter these novel habitats (e.g., Ling et al. 2009; Ling and Johnson 2012; Bates et al. 2013). Factors controlling range limits may also be determined by artificially transplanting individuals beyond their existing range (e.g., Arrontes 2002; Wethey 2002), but this approach risks substantial ecological impacts if transplanted individuals escape and proliferate.

1.4 Tropical reef fish and established mechanisms structuring their range expansions

Tropical marine fishes, colonising temperate regions with human-driven changes to ocean climates, may shed light on how novel reef habitats constrain poleward redistribution of marine species. Sea surface warming may eventually lead to widespread range expansions of tropical reef fishes (Figueira and Booth 2010), but at present, many of these fishes are firstly colonising coastal temperate reefs in conjunction with intensifying poleward flowing boundary currents (Feary et al. 2014). Although there have been historical accounts of tropical or subtropical species being recorded within temperate regions (i.e., Vladykov 1935), poleward redistribution of tropical fishes is increasingly being reported globally, with increases in the abundance and/or diversity of tropical fishes (i.e., new settlers and/or individuals at later life stages) within temperate regions reported during the past decade on five continents (Table 1.1). Long term datasets of fish assemblages in regions such as W Japan, where fish assemblages have been regularly sampled since the early 1960's, ensure that, at least in some locations, tropicalization of fish assemblages on temperate reefs is not merely an artefact of sampling (Nakamura et al. 2013). Such increases in tropical fish communities within temperate regions has been typically associated with intensification in the strength and poleward extension of boundary currents (ocean currents with dynamics influenced by the presence of a coastline; Thurman and Burton 1997). For instance, the East Australian Current (Australia), the Leewin Current (Australia), the Kuroshio Current (Japan), the Gulf Stream (USA), the Brazil Current (Brazil) and the Aghulus Current (Africa) are all intensifying with climate change, which has been attributed to driving poleward redistribution of tropical fishes (Table 1.1, Fig. 1.1). These boundary currents (mostly western) are strengthening in response to systematic changes in mid-latitude winds of both hemispheres with recent warming of the atmosphere (Wu et al. 2012). In effect, this increased poleward transport of warm water, originating from lower latitudes, is facilitating poleward redistribution of many tropical fishes by not only increasing the potential larval connectivity between temperate and tropical systems (Vergés et al. 2014; but see Munday et al. 2009), but also increasing the thermal suitability of temperate waters for tropical fishes (Figueira et al. 2009;

Figueira and Booth 2010). Hereafter, this trend in poleward redistribution of tropical fishes will be referred to as 'range expansions' since redistribution at the lower latitude limit of most tropical fishes, constituting a range-shift or -contraction, are so far largely unreported – although declines in equatorial populations of many species are shortly anticipated (Munday et al. 2008).

Despite the increasingly common detection of tropical fishes in many temperate regions (Fig. 1.1), as well as emerging threats this redistribution may pose for temperate ecosystems (e.g., increased herbivory; Vergés et al. 2014), factors controlling the poleward expansion of tropical fishes are largely unresolved (Feary et al. 2014; Fig. 1.2). Certainly, at a regional extent, the supply of tropical fishes to temperate regions is a key prerequisite to their range expansion (Booth et al. 2007). For example, Booth et al. (2007) found that the richness and density of tropical fish recruits reduced along the southeastern (SE) Australian coast with increasing distance away from tropical larval sources, such as the Great Barrier Reef. Hence, larval supply appears to be important in determining recruitment success of tropical fishes within SE Australia, at least at regional spatial scales. Species traits may also influence which species may be transported to and settle into temperate regions. For instance, tropical fishes most likely to colonise temperate regions (i.e., those with the widest latitudinal range and are commonly expatriated to temperate reefs) have relatively large body sizes, nocturnally feed and form schools (Luiz et al. 2013; Feary et al. 2014). These behaviours and a relatively large body size are believed to reduce predation risk, promoting individual survival in temperate regions (Luiz et al. 2013). Furthermore, fish species with a generalised diet (e.g., herbivores, planktivores and omnivores) are usually more successful in temperate reefs than coral-dependant species. This is despite coral dependent species comprising a relatively high percentage of the tropical reef fish composition (~10% of all tropical reef fishes; Pratchett et al. 2011), including obligate coral feeders and those that use live coral as a settlement cue. Such low abundance within temperate regions is attributed to the rarity or absence of corals in coastal temperate regions (Feary et al. 2014). Pelagic larval duration (PLD) may also influence the dispersal potential of tropical fishes, with a positive relationship suggested between PLD and the distance larvae may disperse (Shanks 2009). However, PLD does not appear to strongly influence range expansions of tropical fishes into temperate regions, since PLDs of many tropical fishes that commonly recruit to temperate coastal reefs of SE Australia and W Japan are usually comparable throughout these regions, regardless of their distance from likely larval sources (Booth and Parkinson 2011; Soeparno et al. 2012).

Variance in water temperature may also strongly influence where tropical fishes colonise, with overwinter mortality associated with low water temperature commonly one of the most important constraints to population establishment within temperate reefs (Feary et al. 2014). For species supplied to temperate regions and capable of accessing necessary resources, low water temperatures during winter may substantially limit their survival. For instance, Figueira and Booth (2010) found the abundance of eight species, belonging to the families Chaetodontidae (butterflyfishes) and Pomacentridae (damselfishes), markedly declined on SE Australian reefs when waters dropped below 17 - 18ºC during winter. In W Japan, substantial reductions in the diversity and richness of the entire tropical fish assemblage were also observed when winter water temperatures dropped below 17 - 18ºC (Hirata et al. 2011; Soeparno et al. 2013). Although reduction in the abundance of tropical fish populations corresponded with cool winter water temperatures in these studies, it is unlikely that such an impact is caused by water temperatures dropping below the lower lethal limit of tropical fishes. This is because closely related species to those found recruiting into temperate reefs (i.e., Pomacentridae; Eme and Bennet 2008) and tropical fishes that commonly recruit to temperate reefs (e.g., *Abudefduf sexfasciatus* and *Pomacentrus coelestis*; H. J. Beck, personal observation; hereafter termed ‘vagrants’) may survive at least short term exposure to water temperatures lower than 15ºC within aquaria. Therefore, *in situ* mortality of tropical fishes at water temperatures above their lower critical thresholds suggests that interactions of tropical fishes with a range of factors, including abiotic conditions and/or temperate fauna, as well as simply a slowed metabolic efficiency during these cool periods may substantially limit their survival. For instance, at the forefront of tropical fishes’ range expansion, cool winter waters reduce the swimming performance of these warm-adapted tropical fishes, which is predicted to impair their capacity to escape attacks by temperate, cool-adapted predators (Figueira et al. 2009).

1.5 How may temperate reefs organise tropical fish recruitment?

To more accurately predict the future distribution of tropical fishes, roles of temperate reef habitats in organising their early life success need to be determined (Munday et al. 2008; Feary et al. 2014; Figs. 1.2 and 1.3). Even if tropical fishes may be readily supplied as larvae to temperate reef habitats where required resources are present, and they may physiologically tolerate the local water temperatures, temperate reef habitats could strongly organise where they can recruit (i.e., survival of individuals from settlement to the reef environment through to maturity). Certainly, such habitat constraints to recruitment of reef fishes may be theoretically overcome, at least to some extent, where larval supply is high - termed traditionally as 'supply-side ecology'(Lewin 1986; Underwood and Fairweather 1989). But at the forefront of species range shifts, where larval supply is likely to be more sparse than within their natal range (Sorte 2013), resource availability and/or interactions with native temperate species and abiotic conditions may strongly impact their recruitment (Fig. 1.4). For example, recruitment success of reef fishes may differ among reef habitats due to spatial and temporal variance in physical stressors, including wave exposure, sunlight, salinity and turbidity, necessary resources such as food (Pitts 1991; Ormond et al. 1996), reef shelter (Beukers and Jones 1998; Gratwicke and Speight 2005) and living space (Sale 1978), whilst competitive (Bay et al. 2001; Ormond et al. 1996) and predatory (Beukers and Jones 1998; Nemeth 1998; Almany and Webster 2006) interactions with individual animals and whole communities (Hixon and Beets 1993; Chase et al. 2002; Hixon and Jones 2005) may also influence where reef fishes may successfully recruit (Fig. 1.4). Hence, recruitment on temperate reefs may be unsuccessful where physical conditions exceed a tropical fishes' physiological thresholds, or required resources are not available or accessible (Fig. 1.4). As a result, habitat-limited recruitment of tropical fishes in temperate reefs may restrict them from shifting with warming waters, since the establishment of permanent populations at temperate latitudes depends strongly on population replenishment by new recruits (Fig. 1.3).

Recruitment success of tropical reef fishes may be spatially variable among temperate coastal reefs, commonly encountered at the forefront of range expansion of many tropical reef fishes (Table 1.1, Fig. 1.2). In addition, factors influencing recruitment success of tropical fishes in temperate coastal regions will likely be spatially dependent. Tropical fish recruitment success may be expected to differ between embayed and exposed coastal reefs, spatially separated by 100s of m to kms, since these two habitats have unique sets of physical conditions and biological communities. For instance, substantial variance in exposure of temperate reefs to wave action may organise early life success of tropical fishes by interacting with their swimming abilities (Fulton and Bellwood 2002; Fulton et al. 2005; Johansen et al. 2007; Johansen et al. 2008). Typically, a greater diversity and densities of reef fishes is supported in more sheltered reef aspects, especially in shallow reefs with moderate to highly energetic wave climates (Friedlander et al. 2003; Fulton and Bellwood 2004). Moreover, in temperate regions where corals may establish, embayed reef habitats may better support recruitment of coral-dependent tropical fishes than wave exposed reefs, since wave-sheltered reefs better support the establishment of structurally complex scleractinian corals (Madin et al. 2014); an important habitat and settlement cue for these fishes (Syms and Jones 2000; Feary et al. 2007a; Feary et al. 2007b).

Tropical fish recruitment may also vary on fine-spatial scales (i.e., < 100 m) within temperate reefs, where wave action is comparable, due to differences in macroalgal cover. Diversity in available habitats and topographic complexity, such as that associated with algal forests, can strongly influence the spatial distribution of both temperate and tropical reef fish assemblages (Choat and Ayling 1987; Curley et al. 2002; Anderson and Millar 2004; Wilson et al. 2010) by determining shelter availability (Shulman 1984, 1985), changing physical stress (Johansen et al. 2007; Johansen et al. 2008) and/or through influencing competition and predation on new recruits (Beukers and Jones 1998; Almany 2004a). The physical motion in the water column of macroalgae may also preclude some tropical reef fishes by potentially causing physical stress and blocking the visual detection of predators (Hoey 2010; Hoey and Bellwood 2011). Hence, spatial differences in reef structure in temperate regions, resulting from the coastline shape and orientation at a broader extent, and macroalgal cover on finer spatial scales, will likely organise where many tropical fishes may successfully recruit.

Even if tropical fishes access temperate reefs with suitable structure, adverse interactions with native predators (Hellmann et al. 2012; HilleRisLambers et al. 2013; Bates et al. 2013), as well as seasonably cool waters (Figueira et al. 2009), may still limit their survival. Temperate piscivores may predate upon tropical fish recruits (Booth and Hixon 1999; Booth and Beretta 2004), but they may also restrict their recruitment success by limiting access to necessary food (Carlsson et al. 2009; Gilman et al. 2010; Estes et al. 2011). Where predator abundance is high, prey fishes' movements are often reduced in the presence of predators, constraining access to food of sufficient quality or quantity (Madin et al. 2010). Over time, this reduced feeding activity may have substantial consequences for the growth, condition, survival of an individual, and ultimately the stability of a population (Lima and Dill 1990; Dill et al. 2003; Preisser et al. 2005). Nevertheless, outcomes of interactions between range expanding prey fishes and native piscivores are likely to vary seasonally due to differential responses between these groups of organisms to environmental temperatures (Davis et al. 1998b; Gilman et al. 2010; Harley 2011; Grigaltchik et al. 2012; Milazzo et al. 2013; Nagelkerken and Simpson 2013). During summer months, the physiological performance, behaviour and space occupancy of both native piscivores and range-expanders may be similar, with both assemblages showing high movement and feeding activity (Pörtner and Peck 2010). Within these warm periods, feeding excursions and bite rates of range expanding fishes may be substantially structured by native predator abundance, as within tropical reefs (e.g., Stallings 2008; Madin et al. 2010). However, range expanding tropical fishes may reduce their feeding activity levels approaching winter in response to cooler waters, irrespective of predation threat, due to poor physiological performance of these warm-adapted fishes (Rijnsdorp et al. 2009; Pörtner and Peck 2010).

1.6 Human modification of reef habitats and implications for tropical fish recruitment

If temperate reef habitat structure and temperate fauna organise tropical fish colonisation, then human actions may indirectly alter the pace of tropical fish range expansion by modifying reefs and temperate species through space and/or time. If the structure of temperate reefs determines tropical fish recruitment, as suggested above (1.5), then creation of reef habitat with suitable structure in temperate regions should facilitate recruitment of these fishes (Fig. 1.5). For example, on broad-spatial scales, if wave exposure of reefs reduces recruitment success of tropical fishes, humans may assist their range expansions by constructing wave-protected reefs, or reducing the wave exposure on established reef habitats. On finer spatial-scales, if the density and diversity of macroalgae structures the recruitment of tropical fishes, then changes in the cover of temperate macroalgae may impact population establishment. For example, warming sea surface temperatures are leading to widespread loss of kelp from temperate reefs (Tait and Schiel 2011; Wernberg et al. 2012b), whilst temperate macroalgae is also being reduced by human-induced changes to grazing pressure (e.g., Ling 2008). Fishing for temperate piscivores may also increase colonisation success of tropical fishes by potentially reducing the incidence of predation for new recruits and by increasing tropical reef fish access to resources, such as food. Hence, an understanding of how temperate reef habitat organise tropical fish recruitment may not only improve our capacity to reliably predict the response of tropical fishes to climate change, but also identify human activities that aid or inhibit this redistribution.

1.7 Thesis aims, hypotheses and layout

The overall goal of this thesis is to provide a foundation for understanding how temperate reef habitats, as well as human activities, spatially organise recruitment of range expanding tropical fishes. Prior to this, however, a suitable method needed to be developed for surveying these fishes, which are often rare and sparsely distributed on temperate reefs (Booth et al. 2007). In Chapter 2, the effectiveness of a Global Positioning System (GPS) – tracked timed swim (distances surveyed measured by GPS) for surveying range expanding tropical fishes was compared to that of belt transects – a traditional method for surveying reef fishes. This study revealed GPS-tracked roaming surveys were preferable for quantifying habitat associations of range expanding tropical fishes. In Chapters 3 and 4, this roaming survey technique was used to explore how temperate reef structure organised the densities, richness and taxonomic and functional diversity of new recruit and early juvenile tropical fishes within two regions that are rapidly warming; SE Australia and W Japan. Based on habitat constraints to reef fish recruitment where wave climate is moderate to high (such as SE Australia and W Japan; see 1.5), it was expected that on broad spatial scales (100s of m to kms) within these temperate regions, recruitment of tropical fishes would be largely influenced by the exposure of reefs to wave action – expecting greater success in more sheltered reefs (Chapter 3). But on finer-spatial scales (10s to 100s m; Chapter 4), where wave action was relatively consistent, the cover of macroalgae was expected to impact recruitment success since the structure of flexible and moving macroalgae may preclude recruitment of many reef fishes (see 1.5). Following these surveys, an aquarium experiment was used to test whether the association of tropical fish recruits with different temperate reef habitats was established by preference at settlement (Chapter 4). Lastly, to determine how temperate predators and cool winter waters impact access of tropical fish recruits to required food, the feeding behaviour of a focal tropical fish was compared between temperate reefs with high and low predator densities, during both summer and winter (Chapter 5). A laboratory experiment was then used to isolate the response of this focal species' feeding activities to temperate predators and seasonal water temperatures. It was anticipated that in warm summer waters, when the energetic requirements of these tropical fishes are relatively high, temperate predators may reduce their foraging activities. But during winter it was expected that tropical fishes would reduce their feeding activities independent of predation threat, since cool water temperatures encountered in temperate regions during winter substantially reduce the energetic demand of these warm-adapted fishes (1.5).

1.8 Tables

Table 1.1 Temperate regions where tropical fish colonisation has been detected and the supporting evidence, as determined by underwater visual surveys and/or fisheries records.

Region	Latitude	Evidence of range expansion	References
Southeastern Australia	28 – 37.5º S	Recruitment of 47 species and increasing diversity	(Booth et al. 2007; Figueira and Booth 2010)
Northern New Zealand	35.5º S	New detection of 20 species tropical and subtropical species	(Francis et al. 1999)
Western Australia	28.8 – 34.2º S	10% increase in tropical and subtropical species with episodic warming; six new species detected	(Wernberg et al. 2012b; Hutchins and Pearce 1994; Hutchins 2011)
Southeastern Africa	28 - 31.6ºS	Recruitment of 16 species, 9% increase over 19 years	(Lloyd et al. 2012)
Brazil	27.3º S	10 new species	(Barneche et al. 2009)
Western Japan and Korea	32.5º - 37º N	85.6% tropical species and breeding of four species in Japan, two new species in Korea	(Nakamura et al. 2013; Kim et al. 2014)
Northern Gulf of Mexico	29.5º - 30.5º N	11 new species	(Fodrie et al. 2010)
Azores Islands	38.4º N	Seven new species	(Afonso et al. 2013)
Portugal	38.25 º N	Increased tropical species	(Horta e Costa et al. 2014)

1.9 Figures

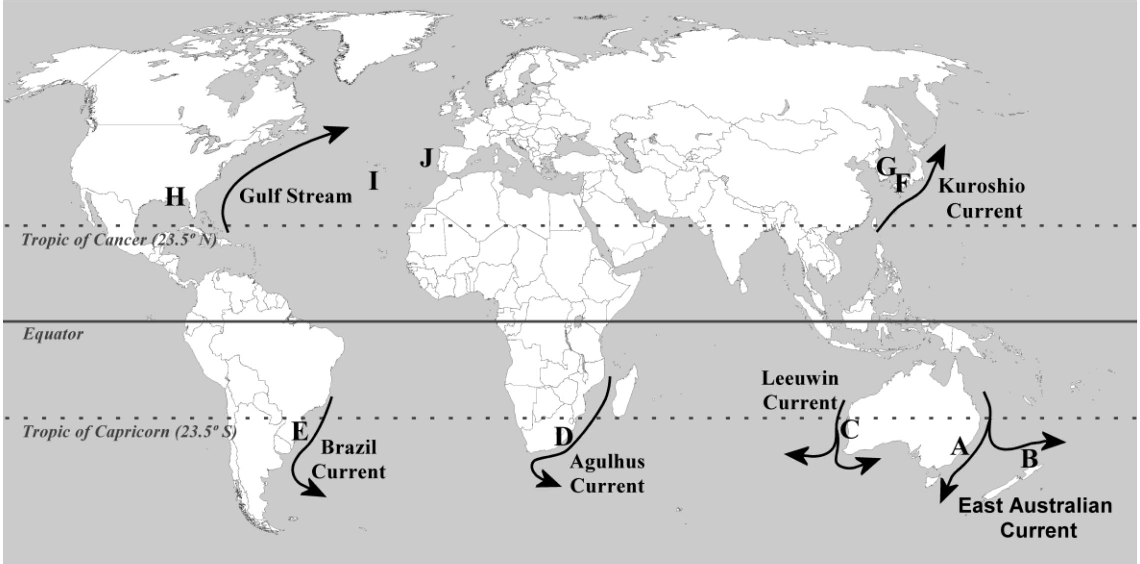

Figure 1.1 Temperate regions where poleward range expansions of tropical fishes have been detected and the associated boundary currents driving this redistribution. Letters denote where new observations and/or increased dominance of tropical fishes have been recorded by underwater census and/or fishing; southeastern Australia (A: Booth et al. 2007; Figueira and Booth 2010), northern New Zealand (B: Francis et al. 1999), Western Australia (C: Wernberg et al. 2012b; Hutchins and Pearce 1994; Hutchins 2011), southeastern Africa (D: Lloyd et al. 2012), Brazil (E: Luiz et al. 2008; Barneche et al. 2009), western Japan (F: Nakamura et al. 2013), Korea (G: Kim et al. 2014), Mexico (H: Fodrie et al. 2010) and the North Atlantic (I and J: Afonso et al. 2013; Horta e Costa et al. 2014).

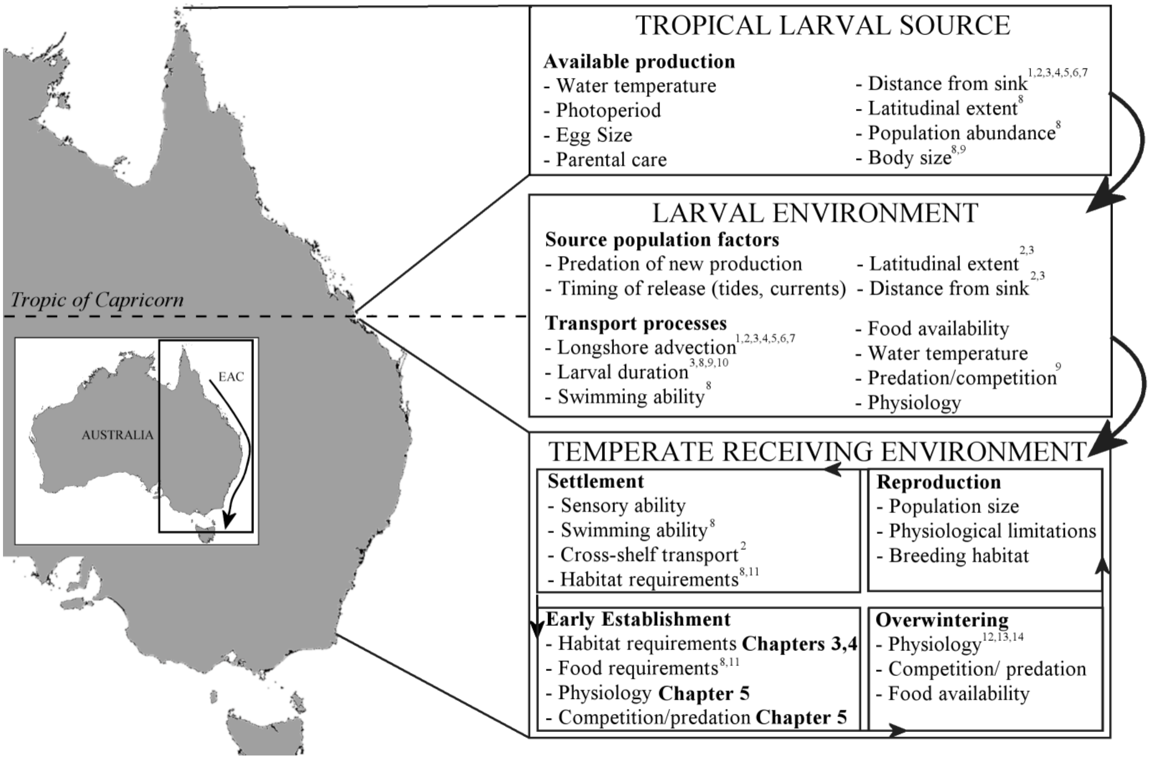

Figure 1.2 Factors potentially limiting the range expansion of tropical fishes into temperate regions, including those influencing the reproductive output from tropical larval sources, oceanic larval transport and early life success within the receiving temperate environments, using SE Australia as a geographic reference – an expanding range for many tropical fishes with intensification of the East Australian Current (EAC). Potential limiting factors were adopted from Feary et al. (2014). Previous studies that empirically explored how these factors limit tropical fish range expansions are denoted by superscripted numbers: [1]McBride and Able 1998 , [2]Booth et al. 2007, [3]Booth and Parkinson 2011, [4]Hare et al. 2002, [5]Nakazono 2002, [6]Hutchins 1991, [7]Hutchins and Pearce 1994, [8]Feary et al. 2014, [9]Luiz et al. 2013, [10]Soeparno et al. 2012, [11]Soeparno et al. 2013, [12]Figueira et al. 2009, [13]Figueira and Booth 2010. This thesis explores how habitat requirements (Chapters 3 and 4) and physiology (Chapter 5) of tropical fishes, as well as predatory/competitive interactions with native species (Chapter 5), may limit the early establishment of their populations (termed ‘recruitment’ here) at temperate latitudes.

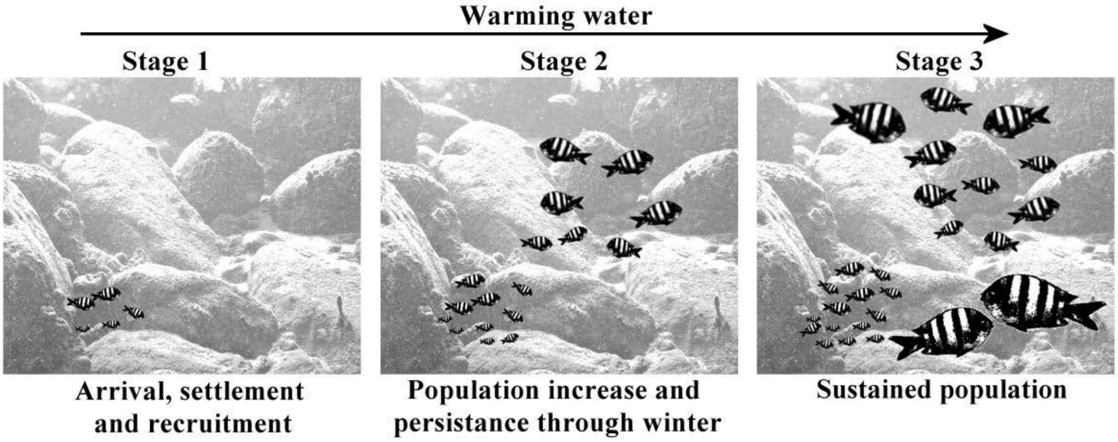

Figure 1.3 Stages of geographic range expansion of tropical fishes into temperate waters, adopted from Bates et al. (2013). The initial stage of range expansion requires the delivery of tropical fish larvae from tropical sources to temperate regions by ocean currents, where they locate, settle and recruit to suitable temperate reef habitats. But ecological limitations, such as cool water temperatures, prevent these transient populations from permanently establishing (e.g., Figueira and Booth 2010). The second stage of expansion requires survival through winter, as the frequency of thermally tolerable winters increase with ongoing climate change, typified by mixed age and size populations composed of recruits, older juveniles and sub-adults. Nevertheless, population stability still depends on input of larvae from tropical regions. Lastly, warming of temperate waters may eventually allow reproductively viable and sustained populations to establish (e.g., Nakamura et al. 2013). Hence, successful recruitment of tropical fishes in temperate regions (i.e., Stages 1 and 2; the focus of this thesis), is necessary before permanent and reproductively viable populations may establish (Stage 3; the final stages of range expansion).

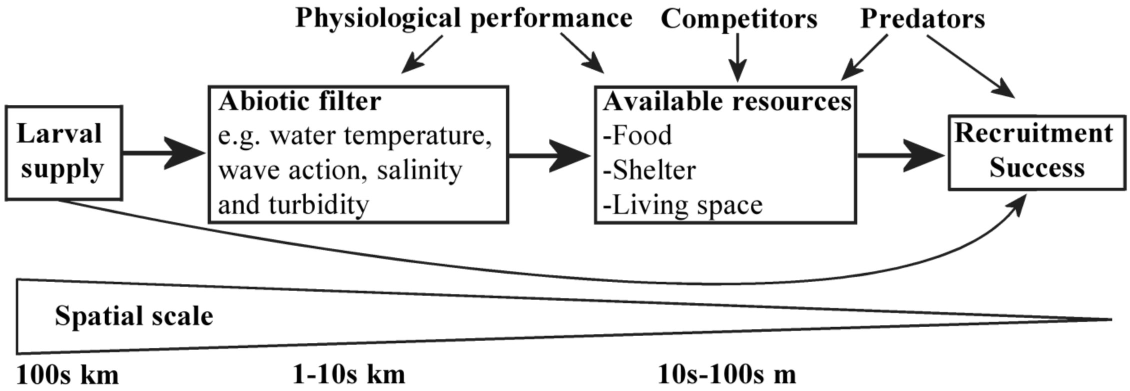

Figure 1.4 Conceptual diagram of how recruitment of marine organisms may be limited by reef habitats, such as tropical fishes on temperate reefs. With a reducing spatial extent, factors influencing recruitment include larval supply, abiotic stressors and resource availability. However, the extent that abiotic conditions influence recruitment success depends largely on the physiological performance of the species. Access to required resources may also depend on the fishes' physiological performance, as well as the strength of both competition and predation pressure. Predators may also limit survival of new recruits by consuming them. Lastly, chances of species overcoming these habitat constraints will likely increase as larval supply increases (i.e., supply-side ecology). Note that many of these factors may interact to influence recruitment success. Diagram modified from Olyarnik et al. (2009).

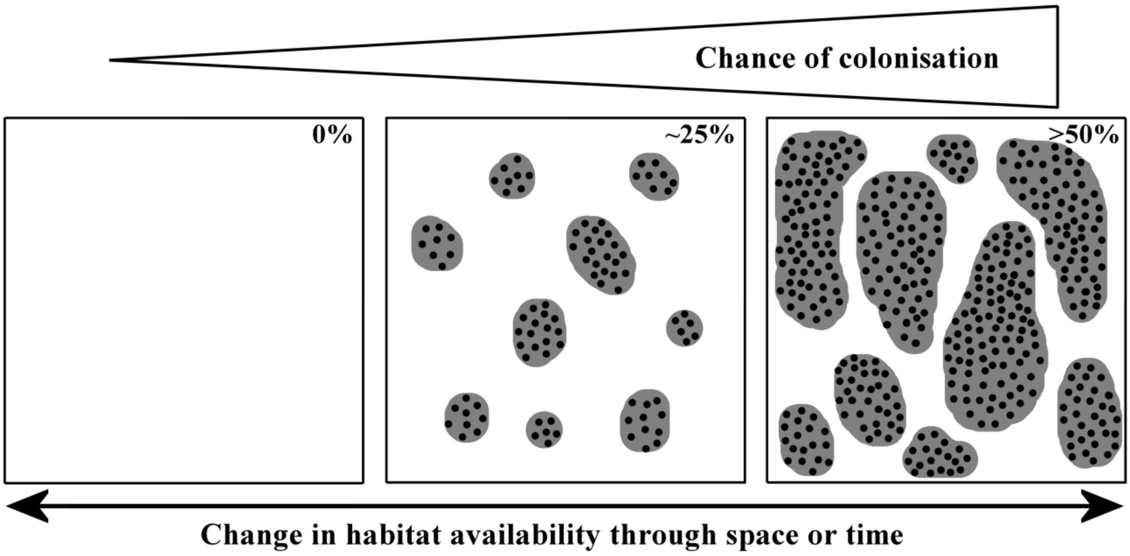

Figure 1.5 Habitat-limited recruitment of organisms within a new range. Although organisms (black dotes) are supplied as larvae to higher latitudes where environmental temperatures are thermally tolerable, they may be limited from recruiting to these new ranges where suitable habitats are not available, including where they cannot access required resources and/or survival is limited by native fauna or abiotic conditions (grey shapes denote suitable habitat availability; white areas denote unsuitable habitat). However, recruitment success may increase in a new range as the availability of suitable habitat increases through space and/or time, which may occur naturally or by human activities (termed disturbance by Olyarnik et al. 2009).

Chapter 2: Assessing range shifts of tropical reef fishes: a comparison of belt transect and roaming underwater visual census methods

Beck HJ, Feary DA, Figueira WF, Booth DJ (2014) Assessing range shifts of tropical reef fishes: a comparison of belt transect and roaming underwater visual census methods. Bulletin of Marine Science 90 (2): 705-721.

Abstract

Accurate, precise, and efficient underwater visual censuses (UVC) are vital for detecting and monitoring range shifts of reef fishes. The present study compared the utility of time-equivalent belt transects and Global Positioning System (GPS) – tracked roaming surveys for assessing populations of range expanding tropical fishes off southeastern Australia. Roaming surveys were significantly more accurate and precise than belt transects in estimating densities of focal damselfish, *Abudefduf vaigiensis*, while the accuracy and precision of density estimates did not significantly differ between methods for the rarer focal species, *Abudefduf whitleyi*. Significantly greater species richness and assemblage diversity were detected by roaming surveys than belt transects. Roaming surveys were also over twice as efficient, defined as the area searched per unit time, as belt transects; mean (SE) efficiency of roaming surveys and belt transects was 33.56 (1.22) and 12.57 (0.66) m^2 min^{-1}, respectively. Results were consistent among observers with varied experience. Reliable density estimates, improved efficiency, and maximised sightings of tropical fishes suggest GPS-tracked roaming surveys are highly suited for detecting and monitoring range shifts of reef fishes.

2.1 Introduction

Changes in ocean climate are leading to substantial poleward shifts in tropical marine fishes (Booth et al. 2007; Figueira et al. 2009; Afonso et al. 2013; Nakamura et al. 2013; Feary et al. 2014). Such poleward shifts are resulting from intensification of western boundary subtropical currents and subsequent warming of ocean temperatures (Wu et al. 2012). Changes in the strength and poleward flow of western boundary currents, which lead to range shifts in tropical fish species, are drastically modifying the function and composition of fish assemblages at temperate latitudes (Johnson et al. 2011; Last et al. 2011; Nakamura et al. 2013). To understand the ecological impacts that range shifts of marine fishes may have within new ranges, detecting and monitoring these shifts is of primary importance, particularly at range edges (Booth et al. 2011). For example, observed ecological changes resulting from distributional shifts of reef fishes off southeastern (SE) Australia has motivated the establishment of long-term monitoring programs, such as the RedMap program (http://www.redmap.org.au) and the Tropical Fish Monitoring Network (Figueira et al. 2012).

An underwater visual census (UVC) is a common tool for detecting and quantifying range shifts of tropical marine fishes (Booth et al. 2007; Booth et al. 2011; Wernberg et al. 2012b; Afonso et al. 2013; Nakamura et al. 2013; Kim et al. 2014). However, the ability of UVC to reliably measure the extent of distributional shifts of tropical reef fishes, both geographically and temporally, may differ substantially between UVC methods. Within high-latitude temperate reefs, where poleward range shifts of tropical fishes are anticipated, tropical reef fishes are usually rare (Booth et al. 2007), and have a spatially heterogeneous distribution because they typically associate with particular temperate benthic habitats (H. J. Beck, personal observation). Colonising populations of tropical fishes also usually have high site fidelity because populations are primarily composed of juveniles (Figueira and Booth 2010), which usually exercise small foraging excursions due to heightened risk of predation (Brown and Kotler 2004). Hence, mobile UVC methods, such as belt transects or roaming surveys, which have capacity to cover a range of habitats and a substantial area of reef, may be better suited to detecting and estimating population parameters of rare and site-attached range shifting tropical fishes than stationary survey techniques, such as point counts or remotely operated video (Murphy and Jenkins 2010). Detecting range shifts of tropical reef fishes also requires surveys to be conducted over large geographic areas and long time-scales, which will likely involve multiple observers with varying experience conducting UVCs, including volunteers (e.g., Last et al. 2011). Hence, to provide reliable species baseline counts and quantify changes in tropical reef fish distribution at temperate latitudes, it is imperative that the UVC method used to survey range shifting tropical fishes minimises sampling error, maximises chance of detecting these rare fishes, and is repeatable by observers with variable UVC experience (Tingley and Beissinger 2009).

Comparing two of the most commonly used mobile UVC methods, transects and roaming surveys (Murphy and Jenkins 2010), differences in efficiency and bias between these methods may make either UVC method more suitable for detecting and monitoring range shifts of tropical reef fishes. Great efficiency within roaming surveys, defined here as the area searched per unit of time (not including data processing time), may increase the likelihood of encounters with rare reef fishes, such as range shifting tropical fishes. In contrast, laying out and retrieving a transect tape when conducting belt transects increases the time spent under water relative to actual time spent surveying (i.e., lower sampling efficiency; Jones and Thompson 1978, Kimmel 1985). Laying out a transect tape prior to the survey has also been shown to disturb some reef fishes, which may reduce the capacity of transects to detect the full community of range shifting tropical fish species (Dickens et al. 2011). Nevertheless, despite the potential usefulness of roaming surveys in detecting the full community of range shifting tropical fishes, by increasing survey efficiency and reducing disturbance, the ability of this UVC method to provide accurate and precise density estimates as compared to traditional belt transects is questionable. Inherent artefacts introduced by diver search patterns and swim speeds within roaming surveys may lead to inaccurate and imprecise estimates of population densities (Kimmel 1985; Sanderson and Solonsky 1986; Lincoln Smith 1988; Ward-Paige et al. 2010). For example, densities of tropical fishes may be overestimated within roaming surveys if observers swim purposely toward fishes or preferentially survey habitat where target species are common (DeMartini and Roberts 1982). Alternatively, fish densities may be underestimated in roaming surveys if observers swim away from fishes or preferentially survey habitat where target species are uncommon.

Despite the potential for observer search patterns to add considerable bias to fish density estimates within roaming surveys, the ability of this UVC method to provide accurate and precise density estimates, as a measure of fish per unit area, as compared to traditional belt transects has not yet been tested. Previously, time-dependent roaming surveys have been used to quantify fish densities using sighting frequency of fishes (DeMartini and Roberts 1982; Schmitt et al. 2002). However, these estimates fail to account for the area searched during surveys. As such, density estimates based on sighting frequencies are likely to be highly inaccurate and imprecise when compared spatially, temporally and among observers, as density values largely depend on survey efficiency (e.g., Kimmel 1985, Schmitt et al. 2002). To control for such differences in area surveyed, the total area searched during roaming surveys needs to be measured. This may be achieved by the use of a Global Positioning System (GPS) device.

In the present study, the utility of roaming surveys, with search areas measured by GPS, was assessed for detecting and monitoring range shifts of tropical reef fishes within SE Australian waters. Presently, tropical reef fish larvae, termed “tropical vagrant fishes,” are frequently transported hundreds of kilometres southward into temperate latitudes within the East Australian Current (EAC) and recruit to the temperate, SE Australian waters during summer (Kuiter 1993; Booth et al. 2007; Figueira and Booth 2010). However, densities of tropical vagrant fishes reduce substantially approaching winter off SE Australia, which constrains establishment of permanent populations of tropical fishes in this region (Booth et al. 2007). Such declines in vagrant densities are attributed to increased risk of mortality as water temperatures reduce (Figueira et al. 2009). However, rapid warming of coastal waters near SE Australia is predicted to facilitate establishment of permanent populations of tropical fishes in the next few decades (Figueira and Booth 2010). Successful detection and monitoring of such range shifts of tropical fishes requires multiple surveyors, so that fish assemblages may be monitored over large geographical areas. Vagrant fishes are also relatively rare (Booth et al. 2007), yet accurate assessment of species densities, richness and diversity is paramount (Booth et al. 2011). Roaming surveys must therefore produce reliable density and diversity/richness estimates of rare-vagrant fishes that are consistent across multiple surveyors for this method to be useful in detecting and monitoring range shifts of tropical fishes into SE Australian waters. Here, the utility of roaming surveys and belt transects for quantifying density, species richness, and diversity of tropical vagrant fishes was examined off SE Australia. It was expected that equivalent-timed roaming surveys would detect a greater richness and diversity of tropical vagrant fishes, due to the higher levels of sampling efficiency and potential to survey a greater diversity of habitat within roaming, than belt transect methods. However, potential for great variance in search patterns among observers and replicates within the roaming survey was also expected to lower precision and accuracy of density estimates compared to belt transects.

2.2 Methods and Materials

2.2.1 Study sites and survey design

The density, species richness, and diversity of all tropical vagrant fishes encountered on rocky reef habitats were estimated using belt transect and roaming UVC methods using snorkel at east and west Shelly Beach, Australia (33°48′01″S, 151°17′52″E; Fig. 2.1). Sites were separated and bounded by sand. Benthic habitats amongst these reefs were primarily composed of either foliose Laminarian algae, such as *Ecklonia radiata* and *Phyllospora comosa*, and areas where folios algae is completely removed by sea urchin grazing and replaced by encrusting coralline algae. Comparison of UVC methods were made on two occasions during austral autumn and winter (25 May and 24 June, 2011), which encapsulated a range of density measures of tropical fishes in concordance with cooling ocean temperatures (Fig. 2.2). On both sampling occasions, three surveyors conducted five, 20 × 2 m belt transects and five, 5 min roaming UVC surveys (with a width of 2 m), at the two sites. Sixty replicates of each method were used in total. A power analysis revealed this replication was sufficient to detect a moderate effect size for all three metrics, according to convention ($\alpha = 0.5$, $f = 0.4$, Power = 0.86; G*Power$^{\text{TM}}$ v3.1.7). Distance estimates were calibrated prior to surveys by repeatedly estimating this 2-m wide search criterion and checking with a tape measure. Belt transects were conducted by fixing the start of the tape to the substrate, swimming out

20 m of tape, swimming back to the start of the tape measure then surveying all tropical vagrant fishes within transect boundaries (e.g., Brock 1954). Routes of all roaming surveys were logged at 5 sec intervals by a GPS unit (Garmin^{TM} GPS 60: accuracy 4 m), towed at a fixed-distance (3 m) behind observers, which allowed shallow dives for closer inspection of fishes. Starting points and survey direction for both methods were randomly assigned prior to surveys. To alleviate tendencies of surveyors to change their course in response to fishes or habitat during roaming surveys, surveys commenced in allocated starting directions to the edge of the plot, which was either the shore or 4 m depth contour, distinguished by geological features of the reef. Surveyors then turned 90°, kicked five times, then returned in the opposite direction. Directions of these turns were alternated between clockwise and counterclockwise to ensure no areas were resurveyed. All tropical vagrant fishes encountered were counted and identified to species. Starting and stopping times of surveys and the time fishes were observed were also recorded. Start time of each belt transect was considered as the commencement of the laying of the transect tape, while finish time for this method was when the tape was retrieved. Six observers participated throughout the present study, with experience in surveying tropical vagrant fishes ranging from 4 months to 10 years. Surveys were conducted during daylight (09:00–13:00) in 0 – 4 m depth, when water visibility was > 7 m and swell was < 1 m.

Comparison of density, diversity, and richness estimates between roaming surveys and belt transects required that the time effort exerted was equal for both UVC methods. To ensure time effort was exerted for both UVC methods equally, all fishes recorded and areas searched during roaming surveys beyond the average time spent completing belt transects were discarded from density and diversity calculations. Average time spent completing belt transects was calculated as the total time spent conducting all belt transects in the present study, across all observers, divided by 60 (total number of transects).

2.2.2 Comparison of density estimates

Control for behavioural response of fishes to surveyors

To compare the precision and accuracy of roaming surveys and transects for estimating densities of vagrant fishes, using multiple surveyors in the same area, it was important to consider the potential effect of repeated exposure of fish to surveyors on fish counts. To ensure observers actions and presence did not influence comparisons of density estimates, a pilot study was conducted, in which the need for minimal sample sizes restricted us to considering two focal species, sergeant major, *Abudefduf vaigiensis*, and whitley's sergeant, *Abudefduf whitleyi* (Table 2.1). Both species are relatively common tropical damselfishes at these sites (Booth et al. 2007).

To control for any behavioural response of *A. vaigiensis* and *A. whitleyi* to repeated visual surveys, video trials were conducted to measure the response of both fishes to exposure and re-exposure to an observer. Eight schools of *A. vaigiensis* [20–100 mm total lengths (TL)] and five schools of *A. whitleyi* (20–60 mm TL) were analysed (Table 2.2, Fig. 2.3). Schools were composed of 6–8 individuals, corresponding to the average size of schools throughout the sites surveyed. Responses of individual fish to diver absence and presence were recorded by high-definition video (GoPro™; with 170° field of view), after placing camera by hand approximately 1 m from schools. Fishes were recorded: (1) for 5 min in absence of an observer, followed by (2) 5 min with an observer displaying typical actions used during UVC surveys (i.e., repeatedly free-diving about 2 m from the school). Response to (1) diver absence, and (2) diver presence were repeated for each school, separated by a 15 min break, to detect behavioural responses of fishes to repetitive surveys.

Five min sections of video containing these pre-exposure, post-exposure, or re-exposure treatments were divided into ten 30 sec interval sections. Maximum numbers of *A. vaigiensis* and *A. whitleyi* observed within video frames during the first 10 sec of each 30 sec section were then recorded (following Dearden et al. 2010). Maximum numbers of individuals per frame were compared among diver absence and presence treatments within each school, using repeated measure one-way analysis of variance (ANOVA).

Total population densities

Total population densities of the two focal species, *A. vaigiensis* and *A. whitleyi*, were estimated to allow calculation of accuracy of density estimates by roaming and transect UVC methods. Total population densities of these species were estimated immediately following the two sampling occasions (25 May and 24 June, 2011) by exhaustive searches of both sites using a slow [mean (SE) = 18.95 (4.23) m^2 min^{-1}] zig-zag search pattern (areas of sites were measured by GPS). By searching the entire survey sites systematically, these thorough searches achieved the best possible estimates of total population densities, without resorting to destructive sampling methods (e.g., McCormick and Choat 1987). These searches were conducted by the principal author (HJB).

Precision and accuracy of density estimates

Accuracy in density estimates of *A. vaigiensis* and *A. whitleyi* within roaming and transect UVC methods were calculated as the difference between the estimated density from the replicate sample and total density estimates (see above) for each species separately. Sample precision for a group of surveys conducted by a single observer (*P*) was estimated by the coefficient of variation for these samples and was calculated as:

$$P = \frac{(\frac{s}{\sqrt{n}})}{\bar{X}},$$

where $\bar{X}$ and s are the mean and standard deviation of estimates from all surveys by the observer and n is the number of surveys by the observer (Southward 1966; McCormick and Choat 1987). Precision was calculated for each species separately for all observers in the study.

Sampling accuracy was then compared among UVC methods (fixed), sites (fixed), days (fixed), and observers (random), as well as among all possible interactions of these factors, by ANOVA with individual surveys as the unit of replication. Sampling precision was compared among UVC methods, sites, and days, as well as among all possible interactions of these factors, by ANOVA with individual observers as the unit of replication (as clarified above). Days were treated as fixed factors because sampling days and locations were chosen to test survey methods against changes in density and diversity (i.e., reductions in both population parameters in response to water temperature decline; Fig. 2.2). Sites were treated as fixed factors, because the diversity and density of vagrant fishes differed between sites prior to study commencement (Booth, D. J., unpublished data). Two-tailed Z-tests were used to test the probability that roaming and transect UVCs over- or underestimated total population densities, within both sites and on both days (n = 15 replicate surveys per method for each site/day).

2.2.3 Diversity and richness

Measurements of richness and diversity of the whole vagrant fish community were also compared between the two UVC methods. Species abundance data were square root transformed prior to analysis to reduce the influence of highly abundant species (Clarke et al. 2006). *K*-dominance plots (i.e., species diversity) were created for each UVC method (Warwick 1986). These plots were constructed individually for each replicate survey by cumulative ranking of species, expressed as a percentage of all species, in decreasing order of their abundance. Pairwise distances between values in *K*-dominance plots were calculated using DOMDIS (PRIMER^{TM} v6 with PERMANOVA+ extension) (Warwick 1986; Clarke 1990; Clarke and Gorley 2006). The dissimilarity matrix, generated by Manhattan metrics, was then used to test for differences in *K*-dominance plots amongst UVC methods (fixed), observers (random), sites (fixed), and days (fixed) using permutational multivariate analysis of variance (PERMANOVA; Type III Sums of Squares; 9999 permutations under the reduced model) (Anderson 2001). This approach to diversity measurement better represents richness and evenness of fish assemblages than a single index (Clarke and Gorley 2006). Total numbers of species (i.e., species richness) encountered were also compared among methods, observers, sites, and days using ANOVA.

2.2.4 Efficiency of roaming and transect methods

Survey efficiency was calculated as the area searched per unit time. Differences in survey efficiency were compared between UVC methods in the same way as accuracy of density estimates (see above). All univariate analyses in the present study were conducted using SPSS^{TM} v19. Where the p-value of a factor was > 0.25, it was removed from the model by pooling this factor with the residual (following Underwood 1997). *A priori*, $p < 0.05$ was the set level of significance for all analyses.

2.3 Results

2.3.1 Comparison of density estimates

Control for behavioural response of fishes to surveyors

The maximum number of fish per frame did not vary significantly among diver pre-exposure, post-exposure, or re-exposure treatments for seven of eight video trials for *A. vaigiensis* and all five trials for *A. whitleyi* (Table 2.2, Fig. 2.3). No effect of diver exposure on fish behaviour was detected in a significant proportion of video trials (one-sided binomial test: *A. vaigiensis*, $p > 0.05$; *A. whitleyi*, $p > 0.05$).

Total population densities

Total density estimates of the two focal species, *A. vaigiensis* and *A. whitleyi*, as determined from exhaustive searches of sites, on both days combined, were 28.7 – 53.4 and 9.5 – 12.4 fish per 1000 m^2 for *A. vaigiensis* and *A. whitleyi*, respectively (Table 2.3).

Precision and accuracy of density estimates

Accuracy of density estimates within both UVC methods did not differ among observers for *A. vaigiensis* (ANOVA: $F_{2,\,114} = 1.923$, $p > 0.05$) or *A. whitleyi* ($F_{2,\,114} = 3.573$, $p > 0.05$), therefore all subsequent analyses used pooled observer data (Underwood 1997). Accuracy of density estimates was greater for roaming surveys than belt transects for *A. vaigiensis* ($F_{1,\,112} = 8.320$, $p < 0.05$), but there was no difference in accuracy between methods for *A. whitleyi* ($F_{1,\,112} = 2.548$, $p > 0.05$) (Fig. 2.4). Accuracy in density estimates did not differ among days or sites for either focal species, nor were any interactions significant ($p > 0.05$ for these terms). Neither roaming nor transects over-estimated densities. Roaming and transect UVCs only underestimated densities (U; Z-test: $p < 0.05$) or there was no difference between estimated and total population density (E; Z-test: $p > 0.05$) (*A. vaigiensis*: U = 1, E = 3; U = 1, E = 3; *A. whitleyi*: E = 4; E = 4; for roaming and transect UVCs, respectively).

There was significantly greater precision in density estimates of *A. vaigiensis* within roaming surveys than belt transects ($F_{1,\,16} = 6.649$, $p < 0.05$; Fig. 2.5). However, there was no significant difference in precision of density estimates between days or sites, while all interactions were non-significant ($p > 0.05$ for these terms). No *A. whitleyi* were detected by four observers during all five replicate transects at both sites combined and thus estimates of precision for these could not be calculated. Based on the remaining surveys, precision of density estimates for *A. whitleyi* was not significantly different between methods ($F_{1,\,10} = 0.598$, $p > 0.05$; Fig. 2.5). All other factors and interactions were not significant ($p > 0.05$ for these terms).

2.3.2 Diversity and richness

Thirteen species of tropical vagrant fishes within four families (Pomacentridae, Acanthuridae, Chaetodontidae, and Labridae) were detected in the present study (Table 2.1). Pomacentridae was the most frequent family observed, followed by Acanthuridae, Chaetodontidae, and Labridae. Roaming surveys detected all 13 species, five of which were only detected using this method. No species were uniquely found within belt transects. Species diversity (*K*-dominance: Psuedo-$F_{3,\,116} = 0.926$, $p > 0.05$) and total species counts ($F_{3,\,126} = 1.073$, $p > 0.05$) did not differ significantly among observers, allowing pooling of observer data prior to further analyses. Estimates of species diversity (i.e., *K*-dominance plots) were significantly greater for roaming surveys than transects (Psuedo-$F_{1,\,112} = 64.29$, $p < 0.001$), but there were no significant differences in diversity between sites or days, nor were interactions among these factors significant ($p > 0.05$ for these terms). Roaming surveys also detected significantly greater species richness (i.e., total species count) than belt transects [$F_{1,\,112} = 45.73$, $p < 0.001$; mean (SE) species richness detected by roaming surveys and belt transects was 1.67 (0.13) and 0.5 (0.12) species per time-equivalent replicate, respectively]. There were no significant differences in species richness among sites or days, nor were interactions between factors significant ($p > 0.05$ for these terms).

2.3.3 Efficiency of roaming and transect methods

Roaming surveys were significantly more efficient than transects on both days (Day 1: $t_{58} = 11.42$, $p < 0.001$; Day 2: $t_{58} = 14.33$, $p < 0.001$). Roaming surveys were over twice as efficient as transects; mean (SE) efficiency of roaming surveys and transects was 33.56 (1.22) and 12.57 (0.66) $m^2\ min^{-1}$, respectively (Fig. 2.6). Survey efficiency did not vary significantly among observers ($F_{2,\,117} = 0.108$, $p > 0.05$), allowing observer data to be pooled. Further analysis revealed that there was a significant interaction between method and days ($F_{1,\,112} = 2.32$, $p < 0.05$), but no difference in efficiency between sites ($F_{1,\,112} = 1.21$, $p > 0.05$). Roaming surveys were significantly more efficient on Day 2 than Day 1 ($t_{58} = -3.623$, $p < 0.001$), but the efficiency of belt transect surveys did not differ between days ($t_{58} = -0.792$, $p > 0.05$).

2.4 Discussion

At the leading edge of an expanding range, individuals are typically rare and have a spatially heterogeneous distribution. Hence, to detect and monitor changes in densities of tropical fishes shifting into a new range, a mobile UVC method is required that maximises detections, while reliably estimates densities of these fishes. In the present study, GPS-tracked roaming surveys achieved greater accuracy and precision in density estimates than belt transects for *A. vaigiensis*, while both methods had similar accuracy and precision in density estimates for *A. whitleyi*. Therefore, GPS-tracked roaming surveys should allow reliable surveys of reef fish densities within new ranges, at least for conspicuous fishes not influenced by divers. Where fishes are strongly diver negative, this may not be the case. Consistency in density estimates of *A. vaigiensis* and *A. whitleyi* across multiple observers also suggested that roaming surveys may be suitable for use in long-term monitoring of shifting marine populations, where multiple observers are commonly required to sample large geographic areas. However, it must be noted that all surveyors had at least 4 months experience in the present study. Therefore, provided observers have been trained in species identification and UVC skills, reliably precise and accurate density estimates of relatively rare tropical fish species may be achieved by utilising GPS-tracked roaming surveys.

Underestimation of focal species densities or lack of difference between estimated and total population densities within roaming surveys suggests that the potential error in density estimates, associated with observers purposely moving toward fishes, was not apparent in the present study. Underestimation of vagrant densities contradicted concerns (e.g., DeMartini and Roberts 1982) that rapid visual survey techniques, such as roaming surveys, risk overestimation of rarer components of fish communities. Nevertheless, studies that attempted to test the utility of roaming UVC either failed to account for the area searched and potential differences in swim speed among observers, did not standardise time spent on different UVC methods, or utilised UVC methods on fishes within their breeding range, where densities are typically higher than within a new range (Jones and Thompson 1978; DeMartini and Roberts 1982; Kimmel 1985; Sanderson and Solonsky 1986; Schmitt et al. 2002).

Within the present study, overestimation of focal fishes' densities within roaming surveys was potentially avoided by measuring areas surveyed using GPS and randomising starting points and swim directions. By randomising surveys, the tendency for surveyors to swim purposely toward focal species, resulting in overestimation of density estimates, were likely reduced. Although various sources of bias may have caused underestimation of fish densities during UVC, underestimation during roaming surveys was likely caused by observers simply failing to encounter focal fishes.

Underestimation of fish densities in UVCs has been previously attributed to failure of surveyors to observe or identify fishes, either due to swim speeds (Lincoln Smith 1988), classification errors (Thompson and Mapstone 1997; Williams et al. 2006), crypsis (Brock 1982; Willis 2001), or mobility of target species (Ward-Paige et al. 2010). However, it was unlikely observers misidentified or missed counting *A. vaigiensis* and *A. whitleyi* during surveys within the present study, since both focal species are non-cryptic and site attached. There were also no significant sheltering or flight responses of these species to diver presence or actions detected during video trials in the present study. Although small-scale behavioural responses of fishes to divers may not have been detected on videos, even small responses, such as slight movement away from observers, were uncommon (H. J. Beck, personal observation) and so likely had little influence on density estimates. Observers also had experience in conducting UVCs of vagrant fishes, so misidentification was unlikely. Other environmental factors that potentially influence UVCs, such as water visibility and swell, were also consistent across sampling days. Underestimation of densities was therefore likely to have resulted from surveyors simply failing to encounter either species during surveys, due to species rarity within the sites. Therefore, randomisation of starting points and directions of surveys, as in the present study, appears to be important in reducing risk of overestimating densities of fishes within new ranges by reducing tendencies of observers to swim toward fishes.

There was a significantly greater total species count and more diverse community surveyed within the GPS-tracked roaming, than the belt transect survey method. In addition, roaming surveys encountered five more species than the belt transect method. Therefore, GPS-tracked roaming surveys may have a greater capacity for accurately surveying the diversity of fish communities comprising relatively rare species, including those that have recently colonised new ranges. Such detection of greater diversity and richness of fishes in roaming, vs belt transect UVCs, was similar to comparisons of other roaming methods with transects (Kimmel 1985; Schmitt et al. 2002; Baron et al. 2004; Holt et al. 2013). However, those previous studies failed to account for the area surveyed. After considering the area searched in our study by tracking roaming surveys using GPS, it appeared that differences in the richness and diversity of tropical vagrant fishes between transect and roaming UVC was likely caused by differences in efficiency (i.e., area searched per unit time) between UVC methods. In the present study, roaming surveys encompassed more than twice as much area than belt transect method over a given time period, thereby increasing the chances of encountering a greater abundance, and hence diversity, of tropical vagrant fishes (Yoccoz et al. 2001).

Greater species diversity and richness within roaming surveys than belt transects may have also been due to fishes being counted upon first contact within roaming surveys. Methods of UVC that document fishes on “first contact,” such as roaming surveys, are likely to be suited to accurately quantify fishes that either positively or negatively respond to a divers’ presence (Dickens et al. 2011). In contrast, any UVC method that does not use “first contact,” such as some belt transect methods, potentially lead to underrepresentation of fishes that flee or hide in response to surveyors disturbance (i.e., while laying a transect tape; Fowler 1987, Sale 1997, Dickens et al. 2011). For example, surgeonfishes (Acanthuridae) exhibit flight responses to divers conducting surveys (Dearden et al. 2010), suggesting instantaneous survey techniques, such as roaming surveys, are a more appropriate UVC method for quantifying this tropical reef fish family. Therefore, methods that record fish when first encountered, such as GPS-tracked surveys, minimise the potential for disturbance to fishes, making them suitable for monitoring range shifts of species that exhibit behavioural responses to surveyors.

UVC methods not used in the present study may affect the reliability of population parameter estimates of range shifting tropical reef fishes. Different search widths than those utilised here may be used for either transects or roaming surveys. Sampling times may also be modified for roaming surveys. However, here we ensured the performance of transects and roaming surveys were directly comparable because sampling time effort was equal between methods, while the same search widths were used for both methods to remove any influence of error associated with estimating distances under water (e.g., Harvey et al. 2004). Moreover, transects may be measured out while counting fishes, thereby reducing the disturbance to fishes (e.g., Bennett et al. 2009). However, we opted to fix the transect measure prior to counting fishes because complex reef structures and water movement on SE Australian coastal reefs increased risk of surveyors becoming tangled by the transect tape when not rapidly fastened to the reef. Nevertheless, we must note that the efficiency and safety of transects may be improved through using an additional observer to measure out the tape while the survey is conducted, or using scuba. UVC methods used here may also perform differently in conditions that differ from the present study, such as when wave action is greater or reef complexity and depth are different. Hence, further work is required to optimise either method for estimating the diversity and density of tropical fishes within a new range by using the UVC methods across a greater range of habitats and conditions, varying search times and dimensions, rolling out the tape while counting within transects, using scuba, as well as for surveying species with distributions and behaviours that differ from those in the present study.

In summary, the rarity and heterogeneous dispersion of tropical reef fishes at range edges present a challenge to monitoring range shifts of these fishes. Monitoring success largely depends on the accuracy and precision of UVC methods in detecting colonisation of tropical species within new ranges, then monitoring changes in densities of these species once colonised. GPS-tracked roaming surveys appear to be a reliable technique for monitoring tropical reef fish range shifts because density estimates of two focal vagrant fishes had at least comparable accuracy and precision to transects. Greater efficiency of the roaming method produced greater species diversity and richness estimates than transects, suggesting roaming surveys will be useful in detecting relatively rare fishes at the vanguard of range expansion. Moreover, capacity to count fishes on first contact using the roaming method suggests that roaming surveys are suited to monitoring range shifts of species that flee or hide in response to surveyors' presence and actions. GPS-tracked roaming surveys may be also useful for surveying any rare reef fishes, not only tropical fishes at their range edge. Reliable accuracy and precision, improved efficiency, as well as the ability to instantaneously count fish using roaming surveys suggests that this method will be suitable for assessing range shifts of tropical reef fishes in response to climate change.

2.5 Tables

Table 2.1 List of tropical fishes detected by roaming (GPS) and belt transect surveys at Shelly Beach, Australia. Frequencies of sightings of species are provided for both methods as a proportion of the total replicates conducted during the study (n = 60 time-equivalent replicate surveys for each method).

	Roaming (GPS)	**Belt transects**
F. Acanthuridae		
Acanthurus dussumieri	7.7%	4.6%
Acanthurus olivaceus	9.3%	3.0%
Acanthurus triostegus	6.2%	-
F. Chaetodontidae		
Heniochus acuminatus	1.5%	-
Chaetodon auriga	6.2%	4.6%
F. Labridae		
Thalassoma lunare	1.5%	-
F. Pomacentridae		
Abudefduf bengalensis	10.8%	6.2%
Abudefduf sexfasciatus	1.5%	-
Abudefduf vaigiensis	78.5%	21.5%
Abudefduf whitleyi	38.5%	23.1%
Pomacentrus australis	3.0%	-
Pomacentrus coelestis	3.0%	3.0%
Stegastes gascoynei	3.0%	1.5%

Table 2.2 Repeated measure ANOVAs testing for differences in maximum numbers of *Abudefduf vaigiensis* and *Abudefduf whitleyi* observed in video replicates with diver absence (pre exposure and pre re-exposure) and presence (exposure and re-exposure), with numbers of individuals observed prior to test (n) and total lengths (TL). Mauchly's Tests of Sphericity indicated data were spherical.

Source	**n**	**TL (mm)**	**d.f.**	**MS**	***F***	***p***
A. vaigiensis						
Trial 1 (20/04/11)	7	20-30	3	1.67	1.41	> 0.05
Trial 2 (20/04/11)	16	20-30	3	5.09	2.41	> 0.05
Trial 3 (20/04/11)	6	20-30	3	1.03	0.97	> 0.05
Trial 4 (20/04/11)	5	20-30	3	32.23	28.11	< 0.001
Trial 4 (01/07/11)	6	60-100	3	1.70	1.35	> 0.05
Trial 5 (01/07/11)	6	60-100	3	5.37	1.35	> 0.05
Trial 6 (01/07/11)	3	40-50	3	1.32	1.83	> 0.05
Trial 7 (01/07/11)	5	50-60	3	0.79	0.84	> 0.05
Trial 8 (01/07/11)	3	50-60	3	2.30	4.16	> 0.05
A. whitleyi						
Trial 1 (20/04/11)	3	20-30	3	0.03	0.60	> 0.05
Trial 2 (20/04/11)	2	20-30	3	0.07	0.47	> 0.05
Trial 3 (01/07/11)	4	60-70	3	0.23	0.30	> 0.05
Trial 4 (01/07/11)	3	50-60	3	0.03	0.04	> 0.05
Trial 5 (01/07/11)	2	50-60	3	0.16	0.31	> 0.05

Table 2.3 Total population densities of *Abudefduf vaigiensis* and *Abudefduf whitleyi* at Shelly Beach East (SBE) and West (SBW), as determined by thorough searches.

Date	**Site**	***A. vaigiensis***	***A. whitleyi***
25/5/11	SBE	34.4	12.4
25/5/11	SBW	39.2	11.1
24/6/11	SBE	53.4	9.5
24/6/11	SBW	28.7	10

2.6 Figures

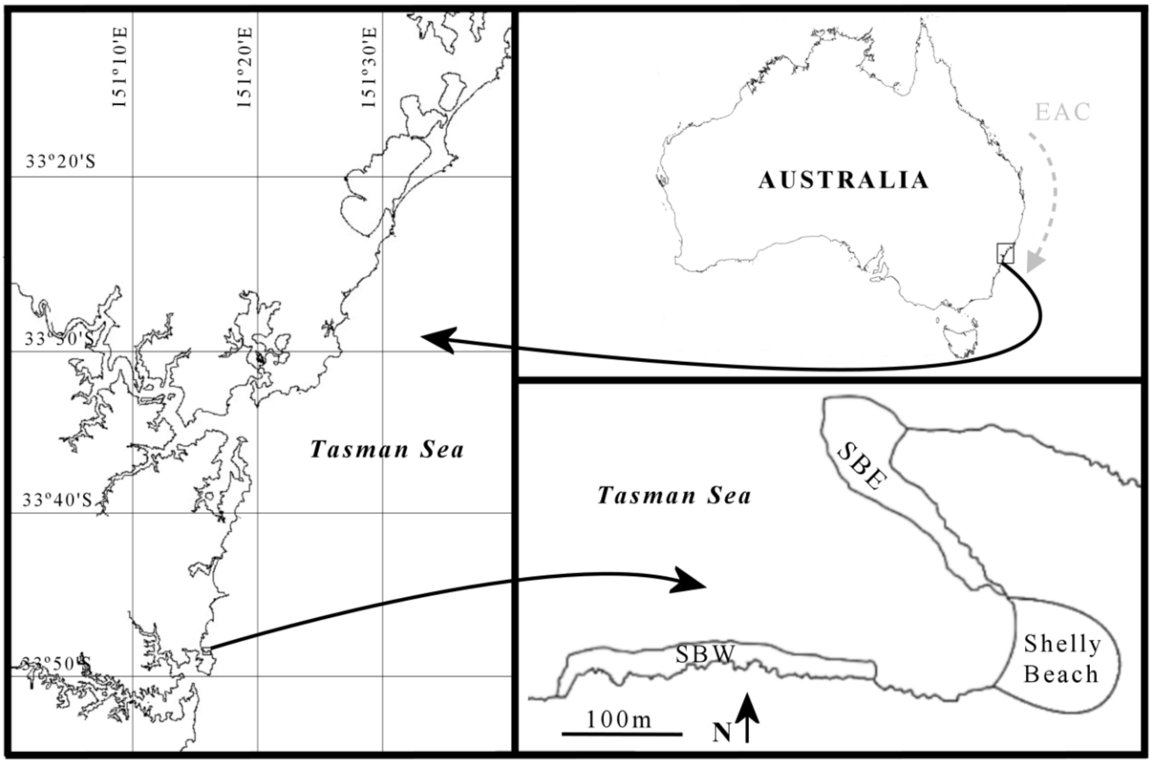

Figure 2.1 Location of east (SBE) and west Shelly (SBW) Beach within southeastern (SE) Australia. The East Australian Current (EAC; dashed grey line) annually supplies tropical fish larvae to SE Australian waters from tropical source populations. Sites were separated by sand.

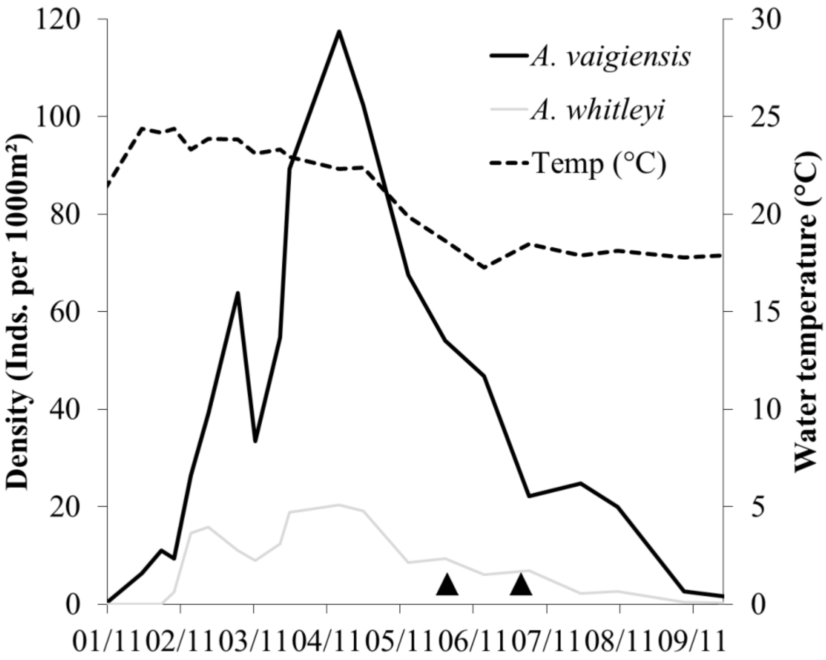

Figure 2.2 Density of *Abudefduf vaigiensis* (black line/axis 1) and *Abudefduf whitleyi* (grey line/axis 1) and mean daily water temperature (dashed line/axis 2) at Shelly Beach, Sydney. Arrows denote occasions when roaming and transect UVC methods were utilised. Fish densities were determined monthly by exhaustive searches of study areas using a slow, zig-zag search pattern as part of the Tropical Fish Monitoring Network (Figueira et al. 2012). Water temperature data were collected by HOBO^{TM} loggers recording at 30 min intervals.

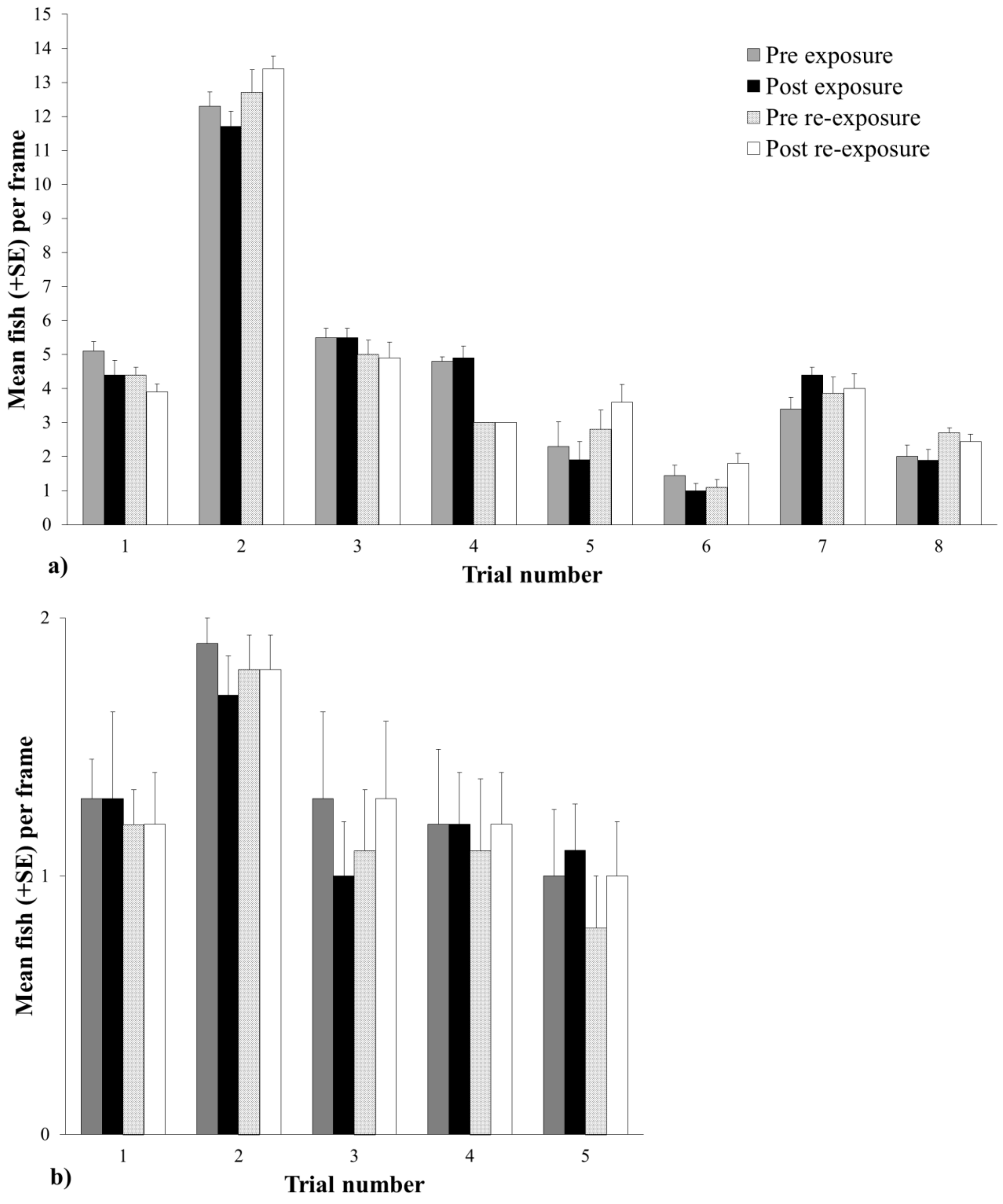

Figure 2.3 Mean (+SE) maximum number of a) *Abudefduf vaigiensis* and b) *Abudefduf whitleyi* per frame during diver absence (pre exposure and pre re-exposure) and presence (exposure and re-exposure). Responses to observers were tested using video analysis for *A. vaigiensis* and *A. whitleyi* on eight and five occasions, respectively.

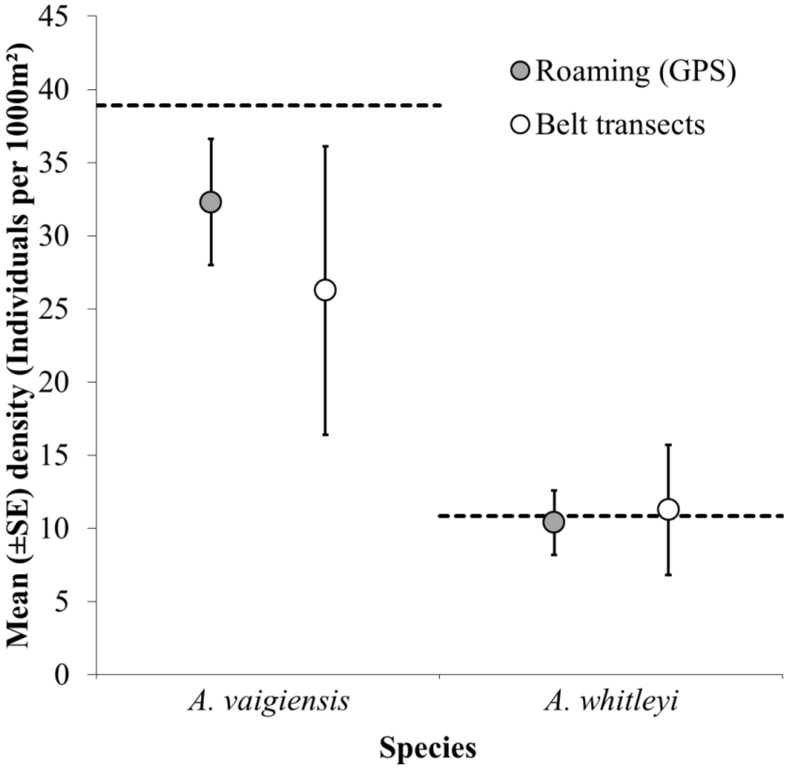

Figure 2.4 Mean (±SE) accuracy of time-equivalent density estimates for *Abudefduf vaigiensis* and *Abudefduf whitleyi* using belt transect (white marker) and roaming survey (grey marker) UVC methods at Shelly Beach (sites, observers, and days pooled). Dashed line represents total population densities, as determined by thorough site searches.

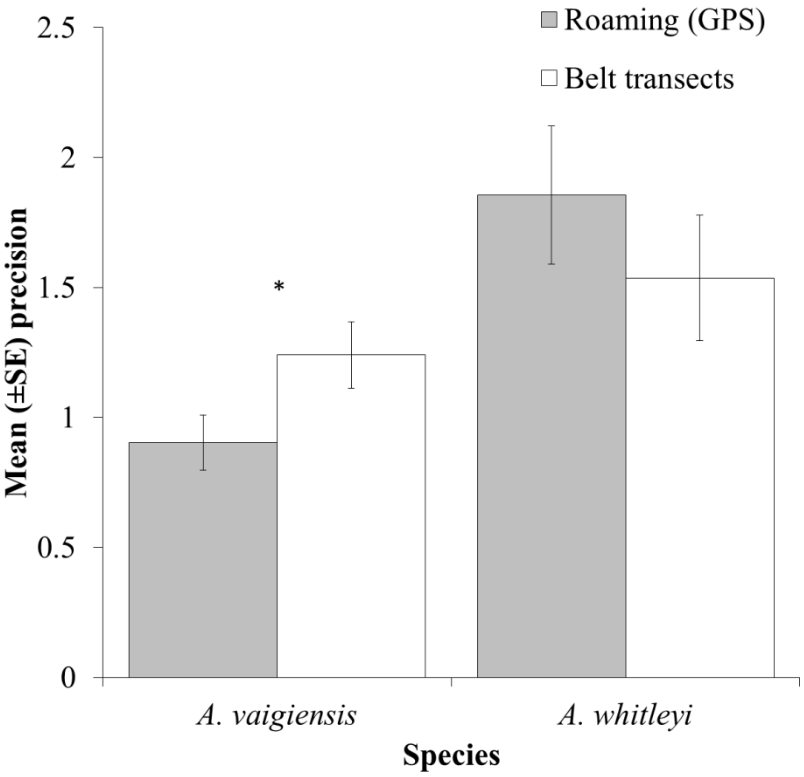

Figure 2.5 Mean (±SE) precision of time-equivalent density estimates for *Abudefduf vaigiensis* and *Abudefduf whitleyi* using belt transect (white bar) and roaming survey (grey bar) UVC methods at Shelly Beach (sites, observers, and days pooled). Note: precision of density estimates increase approaching zero. * indicates significant difference between methods: $p < 0.05$.

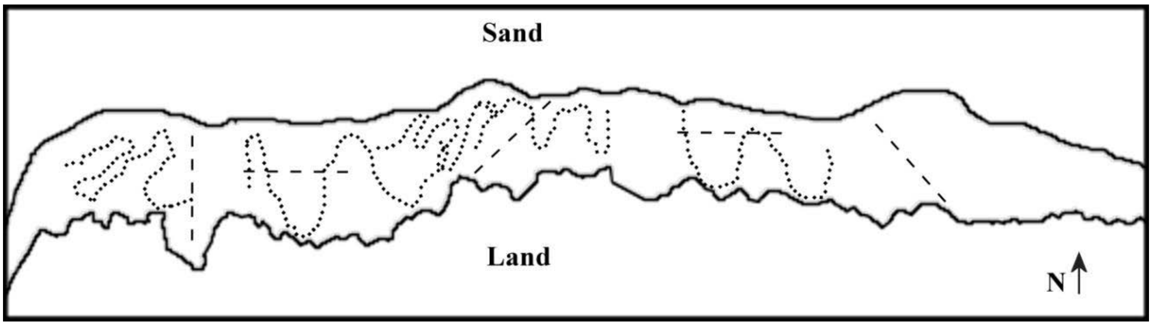

Figure 2.6 Survey paths of an observer within the Shelly Beach west site boundaries (black line), using five roaming surveys (dotted lines) and belt transect (dashed lines). At each site, each observer completed five roaming surveys and belt transects. Note: transects were 20 m long.

Chapter 3: Wave regime of temperate reefs influences recruitment and poleward expansion of tropical fishes

Beck HJ, Feary DA, Nakamura Y, Booth DJ (*Submitted*) Wave regime of temperate reefs influences recruitment and poleward expansion of tropical fishes. Oecologia.

Abstract

Poleward range shifts of species, facilitated by global warming, will be compromised if suitable habitats are not available at higher latitudes. For tropical reef fishes, reef structure may mediate range expansion into temperate regions, however an understanding of the key habitat requirements for colonisation is currently lacking. Here we show that wave exposure in temperate regions reliably predicted density and species richness of newly-recruited tropical reef fishes in two regions undergoing rapid ocean warming, southeastern (SE) Australia and western (W) Japan. Specifically, embayed temperate reefs (with low wave action) supported more tropical fishes with higher taxonomic and functional diversity than exposed reefs. Fish species included trophic generalists (e.g., planktivores and herbivores) and specialists (corallivores). Difference in wave exposure between temperate reefs was a stronger predictor of the density and richness of recruit fish assemblages than water temperature, latitude, and a suite of other habitat predictors. Only 14% of SE Australian and 21% of W Japanese nearshore reefs may provide suitable sheltered habitat, highlighting the importance of considering wave exposure of reefs when predicting the geographic response of many tropical fishes to climate change.

3.1 Introduction

Anthropogenic warming of terrestrial and aquatic environments threatens the existence of species globally (Parmesan and Yohe 2003). If species fail to acclimate or adapt to rising environmental temperatures (Bradshaw and Holzapfel 2006; Munday et al. 2013), they may shift elevation (altitude/depth; Dulvy et al. 2008; Lenoir et al. 2008) or poleward to more suitable climates to avoid extinction (Walther et al. 2002; Parmesan and Yohe 2003; Parmesan et al. 2005; Parmesan 2006; Sorte 2013). Hence, accurate predictions of where and when species may colonise are required to guide species conservation, as well as the management of adverse impacts to receiving ecosystems that result from this redistribution (Gilman et al. 2010). However, many factors controlling the geographical response of species to climate change are poorly understood, so that species' range expansions are still difficult to accurately predict (HilleRisLambers et al. 2013). There is mounting evidence that propagule pressure and the physiological tolerance of species to environmental temperatures may organise species redistribution (Parmesan and Yohe 2003; Parmesan 2006; Pinsky et al. 2013; Sorte 2013; Burrows et al. 2014). However, the availability of suitable habitat, encapsulating the full suite of biological and physical factors required to support survival of a species, including all life stages, may ultimately determine if species can redistribute poleward with shifting isotherms (Opdam and Wascher 2004; Bennie et al. 2013). For instance, early life (post-recruitment) success of a species within a new range may be highly influenced by spatial heterogeneity in abiotic stressors (Helmuth et al. 2006; Lenoir et al. 2010), resource availability (Hill et al. 2001; Warren et al. 2001; Schweiger et al. 2008) and/or interactions with resident fauna (Davis et al. 1998a; Ling and Johnson 2012; Bates et al. 2013; HilleRisLambers et al. 2013).

For tropical marine organisms expanding into temperate latitudes, the abiotic and biotic environment structuring habitats within destination latitudes may largely constrain colonisation (Cheung et al. 2010; Sommer et al. 2014). Many tropical reef fishes are expected to shift their range in response to increased poleward supply of tropical and subtropical water to temperate regions, associated with strengthening of poleward flowing boundary currents in Australia (Booth et al. 2007; Figueira and Booth 2010; Wernberg et al. 2012b; Feary et al. 2014; Vergés et al. 2014). However, despite strong evidence that many tropical fishes could physiologically tolerate temperate waters (Eme and Bennett 2008; Figueira et al. 2009), and that larval supply could be sufficient to support colonisation of a range of species at higher latitudes (Figueira and Booth 2010), many temperate reef habitats may not support the successful settlement and recruitment of tropical fishes (Feary et al. 2014). For example, the absence of coral habitats within temperate reefs (Nakamura et al. 2013; Soeparno et al. 2013; Feary et al. 2014) may strongly limit recruitment of obligate coral-feeding fishes (i.e., corallivores, hereafter termed 'habitat specialists'), which depend on live corymbose corals for food and shelter (Syms and Jones 2000; Feary et al. 2007b). In contrast, the absence of coral resources may not restrict recruitment of trophic generalists, such as those that graze on algae, or prey upon benthic invertebrates and/or fishes in temperate reefs (Nakamura et al. 2013; Feary et al. 2014). However, even for these generalists, heterogeneity in reef structure arising from macroalgal cover may organise recruitment success, at least on fine-spatial scales, as hypothesised by Feary et al. (2014).

Within coastal reef systems, differences in the strength of wave action structures the diversity and composition of marine communities by predominantly interacting with an organisms' physiological tolerance and body morphology (Underwood 1975; McQuaid and Branch 1985; Friedlander et al. 2003; Fulton and Bellwood 2004). Despite this understanding, however, the importance of wave exposure in structuring recruitment success of tropical reef fishes within temperate reefs remains uninvestigated. Within regions prone to high wave energy such as in Hawaii and southeastern (SE) Australia, the diversity and abundance of reef fishes are typically greater in wave-sheltered than exposed reef aspects, at least in shallow waters, where wave action is strongest (Friedlander et al. 2003; Fulton and Bellwood 2004). Wave action may also influence recruitment of tropical fishes indirectly by determining habitat distribution and composition (Floeter et al. 2007; Santin and Willis 2007). For instance, wave action shapes the structure and composition of habitat forming benthic organisms, including corymbose corals and macroalgae, which strongly influences the distribution of many reef fishes (Feary et al. 2007a; Jones 1992; Syms and Jones 2000); more structurally elaborate and topographically complex morphologies of coral and macroalgae typically form in reef aspects sheltered from wave action (Fowler-Walker et al. 2006; Madin et al. 2014). Recruitment success of tropical reef fishes may be organised by a range of abiotic and biotic factors which covary with the degree of wave action. For instance, embayed temperate reefs in coastal regions may be substantially influenced by freshwater runoff and/or tides, which can restrict recruitment of some tropical fishes where water parameters, such as turbidity, oxygen and temperature, exceed their physiological tolerance (Figueira et al. 2009; Wenger et al. 2013). Near-shore embayed reefs can also contain high piscivore densities, leading to high mortality of tropical fishes at recruitment (Baker and Sheaves 2005, 2006 and 2009). Hence, there are a range of both biotic and abiotic factors which pose various constraints to tropical fish recruitment, which may differ considerably between embayed and exposed temperate reef habitats. These may ultimately determine whether tropical fishes can expand their geographic range with sea surface warming.

The influence of embayed and exposed shallow temperate reefs, and the abiotic and biotic factors differing between them, on recruitment success of tropical reef fishes was explored by underwater visual surveys within SE Australia and W Japan. Since both regions are at the forefront of the range expansion of many tropical fishes, they provide a unique opportunity to explore the influence of temperate reef habitats in structuring recruitment success of tropical fishes (Feary et al. 2014). Each summer, expatriating tropical reef fish larvae (hereafter termed ‘vagrants’) are transported 100s to 1000s of km into these temperate regions by poleward flowing boundary currents (East Australian Current (EAC) in Australia, and the Kuroshio Current in Japan), where they recruit to coastal reef habitats (Booth et al. 2007; Feary et al. 2014). Although coastal waters in SE Australia and W Japan are warming at over two times the global average (Wu et al. 2012), and may facilitate colonisation of tropical fishes by reducing severity of winter water temperatures (Figueira and Booth 2010), variability in physical and abiotic stressors associated with embayed and exposed temperate reefs may essentially block this redistribution by limiting recruitment. Due to the strong influence of wave action on the distribution of reef fishes in regions with moderate to high wave regimes, such as W Japan and SE Australia, we predicted that the density, richness and diversity of vagrant fish assemblages would be greater in embayed than exposed temperate reefs. However, for the successful recruitment of habitat specialists dependant on coral, we also expected structurally complex corals to be present.

3.2 Material and methods

3.2.1 Density and distribution of tropical fishes in temperate reefs

Underwater visual surveys were conducted to examine the richness, diversity and density of new recruit and juvenile vagrant tropical fishes in exposed and embayed temperate reef habitats of SE Australia and W Japan (Kuiter 1993; Allen et al. 2003) (Fig. 3.1). Both regions hold sub-tidal coastal reefs within areas that have moderate to high energy wave climates (Young et al. 2011). Surveys were conducted during recruitment of tropical fishes in both 2011 and 2012 in SE Australia (i.e., March to May) and 2013 in W Japan (i.e., June to November) (Kuiter 1993; Booth et al. 2007; Figueira et al. 2009; Nakamura et al. 2013; Soeparno et al. 2013). Vagrant fishes were surveyed during 30 min timed swims in 0 - 4 m water depth whilst snorkelling. To standardise survey effort and calculate fish densities, paths swam were measured at 5 sec intervals by towing a GPS (Garmin^{TM} GPS 60; accuracy of 3 m) at a fixed-distance (3 m) (following Chapter 2; Beck et al. 2014). This survey method allows greater detection of sparsely-distributed vagrant fishes than traditional belt transects and more reliable density estimates (Chapter 2; Beck et al. 2014). Starting positions and swim patterns were haphazardly determined prior to surveys. All tropical fishes observed within 1 m either side of the observer were recorded by hand. Individuals were classified as new recruits or juveniles based on family specific length-age criteria (established by Booth et al. 2007), while functional groupings were determined using Froese and Pauly (2014) (Table 3.1). Tropical species were defined by the latitudinal range of a species; only found as breeding-aged adults between the Tropics of Cancer and Capricorn; 23°27’ N and S, respectively (Froese and Pauly 2014). Surveys were conducted by HJB at a constant speed between 09:00 and 17:00 when water visibility was > 5 m and swell was < 1 m. These conditions were chosen to minimise any potential bias to visual surveys associated with inherent differences in wave action and water visibility between exposed and embayed reefs.

3.2.2 Study locations

To test the influence of wave climate on vagrant assemblage structure, vagrant fishes were surveyed at four locations in SE Australia separated by 100s km; Nambucca (NB), Camden (CA), Forster (FO) and Swansea (SW) (Fig. 3.1). Within W Japan, vagrant fishes were surveyed in Otsuki (OT), Yokonami (YO), Tei (TE) and Nahari (NA), separated by 10s - 100s of km (Fig. 3.1). Within each location, vagrant fishes were surveyed by conducting one 30 min timed swim in two or three embayed and three exposed rocky reef sites. Sites were separated by > 100 m. Embayed reefs in SE Australia were positioned within estuary mouths (predominantly formed by artificial rockwalls), while embayed reefs surveyed in W Japan were naturally formed, with little freshwater influence. Exposed reefs in both regions were exposed or partially-exposed to ocean swell. In total, forty-two and twenty-one 30 min visual surveys were undertaken in SE Australia and W Japan, respectively.

3.2.3 Temperate reef habitat variables

To assess the role of biophysical factors in determining the composition and density of vagrant fishes amongst locations and reef habitats, *in situ* density of predatory fishes (identified according to Froese and Pauly 2014) were surveyed within each site using timed swim surveys (as above), water temperature (measured at half-hour to hourly intervals by permanent loggers installed at ~2.5 m below MSL), topographic complexity (using the ratio of surface distance to linear distance of a 5 m chain within 10 haphazardly selected areas within each location), and substrate composition [within 30 haphazardly selected 0.25 m^2 quadrats, with benthic habitats quantified using Underwood et al. (1991) and Bradbury and Young (1981)] were recorded. Benthic habitats measured were macroalgae, turfing algae, folios algae, encrusting algae, invertebrate cover (including sea urchins, ascidians, mussels and oysters), bare rock, silt and sand, as well as branching, plate and encrusting corals. Wave-exposure for each site was calculated using a fetch-based index with MicroStation^{TM} GIS. Fetch lines were constructed with 7.5° spacing around the midpoint of survey sites to a maximum of 650km (i.e., minimum fetch distance for fully developed seas to form) and divided by the sum of fetch distances by the maximum possible total; index units are dimensionless, with exposure increasing from 0 to a maximum exposure value of one (Hill et al. 2010). In addition, as a proxy for water parameters subjected to fishes within estuaries (e.g., nutrients, turbidity, oxygen etc), Google Earth^{TM} was used to calculate the distance of each site from the mouth of nearest estuary (i.e., minimum manhattan distance).

3.2.4 Statistical analyses

Because the number of survey occasions, locations and sites surveyed differed between SE Australia and W Japan, density, richness and the diversity of vagrant fish assemblages were analysed separately for each region. Overall assemblage densities (i.e., individuals per m^2) and species richness (i.e., total number of species per m^2) for vagrant fish assemblages were compared between habitats (exposed, embayed: fixed), recruitment years (2011, 2012: random; Australia only) and amongst locations (4 locations in both Australia and Japan: fixed) using permutational multivariate analysis of variance (PERMANOVA; Type III Sums of Squares; 9999 permutations under the reduced model, Anderson, 2001).

K-dominance plots were used to test whether species and functional group diversity of vagrant fish assemblages differed between embayed and exposed reef habitats, years (SE Australia only), and locations (Clarke and Gorley 2006). As a diversity measure, *K*-dominance plots better account for species and functional group evenness than single value diversity indexes (Lambshead et al. 1983). *K*-dominance plots were constructed individually for survey replicates by cumulatively ranking fourth root transformed species and functional group densities, expressed as a percentage of all species density, in decreasing order of their density. Fourth root transformations were used since there were many low and some high fish counts within survey replicates; as recommended by Quinn and Keough (2002). Pairwise distances between values in *K*-dominance plots were calculated using DOMDIS (PRIMER^{TM} v6 with PERMANOVA+ extension) (Warwick 1986, Clarke 1990, Clarke and Gorley 2006). *K*-dominance plots, both for species and functional diversity, were compared between years (SE Australia only), habitats and amongst locations by PERMANOVA (as above). Functional groups, grouped by primary trophic preference according to Froese and Pauly (2014), that were important contributors to dissimilarity of fish assemblages between habitats were identified using the similarity percentages routine (SIMPER; Clarke 1993) then graphically explored by principle coordinate analysis (PCO) using Spearman's rank correlation. We considered functional groups with % $\overline{\delta}_i > 10\%$ and $\overline{\delta}_i / SD(\overline{\delta}) > 1$ as important contributors to overall dissimilarity between habitats; where $\overline{\delta}_i$ is the average contribution of the *i*th functional group to the overall dissimilarity [$\overline{\delta}$] between the two groups and SD is the standard deviation. Densities of these functional groups, found by SIMPER as important contributors to variance in fish assemblages, were then compared between years (SE Australia only), habitats and sites using PERMANOVA (as above).

All survey data were inspected for homogeneity of variance using the PERMDISP procedure (PRIMER^{TM} v6 with PERMANOVA+ extension), with data ln(X+1) transformed where required. PERMANOVA was used as it is more robust to heterogeneity of variances and assumptions of data normality than parametric analyses (Underwood 1997; Anderson and Walsh 2013). For all univariate analyses, factors were pooled with the residual, pertaining to the rule of pooling when $p > 0.25$ (Underwood, 1997). *Post hoc* pair-wise tests were performed to identify differences in assemblage densities, richness and diversity amongst locations.

To determine the combination of environmental variables (i.e., minimum, maximum and mean water temperature, benthos composition, habitat rugosity, predator density, distance from estuary mouth, wave exposure and latitude), that best predicted variance in generalist and specialist fish assemblages between embayed and exposed temperate reef habitats, the best-fit distance based linear modelling (DistLM) (PERMANOVA; 9999 permutations pertaining to the Akaike information criterion with a correction for finite sample sizes - AIC_c; maximum of 10 variables) was conducted using Bray-Curtis similarity measures on fourth root transformed fish abundance data for all years, locations, habitats and species (Clarke and Gorley 2006). Environmental data were checked for multicollinearity and dispersion using draftsmen plots, ln(X+1) transformed where required, then normalised prior to analysis. *A priori*, $p < 0.05$ was the set level of significance for all analyses.

3.3 Results

A total of 8204 vagrant tropical fishes were surveyed within SE Australia and W Japan, encompassing 13 families and 75 species (Table 3.1). There was a 28% overlap in species between countries, with six families (i.e., Acanthuridae, Chaetodontidae, Labridae, Ostraciidae, Pomacentridae and Zanclidae) encompassing 22 species observed in both countries.

3.3.1 Association of vagrant assemblage with embayed and exposed temperate reefs

Within both SE Australia and W Japan, the overall density (total individuals), species and functional diversity (*K*-dominance) and species richness (total species) of vagrant fishes were significantly greater in embayed then exposed reefs (PERMANOVA, $p < 0.05$ for these four metrics, Table 3.2, Fig. 3.2). Density and richness of vagrants was over 2.5 and 1.5 times greater, respectively, within embayed than exposed reefs for SE Australia and W Japan, after pooling data at the year (SE Australia only), location and site level (Fig. 3.2). Factors ‘location’ and ‘year’ (SE Australia only) did not significantly explain patterns of vagrant density, richness and diversity ($p > 0.05$ for both factors; Table 3.2).

3.3.2 Association of trophic guilds with embayed and exposed temperate reefs

In SE Australia, the most common benthic habitats were folios (47.8%) and turfing algae (33.2%), whilst no coral was detected. In W Japan, turfing algae was also common (46%), but coral (26.5%) and encrusting algae (18.9%) were dominant benthic habitats, whilst folios algae was rare (<1%).

Trophic generalists comprised the entire vagrant assemblage in SE Australia and 98% of assemblages in W Japan. Planktivores were the most common generalist trophic guild in both SE Australia (54.4%) and W Japan (85.2%), followed by herbivores (22.5% Australia; 5.1% Japan), benthivores (16.5% Australia; 6.02% Japan), omnivores (4% Australia; 1.6% Japan), parasite cleaners (1.4% Australia; 0.3% Japan) and piscivores (1.2% Australia; 0.1% Japan). Corallivores made up the remaining ~2% of vagrant assemblages in W Japan, but were never found within SE Australia. There was clear separation in trophic group composition along PCO axis 1 between embayed and exposed temperate reefs in both SE Australia and W Japan (Fig. 3.3), with trophic group explaining 65.7% and 54.9% of variance in assemblages, respectively.

Planktivores (Australia and Japan), herbivores (Australia and Japan), benthivores (Australia and Japan), omnivores (Australia and Japan) and corallivores (Japan only) primarily accounted for division of assemblages between habitats (SIMPER; % $\bar{\delta}_i >$ 10%, $\bar{\delta}_i / \mathrm{SD}(\bar{\delta}_i) > 1$) and were positively associated with PCO axis 1 (Spearman's rank correlation, $r_s > 0.32$, $p \leq 0.01$ for each trophic group in both countries; Fig. 3.3), with exception of omnivores in Japan ($r_s = -0.008$, $p = 0.69$). Embayed reefs supported greater densities of herbivores (Australia: *Pseudo*-$F_{1,31} = 92.91$, $p = 0.001$, Japan: *Pseudo*-$F_{1,13} = 16.43$, $p = 0.002$), benthivores (Australia: *Pseudo*-$F_{1,32} = 38.75$, $p = 0.0001$, Japan: *Pseudo*-$F_{1,13} = 8.08$, $p = 0.01$), omnivores (Australia: *Pseudo*-$F_{1,32} = 75.83$, $p = 0.0001$, Japan: *Pseudo*-$F_{1,13} = 6.57$, $p = 0.02$) and corallivores (Japan: *Pseudo*-$F_{1,13} = 6.13$, $p = 0.03$) than exposed reefs. Planktivores were in greater densities in embayed than exposed reefs in SE Australia (*Pseudo-*$F_{1, 32}$ = 34.11, p = 0.001), and greater (but not significant) densities in embayed W Japanese reefs (*Pseudo-*$F_{1, 13}$ = 2.78, p = 0.12).

Interactions of the factor ‘habitat’ with other terms in models were non-significant for all trophic groups reported here in both countries (i.e., $p < 0.05$ for all interactions between ‘habitat’ and ‘location’ and ‘year’ (SE Australia only).

3.3.3 Environmental correlates and recruitment of tropical fishes to temperate reefs

Wave exposure best predicted variance in generalist fish composition (i.e., non-obligate feeders) between embayed and exposed reefs within both SE Australia (23.2%; AIC_c = 301.89) and W Japan (23%; AIC_c = 155.13). The richness and density of generalist assemblages in both countries monotonically increased as the exposure of reefs reduced below a fetch-based index 0.1 (Figs. 3.4 and 3.5; Hill et al. 2010). In W Japan, wave exposure, independent of any other measured factor, best explained variance in the composition of trophic generalists. In SE Australia, the overall best combination of factors explaining variance in vagrant assemblage also included predator density (20.5%) and latitude (9%) (AIC_c = 296.38). Richness and density of SE Australian generalist assemblages was significantly and positively correlated with predator density (density: r_s = 0.64, p = 0.001, richness: r_s = 61, p = 0.001); predators were also more commonly observed in embayed reefs (Table 3.3). There was no significant correlation of fish assemblage density or richness with latitude (density: r_s = -0.15, p = 0.35; richness: r_s = -0.09, p = 0.59).

Presence of branching coral cover in W Japan best explained differences in densities of corallivore fishes amongst sites (38.7%; AIC_c = 136.97), independent of any other factor measured. Richness and densities of corallivores were significantly and positively correlated with branching coral cover (density: r_s = 0.82, p = 0.001; richness: r_s = 0.83, *p* = 0.001; Fig. 3.6a). Branching corals were only found within highly embayed reefs, with sites with branching corals showing a fetch-based wave exposure index values < 0.1 (Fig. 3.6b; Hill et al. 2010).

3.4 Discussion

Poleward range expansion of tropical reef fishes is expected with ongoing sea surface warming (Figueira and Booth, 2010). However, based on thresholds of wave exposure for reefs supporting high tropical fish recruitment success (i.e., reefs with an exposure index < 0.1; Hill et al. 2010), and using aerial photographs and bathymetric profiles (Google-Earth^{TM}), we estimate over 80% of temperate reefs in SE Australia and W Japan may be too wave-exposed to support recruitment of many species. Specifically, we found that the density, species richness and diversity of newly recruited tropical fish communities was substantially lower on exposed compared to embayed temperate reefs, within both SE Australia (across 2 years) and W Japan (during 1 year). Prior to this study, larval supply (Booth et al. 2007; Soeparno et al. 2012), water temperatures (Figueira et al. 2009; Figueira and Booth 2010) and species traits (e.g., life history and diet: Luiz et al. 2013, Feary et al. 2014) were considered the major factors influencing range expansions of tropical fishes into temperate regions. However, our results show that even if tropical fishes are supplied as larvae to temperate regions where they may physiologically tolerate local water temperatures (Eme and Bennett 2008; Figueira et al. 2009) and potentially access necessary resources (Feary et al. 2014), recruitment success may be strongly determined by the availability of moderately to highly embayed reefs. Hence, the establishment of permanent populations may be constrained in temperate regions where embayed reefs are sparsely distributed and/or rare (Bates et al. 2014).

Wave exposure was the primary factor organising tropical fish recruitment between embayed and exposed temperate reefs in our study, since the density and richness of tropical fish assemblages was highly correlated with the degree of protection from wave action. This influence of wave exposure on tropical fish recruitment among temperate reefs appeared to outweigh other measured abiotic and biotic factors that have been shown to strongly organise reef fish recruitment elsewhere. For example, habitat complexity, which may influence survival of reef fish recruits by determining refuge from predators, competition strength and/or environmental stress (Almany 2004b; Johansen et al. 2008), did not explain differences in tropical fishes assemblages among sites. Water temperatures and distance from river mouth (i.e., estuarine influence) also did not explain such strong association with embayed reefs, despite the greater potential for physiological stress associated with high salinity, oxygen, thermal and nutrient flux associated with low flushing and rainfall influences to occur within these habitats (Wenger et al. 2012; Johansen and Jones 2013; Wenger et al. 2013). Wave exposure was also a better predictor of tropical fish recruitment success than benthic habitats. For instance, macroalgal cover of reefs did not explain variance in vagrant recruitment between embayed and exposed reefs, even though macroalgal cover may be strongly influenced by wave action and influence reef fish recruitment (Jones 1992; Fowler-walker 2006). This is clear in W Japan, where tropical fishes associated strongly with embayed reefs despite rarity of folios algae; folios algae covered <1% of the reefs surveyed. Furthermore, although there is evidence that native predators may constrain colonisation of range expanding marine fishes (Bates et al. 2013; Luiz et al. 2013), the diversity and density of temperate predators also appeared here to have little influence on tropical fish recruitment to embayed reefs, as densities of tropical fish recruits were positively correlated with predators in SE Australia, whilst vagrant assemblage composition did not vary with predator densities in W Japan.

Wave exposure of temperate reefs appeared to be more important than larval supply on tropical fish recruitment, at least on spatial scales of 100s m to kms - studied here. Larval supply of tropical fishes is often strongly influenced by ocean current flow direction and speed (Shanks 2009). Although larval supply of fishes is spatially patchy throughout the W Japanese coast due to the almost perpendicular orientation of this coastline to the Kuroshio current and chaotic nearshore flow (Waseda and Mitsudera 2002), the East Australian Current (EAC) typically flows along the SE Australian coast, leading to reducing diversity and density of tropical fish recruits from north to south

(Booth et al. 2007). Nevertheless, wave exposure of temperate reefs in SE Australia better explained spatial variation in tropical recruit assemblages among sites than did latitude. It is possible that latitudinal trends in larval supply may be masked by sporadic, but reoccurring eddies in SE Australia (Mullaney et al. 2011; Matis et al. 2014), which form where the EAC encounters particular topographic features of the continental shelf and coastline in this region (Ridgway and Dunn 2003). However, patchiness of embayed and exposed reefs is at a much smaller scale than eddies (kms vs 100s of kms) so eddy effects did not confound our results. Hence, although larval supply is an important precursor/prerequisite to range expansions of tropical fishes, influence of temperate reef habitats on recruitment success, such as exposed and embayed reefs, may ultimately control/limit colonisation at local scales.

The effects of wave exposure on temperate establishment of tropical reef fishes may be mediated through wave motion effect on fish swimming ability. Many new recruits and early juvenile tropical fishes seek shelter from hydrodynamic stress to reduce energetic demand (Johansen et al. 2008) and/or to feed more efficiently (MacKenzie and Kiørboe 2000). Although there is considerable variance in swimming performance within and among tropical fish families (Fulton and Bellwood 2004; Fulton et al. 2005; Fulton and Bellwood 2005; Fulton 2007; Fulton et al. 2013), the majority of tropical fishes, independent of their potential swimming performance, may be forced into sheltered aspects of shallow reefs when the wave climate is high (Friedlander et al. 2003; Fulton and Bellwood 2004). Alternatively, fishes may avoid hydrodynamic stress associated with wave action by moving to deeper reefs (Fulton and Bellwood 2004). However, a depth response to wave action by these range expanding fishes was unlikely, at least at the forefront of their redistribution, since isotherms are typically warmer toward the surface, which best supports colonisation success of such warm-adapted, range expanding species (Bates et al. 2014). Hence, the high wave energy of SE Australian and W Japanese reefs in this study may have been sufficient to force the majority of tropical fish recruits into highly wave sheltered regions, and exclude them from using exposed sites due to the wave action exceeding these fishes' physiological tolerance for water movement, while also limiting their access to suitable resources.

As well as directly structuring tropical fish recruitment, where corals are also undergoing range-expansion, wave action may also further organise colonisation success of these fishes by determining the distribution and morphology of coral habitats at temperate latitudes. At least in W Japan, where many corals are rapidly shifting poleward (Nakamura et al. 2013), densities and richness of corallivore fishes were positively associated with branching corals. In SE Australia, corallivores were not detected, likely due to rarity of hard tropical corals in this region (Feary et al. 2014). This was consistent with our expectation, since corallivores typically depend on hard branching corals for food, but also living space and refuge (Syms and Jones 2000; Feary et al. 2007b). However, branching corals were only found within highly embayed temperate Japanese reefs (i.e., wave exposure < 0.1). Although branching coral cover increased monotonically with reducing wave action, so the positive response of tropical fishes to embayments may have been driven by hydrodynamic stress rather than coral habitats, we are confident that coral structure was important since all observed individual corallivores were found amongst branching corals (H. J. Beck, unpublished data). Factors organising the range expansions of corals and their morphology are largely untested, however we may expect that low wave action in these embayed Japanese reefs was important for the establishment of branching coral habitats. Complex growth forms of corals, such as fine branching, are often preferred by fishes but are highly prone to hydrodynamic stress (Madin et al. 2014), so that at least in shallow coastal waters with a high wave climate, they often best establish in reef aspects protected from wave action (Smith and Simpson 1992; Harriott 1999; Sommer et al. 2014). Hence, by supporting the establishment of structurally suitable corals, embayed temperate reefs may indirectly assist the colonisation of tropical fishes that depend on these corals for resources.

This study identified the importance of embayed and exposed reefs in organising tropical fish colonisation in regions with moderate to high wave energy, yet these habitat influences will likely be weaker where regional and/or seasonal (i.e., through summer recruitment) wave action is lower. However, while progressive warming of oceans may eventually lead to poleward expansions in temperate regions globally, where shifts have so far been documented, wave action should be sufficient to limit recruitment success since many regions prone to tropical fish range expansions have high-energy wave climates. For example, the eastern continental boundaries of South America, Africa and USA, as well as the West Australian coast, where poleward expansions of many tropical fishes are most rapid (Lloyd et al. 2012; Wernberg et al. 2012b; Luiz et al. 2008; Barneche et al. 2009; Fodrie et al. 2010), all have moderate to high wave climates (Young et al. 2011), which are similar to that of the SE Australian and W Japanese coasts studied here. Furthermore, even for temperate regions with low wave energy, where wave action may not currently constrain tropical fish recruitment, forcing of wave action on tropical fishes recruitment may increase on the whole because the frequency of extreme wave events may increase with ongoing climate change (Young et al. 2011), but see Dowdy et al. (2014).

Based on the threshold of wave exposure detected here, we estimate that only 13.9% of SE Australian and 20% of W Japanese nearshore reefs may be adequate for supporting recruitment of many tropical fishes (depths < 10m; Google-Earth^{TM}). Tropical fishes may access suitable shelter from wave action naturally, where headlands and offshore reefs block swell. However, anthropogenic disturbance associated with the development of rocky sea walls and other wave barriers may increase the availability of embayed reef in temperate regions, and hence assist tropical fish redistribution. For instance, in W Japan, ~70% of shallow, embayed reefs are afforded by artificial wave barriers, which include harbours, jetties, seawalls and detached breakwaters (depths <10 m; Google-Earth^{TM}; Walker and Mossa 1986). Protection of reefs from wave action, afforded by such construction, may also promote colonisation of corallivore fishes because these relatively calm environments facilitate the establishment of branching coral habitats (Iwas 2004).

We predict that embayed reef habitats will substantially constrain range expansions of tropical fishes into SE Australia and W Japan since the availability of embayed reefs appears to be greater in the source tropical range for tropical fishes in these regions (cf. Bates et al. 2014). Along eastern Australia, embayed habitats are most abundant throughout the Great Barrier Reef (GBR), a vast habitat for Indo-Pacific tropical fishes and the primary larval source of tropical fishes for vagrant fishes in this region (Kuiter 1993; Allen et al. 2003). Within the GBR, mid- and inner-shelf reefs are largely protected from ocean swells by the outer reef. For example, from ~16º to ~9º S, the outer reef runs almost continuously north, blocking ~80% of reefs leeward from the outer edge from direct exposure to regular ocean swells (Lewis 2001). Similarly, an island chain that extends from the Philippines to the Ryukyu Islands, which composes the primary historic range for tropical fishes colonising W Japan (Soeparno et al. 2012), provides substantial protection from wave action since reefs bordering western shores are considerably protected from the dominant, east swell; wave energy is at least half that on the westward than eastward sides of these islands (Barstow et al. 2009). Moreover, although development of a barrier reef system at higher latitudes may reduce constraints of wave action for range-expansions of tropical fishes, geological formations that support substantial barrier reef development in SE Australia and W Japan are largely absent. Hence, the general incidence of embayed reefs is reduced approaching the poles in both eastern Australian and W Japan, with high potential to impact capacities of tropical fish populations to shift with sea surface warming.

Accurate predictions of species' range expansions are required for effective management of climate change impacts in natural ecosystems, but reliable projections of species' geographic responses to climate change are currently elusive (Russell et al. 2011; Urban et al. 2013). Although propagule supply and species thermal requirements are important considerations (Sorte 2013; Pinsky et al. 2013), the timing and location of species range expansions may be more accurately predicted by determining habitat requirements of species at higher latitudes (Cheung et al. 2010), yet field-based studies that test this are largely lacking (Wernberg et al. 2012a). This study highlights the importance of understanding habitat constraints to recruitment of tropical species, such as wave action, not only larval supply and local environmental temperatures, when predicting where and when they may colonise with ongoing climate change. For instance, we show here that for many tropical fishes, failure to consider wave exposure of temperate reefs when predicting their future distribution may lead to vast over-estimates of their range expansion success.

3.5 Tables

Table 3.1 Species, primary trophic guild and country tropical reef fishes were detected. Trophic guilds allocated according to Froese and Pauly (2014). A = southeastern Australia; J = western Japan.

Species	Primary trophic guild	Region
F. Acanthuridae		
Acanthurus dussumieri	Herbivore	A, J
Acanthurus lineatus	Herbivore	A, J
Acanthurus mata	Planktivore	A
Acanthurus nigrofuscus	Herbivore	A, J
Acanthurus olivaceus	Herbivore	A, J
Acanthurus triostegus	Herbivore	A, J
Ctenochaetus binotatus	Herbivore	A, J
Ctenochaetus striatus	Herbivore	J
Naso unicornis	Herbivore	A, J
F. Balistidae		
Sufflamen chrysopterus	Benthivore	A
F. Chaetodontidae		
Chaetodon auriga	Benthivore	A, J
Chaetodon auripes	Benthivore	J
Chaetodon citrinellus	Benthivore	A
Chaetodon flavirostris	Benthivore	A
Chaetodon guentheri	Benthivore	A
Chaetodon kleinii	Benthivore	A
Chaetodon melannotus	Corallivore	J
Chaetodon plebeius	Corallivore	J
Chaetodon selene	Corallivore	J
Chaetodon speculum	Corallivore	J
Chaetodon trifasciatus	Corallivore	J
Chaetodon vagabundus	Omnivore	A, J
Heniochus accuminatus	Planktivore	A

F. Gobiesocidae		
Diademichthys lineatus	Benthivore	J
F. Labridae		
Anampses caeruleopunctatus	Benthivore	A, J
Anampses melanurus	Benthivore	J
Anampses meleagrides	Benthivore	J
Cirrhilabrus temminckii	Benthivore	J
Coris gaimard	Benthivore	J
Gomphogus varius	Benthivore	J
Halichoeres margaritaceus	Benthivore	J
Halichoeres nebulosus	Benthivore	J
Hologymnosus annulatus	Benthivore	J
Labroides dimidiatus	Parasite cleaner	A, J
Pseudocheilinus hexataenia	Benthivore	J
Stethojulis bandenensis	Benthivore	A, J
Stethojulis interrupta terina	Benthivore	J
Stethojulis strigiventer	Benthivore	J
Thalassoma amblycephalum	Plankivore	J
Thalassoma hardwicke	Benthivore	J
Thalasoma jansenii	Benthivore	A
Thalasoma lunare	Benthivore	A, J
Thalasoma lutescens	Benthivore	A, J
F. Lutjanidae		
Lutjanus argentimaculatus	Piscivore	A
Lutjanus russellii	Piscivore	A
F. Ostraciidae		
Ostracion cubicus	Benthivore	A, J
F. Pomacentridae		
Abudefduf bengalensis	Omnivore	A
Abudefduf sexfasciatus	Plankivore	A, J
Abudefduf sordidus	Omnivore	A

Abudefduf vaigiensis	Planktivore	A, J
Abudefduf whitleyi	Planktivore	A
Amphiprion clarkii	Planktivore	J
Chromis notata	Planktivore	J
Chromis flavomaculata	Planktivore	J
Chromis fumea	Planktivore	A
Chromis margaritifer	Planktivore	A, J
Chromis weberi	Planktivore	J
Chrysiptera starcki	Omnivore	J
Chrysiptera unimaculata	Herbivore	J
Dascyllus reticulatus	Omnivore	J
Dascyllus trimaculatus	Omnivore	J
Plectroglyphidodon leucozonus	Herbivore	A, J
Pomacentrus coelestis	Planktivore	A, J
Pomacentrus nagasakiensis	Planktivore	A, J
Pomachromis richardsoni	Benthivore	J
Stegastes gascoynei	Omnivore	A
F. Scaridae		
Scarus forsteni	Herbivore	J
F. Scorpaenidae		
Pterois volitans	Piscivore	J
F. Serranidae		
Cephalopholis argus	Piscivore	A
Diploprion bifasciatum	Piscivore	A
Grammistes sexlineatus	Piscivore	A
Pseudanthias squamipinnis	Planktivore	J
F. Tetraodontidae		
Canthigaster rivulata	Omnivore	J
Canthigaster valentini	Omnivore	J
F. Zanclidae		
Zanclus cornutus	Benthivore	A, J

Table 3.2 Results of permutation analysis of variances testing for differences in total vagrant tropical fish assemblage density, richness and diversity (i.e., *K*-dominance) between embayed and exposed temperate reefs (Habitat), locations and years (Australia only), and interactions amongst these factors, within a) SE Australia and b) W Japan. Bold *p*-values denote a significant difference of $p < 0.05$. Where variable was $p > 0.25$, it was pooled with the residual.

	Effects of variable								
	Habitat (H)			**Other variable's *p*-values**					
Parameter	***Pseudo-F***	**d.f.**	***p***	**L**	**L x H**	**Y**	**Y x H**	**Y x L**	**L x Y x H**
a) SE Australia									
Density	68.11	1, 39	**0.0001**	0.16	0.13	0.36	0.51	0.73	0.21
Species richness	57.08	1, 39	**0.0001**	0.39	0.51	0.30	0.66	0.88	0.21
Species diversity	34.42	1, 35	**0.0001**	0.69	0.87	0.79	0.75	0.45	0.25
Functional diversity	15.83	1, 28	**0.0001**	0.13	0.19	0.62	0.51	0.52	0.83
b) W Japan									
Density	5.65	1, 13	**0.03**	0.62	0.19	-	-	-	-
Species richness	12.47	1, 13	**0.003**	0.49	0.23	-	-	-	-
Species diversity	17.90	1, 13	**0.03**	0.86	0.65	-	-	-	-
Functional diversity	6.56	1, 13	**0.02**	0.62	0.46	-	-	-	-

Table 3.3 Mean (SE) piscivore densities within embayed and protected reef habitats within a) SE Australia and b) W Japan. * denotes significant difference in densities between habitats (PERMANOVA; $p < 0.05$).

Species	Common name	Embayed reef	Exposed reef
a) SE Australia			
Acanthopagrus australis	Yellowfin Bream	45.64 (7.82)*	4.91 (1.65)
Argyrosomus japonicus	Jewfish	0.32 (0.33)	0.00
Brachaelurus waddi	Blind shark	0.00	0.03 (0.03)
Dinolestes lewini	Longfin Pike	2.12 (1.55)	1.20 (0.60)
Epinephelus coioides	Estuary cod	0.24 (0.14)	0.00
Epinephelus daemelii	Black cod	0.16 (0.17)	0.03 (0.03)
Gymnothorax prasinus	Green Moray	0.23 (0.24)	0.00
Lutjanus argentimaculatus	Mangrove Jack	0.12 (0.13)	0.00
Lutjanus russellii	Moses' snapper	4.88 (2.11)	1.71 (1.71)
Platycephalus bassensis	Sand flathead	2.67 (2.37)	0.03 (0.03)
Platycephalus fuscus	Dusky flathead	0.80 (0.53)	0.09 (0.09)
Sepia plangon	Mourning cuttlefish	0.20 (0.21)	0.00
Sepia sp.	Unidentified cuttlefish	0.00	0.09 (0.09)
	Total	57.54 (8.69)*	8.09 (2.28)
b) W Japan			
Acanthopagrus schlegelii	Japanese black porgy	0.13 (0.13)	0.44 (0.25)
Apagon sp.	Unidentified cardinal fish	19.29 (9.88)	4.16 (4.16)
Gymnothorax sp.	Unidentified morey eel	0.13 (0.13)	0.00
Lethrinus genivattatus	Thread-finned emperor	0.15 (0.15)	0.00
Lethrinus nebulosus	Spangled emperor	0.12 (0.12)	0.56 (0.56)
Lutjanus russelli	Moses’ snapper	0.13 (0.13)	0.00
Lutjanus stellatus	Star snapper	0.23 (0.15)	0.10 (0.10)
Plectropomus leopardus	Coral trout	0.10 (0.10)	0.00
Pterois volitans	Red lionfish	0.10 (0.10)	0.00
Scolopsis affinis	Monocole bream	0.15 (0.15)	0.35 (0.35)
Sphyraena japonica	Japanese barracuda	2.52 (2.52)	1.76 (1.76)
Synodus ulae	Red lizard fish	0.61 (0.47)	0.07 (0.07)
	Total	25.49 (9.10)	5.63 (3.13)

3.6 Figures

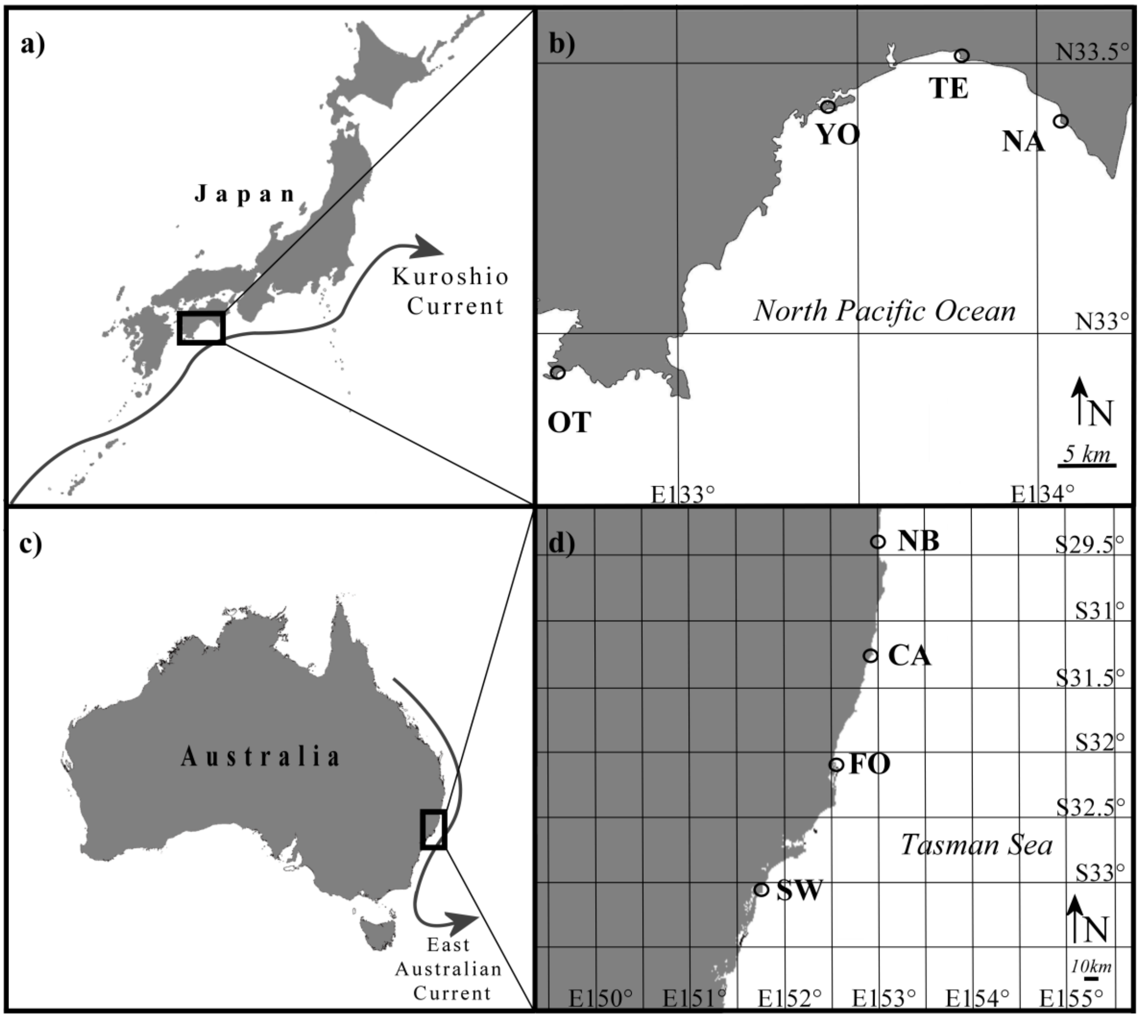

Figure 3.1 Location of survey locations within western (W) Japan, insets a) and b), and southeastern (SE) Australia, insets c) and d). Within each location, two to three 30 min underwater visual surveys of tropical vagrant were conducted in both embayed and exposed temperate reefs. Vagrant tropical fishes are supplied through summer from tropical fishes to temperate reefs by the poleward flowing a) Kuroshio and c) East Australian Currents within SE Japan and Australia, respectively. Flow path and direction illustrated by arrows; insets a) and b). Surveys conducted for two recruitment seasons in SE Australia and one in W Japan. CA = Camden Haven, FO = Forster, NA = Nahara, NA = Nambucca, OT = Otsuki, SWA = Swansea, TE = Tei, YO = Yokonami.

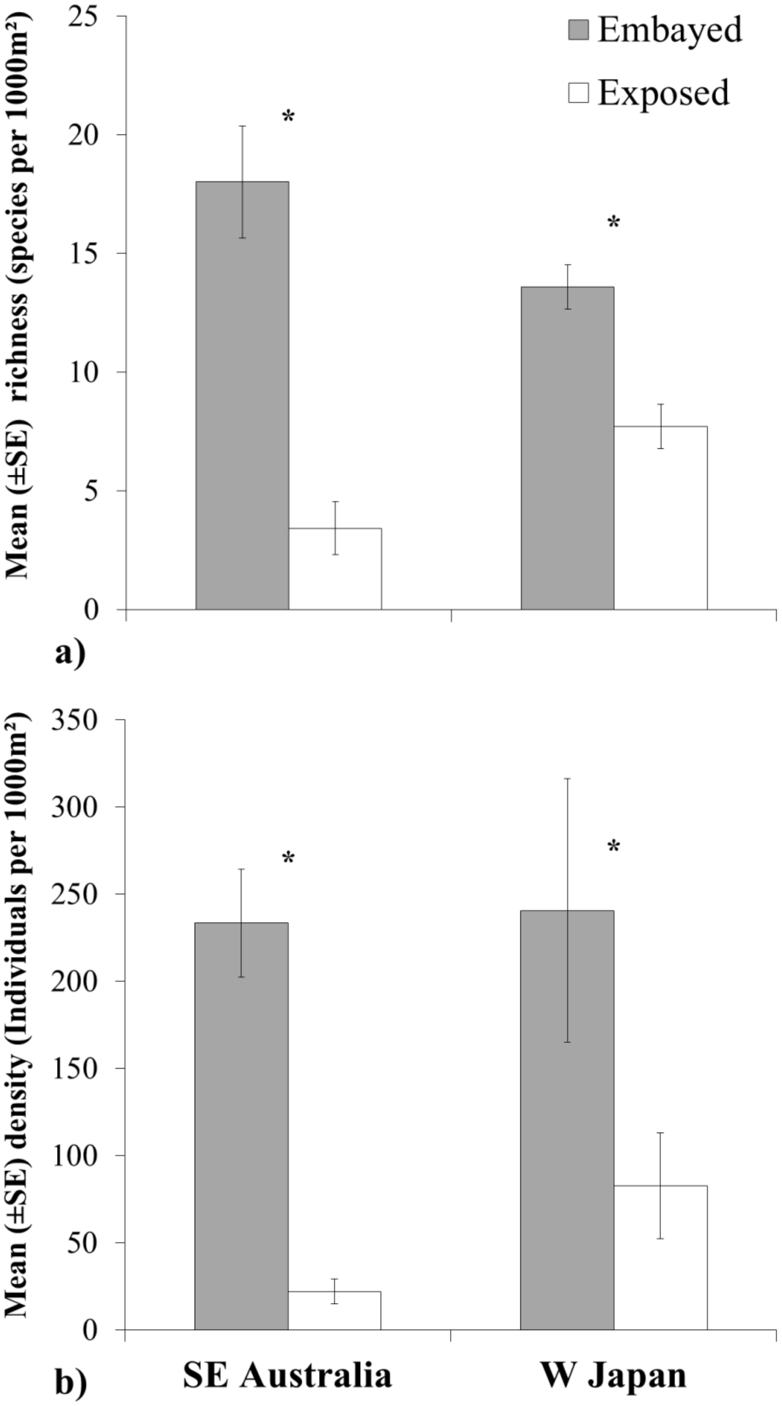

Figure 3.2 Mean (±SE) density and species richness of vagrant tropical fishes within embayed (grey bars) and exposed (white bars) reef habitats of SE Australia and W Japan. * denotes a significant difference of $p < 0.05$.

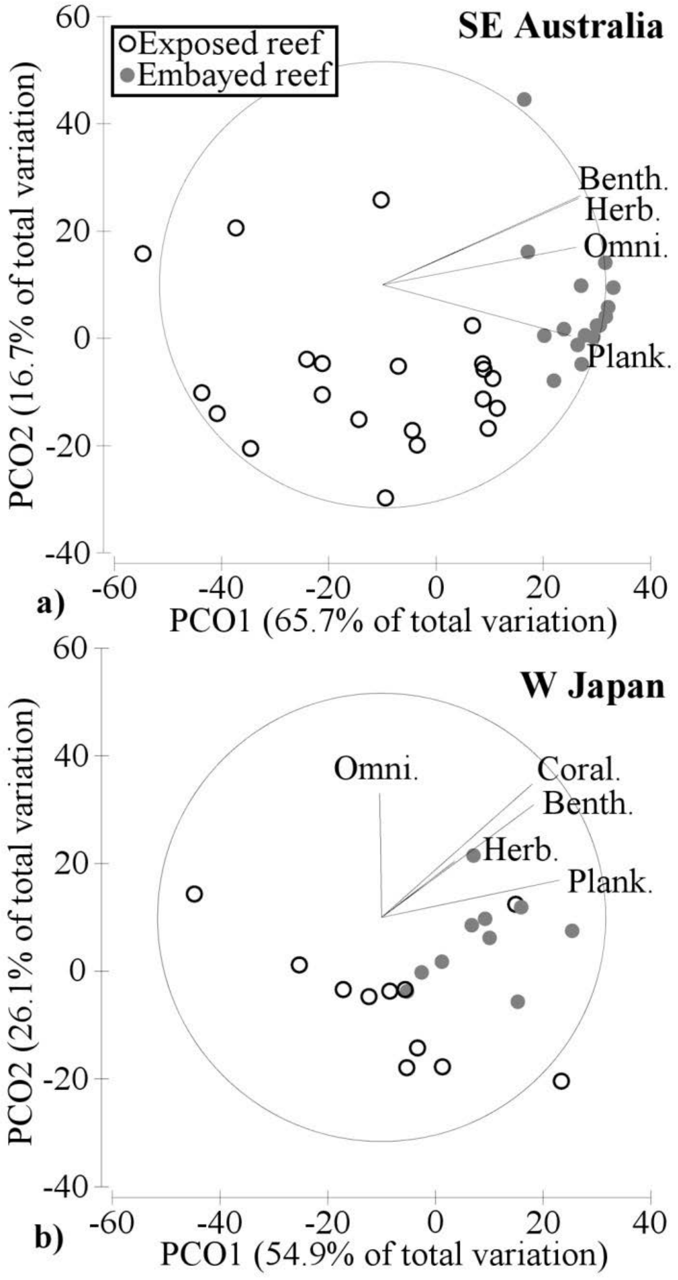

Figure 3.3 Principal co-ordinate analysis of tropical vagrant fish functional groups within wave exposed (open markers) and embayed (grey markers) sites of a) SE Australia and b) W Japan. Vectors overlaid display the primary groups responsible for division of sites along PCO axis 1, determined by SIMPER analysis (result reported in text). n = 40 and 21 replicate 30 min timed swims within SE Australia and W Japan, respectively.

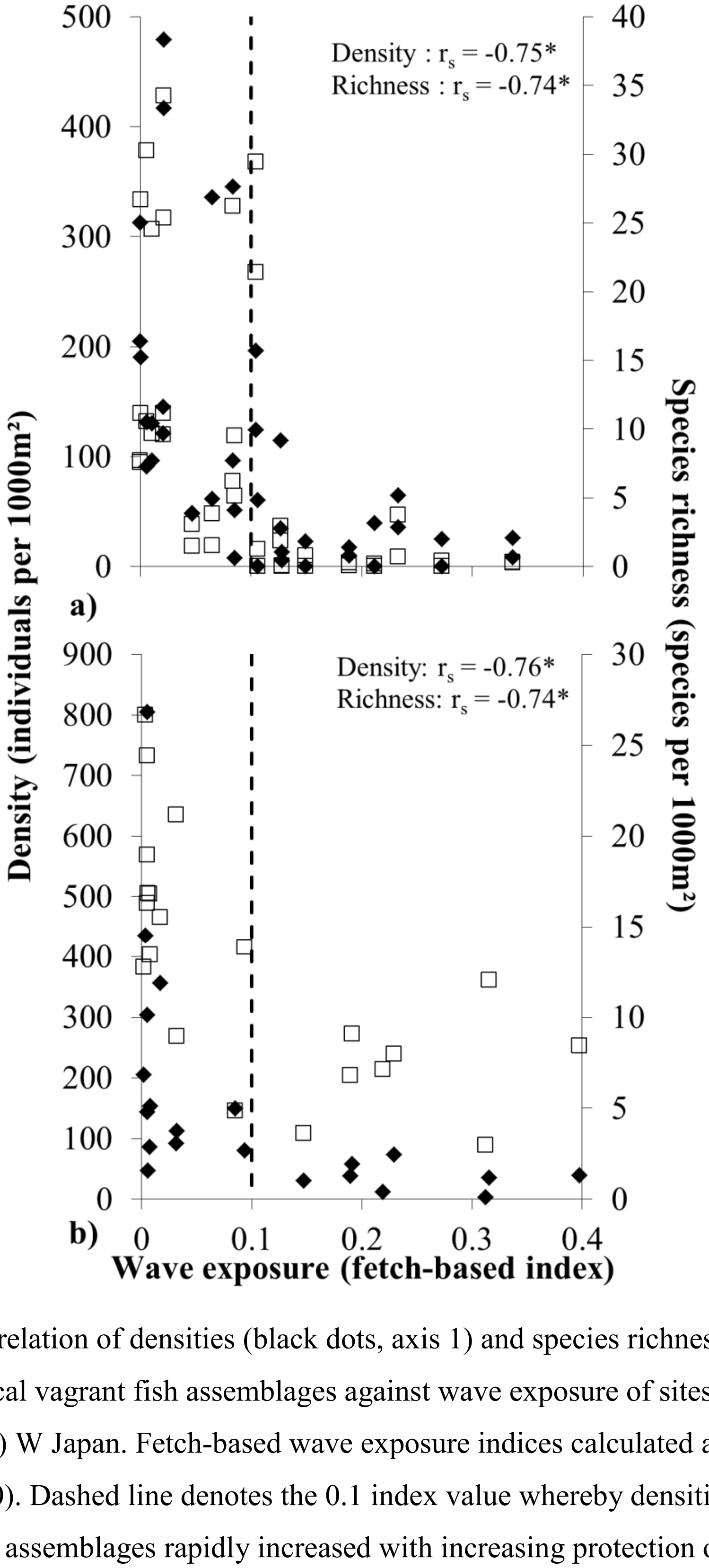

Figure 3.4 Correlation of densities (black dots, axis 1) and species richness (open dots, axis 2) of tropical vagrant fish assemblages against wave exposure of sites within a) SE Australia and b) W Japan. Fetch-based wave exposure indices calculated according to Hill et al. (2010). Dashed line denotes the 0.1 index value whereby densities and richness of fish assemblages rapidly increased with increasing protection of sites from wave action. n = 40 and 21 replicate 30 min timed swims within SE Australia and W Japan, respectively. Spearman's rank correlation statistic (r_s) is included for each regression, with * denoting a significant relationship with $p < 0.001$.

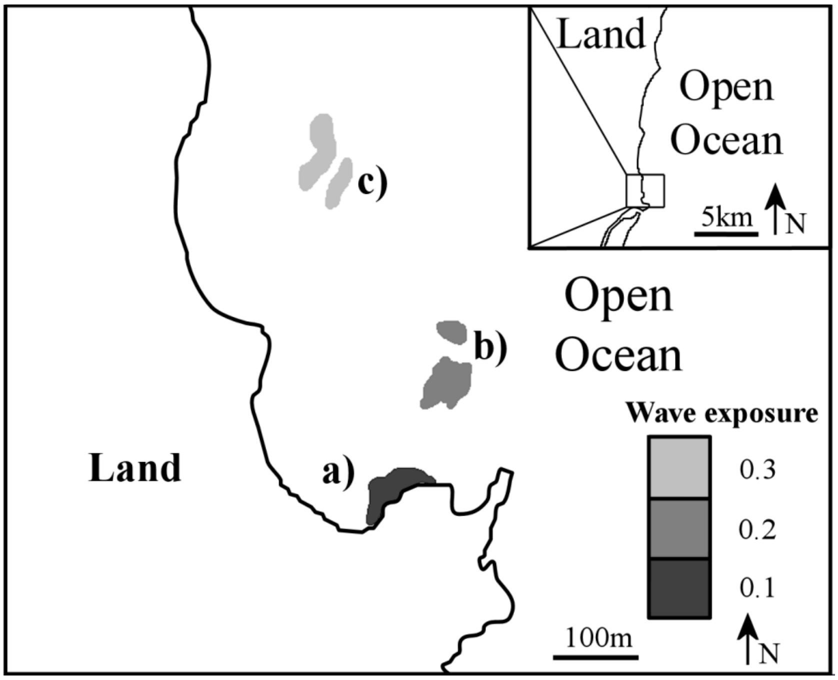

Figure 3.5 Examples of wave-exposure index values for patch reefs surveyed within Nambucca, SE Australia. Survey sites a), b) and c) correspond to wave exposure indices of ~ 0.1, 0.2 and 0.3 out of a maximum exposure value of 1, respectively. Index values were constructed with 7.5° spacing around the midpoint of survey sites to a maximum of 650 km, the minimum fetch distance for fully developed seas to form, according to Hill et al. (2010).

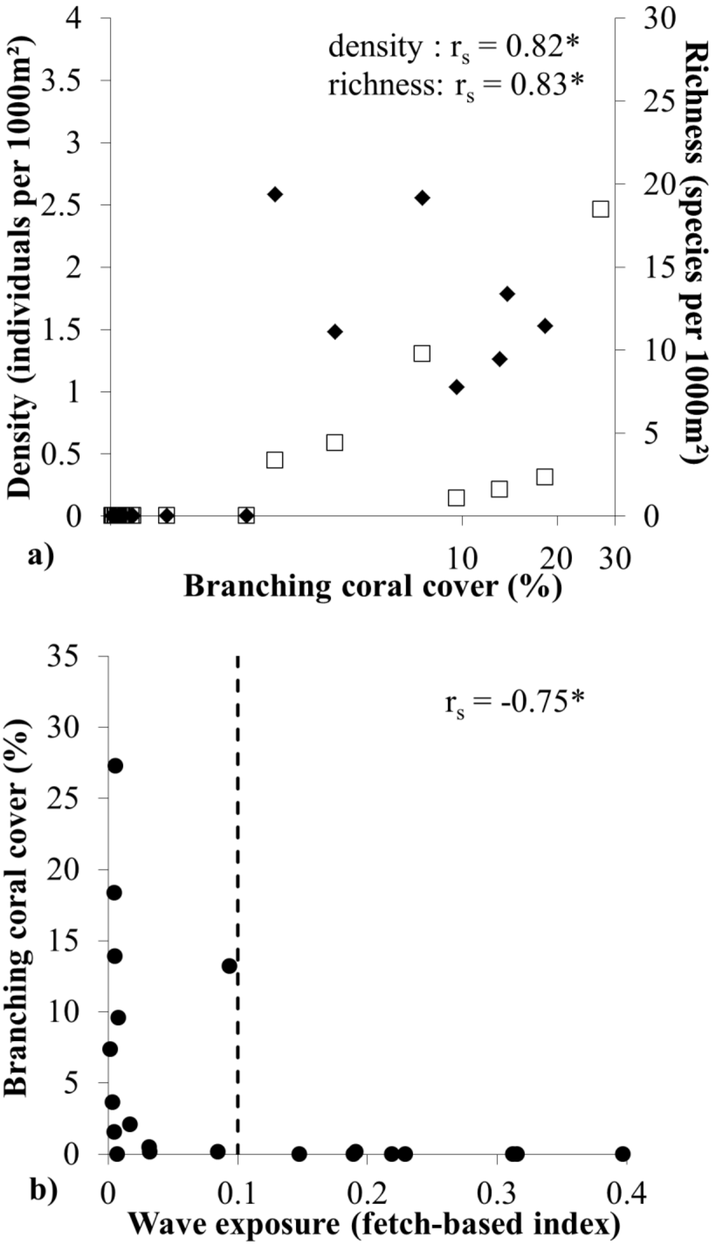

Figure 3.6 Regression of a) densities (black diamonds, axis 1) and species richness (open squares, axis 2) of corallivores with mean branching coral cover of reefs within W Japan, and b) branching coral cover (black dots) and wave exposure within sites of W Japan. n = 21 sites; within each site, fishes quantified by one 30 min timed swim survey and coral cover was quantified 20 haphazardly arranged 0.5 m^2 quadrates. Vertical dashed line denotes the 0.1 index value cut-off where by branching corals were not observed with any further exposure. Fetch-based wave exposure indices calculated according to Hill et al. (2010). Spearman's rank correlation statistic (r_S) is included for each regression, with * denoting a significant relationship ($p < 0.05$).

Chapter 4: Tropical fishes associate with temperate reef lacking macroalgae, suggesting climate-driven macroalgal loss facilitates their range-expansion

Beck HJ, Feary DA, Nakamura Y, Booth DJ (*Submitted*) Tropical fishes associate with temperate reefs lacking macroalgae, suggesting climate-driven macroalgal loss facilitates their range-expansion. Coral Reefs.

Abstract

Habitat-limited recruitment and settlement can be a major factor impeding species from shifting poleward with climate change. Therefore, responses of local autogenic ecosystem engineers to climate change may indirectly control species' range expansions by altering availability of habitats that support range expanders' early life success. We tested the effect of climate-mediated temperate macroalgal loss on recruitment of range expanding tropical fishes within two coastal regions undergoing rapid warming; southeastern (SE) Australia and western (W) Japan. Underwater surveys of temperate reefs revealed that the density and richness of new recruit and juvenile tropical fishes was over seven times greater in non-macroalgal than macroalgal reef habitat (i.e., > 75% cover), across one and three year/s in coastal W Japan and SE Australia, respectively. Species and functional diversity of tropical fishes (i.e., *K*-dominance) were also greater in non-macroalgal habitat in both regions. The abundance and diversity of tropical fish assemblages were negatively related to the proportion of reef covered by macroalgae and positively related to reef cleared of all branching algae. Aquarium experiments indicated that non-macroalgal habitats were the preferred temperate settlement habitat for at least one tropical fish, *Pomacentrus coelestis*. Reductions in macroalgal cover associated with rapidly warming temperate regions may facilitate tropical reef fish colonisation by increasing the availability of non-macroalgal reef habitats. This study highlights that an understanding of responses of habitat engineers to environmental warming may be required to reliably predict where and when species will colonise with ongoing climate change.

4.1 Introduction

Anthropogenic warming of aquatic and terrestrial environments is leading to widespread poleward shifts in the geographic distribution of species (Thomas et al. 2004; Harley et al. 2006). Such poleward redistribution of organisms is altering the composition and food web structure of natural ecosystems, negatively impacting societies that depend on these ecosystems (Cheung et al. 2009; Pereira et al. 2010). To manage ecological impacts of climate change, and alleviate unwanted socioeconomic impacts of species' range expansions (Burrows et al. 2014), accurate predictions of the timing and location of species redistribution are required (Frusher et al. 2014). Despite the importance of this information, factors regulating species' range expansions are largely unresolved (Hellmann et al. 2012; HilleRisLambers et al. 2013; Urban et al. 2013). Recent evidence suggests that the supply of propagules to a new range (i.e., propagule pressure, Gaylord and Gaines 2000; Keith et al. 2011) and underlying climactic conditions at higher latitudes (i.e., which will impact species climate envelope, Pinsky et al. 2013) may substantially determine capacities of species to range-shift with shifting isotherms. However, independent of propagule input and background abiotic conditions, we can expect that availability of habitats that support recruitment may ultimately determine whether a species successfully colonises higher latitudes (Hill et al. 2001; Warren et al. 2001; Honnay et al. 2002; Travis 2003; Cheung et al. 2010; Mair et al. 2014).

Climate change may directly influence species' range expansions by making higher latitudes more thermally tolerable, but also indirectly, by altering the structure of habitats within a new range (HilleRisLambers et al. 2013). For example, the response of autogenic ecosystem engineers to climate change may alter the geographic distribution, cover, abundance and three-dimensional structure of both marine (i.e., scleractinian coral, kelp) and terrestrial habitat (i.e., trees) (Hoegh-Guldberg et al. 2007; Brierley and Kingsford 2009; Yamano et al. 2011; Harley et al. 2012; Martin and Maron 2012). Such changes to autogenic ecosystem engineers may substantially control species' capacity to colonise higher latitudes by impacting the availability of suitable habitat resources, such as shelter and living space, within the receiving environment (Hodgson et al. 2011a; Travis et al. 2013). The response of autogenic ecosystem engineers to climate change may then facilitate species' range expansions if suitably structured habitats increase in extent (Hodgson et al. 2011b; HilleRisLambers et al. 2013), or restrict range expansions if habitats supporting colonisation are disturbed or degraded (Travis 2003). Despite this, roles of thermally-driven habitat change in facilitating or constraining species' range expansions are largely unknown, and need to be understood before impacts of climate change on natural ecosystems may be accurately predicted.

Many temperate marine ecosystems are undergoing substantial changes in function and composition, resulting from the colonisation of tropical reef fishes (Nakamura et al. 2013; Feary et al. 2014; Vergés et al. 2014), amid substantial reductions in biogenic habitat structure (Schiel et al. 2004; Ling 2008; Tait and Schiel 2011). Such ecological changes are being driven by intensification of poleward flowing boundary currents with climate change, resulting in increased poleward supply of warm subtropical and tropical water along western continental boundaries (Wu et al. 2012). As coastal waters warm, the multi-dimensional structure associated with temperate macroalgal forests (i.e., canopy, subcanopy and basal layers) is shifting to algal turf and/or barren reef, covered by ephemeral or encrusting algae (Tait and Schiel 2011; Harley et al. 2012), at least prior to colonisation of tropical macroalgae (Tanaka et al. 2012). In unison, tropical fishes are increasingly colonising thermally-marginal temperate reefs, driven by increased connectivity between tropical and temperate systems and reduced severity of winter water temperatures (Figueira et al. 2009; Figueira and Booth 2010). Such changes in temperate marine ecosystems are occurring along the southeastern (SE) Australian and western (W) Japanese coastlines (Hobday et al. 2007; Tanaka et al. 2012; Nakamura et al. 2013; Feary et al. 2014); two hotspots of warming (i.e., ~1.3ºC increase in sea surface temperatures from 1900 to 2008; Wu et al. 2012) that results from the strengthening of the East Australian Current (Australia) and the Kuroshio Current (Japan) (Wu et al. 2012).

Decline in habitat structure, resulting from loss of temperate macroalgae, may substantially impact early life success of range expanding tropical fishes. Although many tropical reef fishes are readily supplied to temperate regions as larvae (Booth et al. 2007) and may physiologically tolerate temperate water temperatures (Eme and Bennett 2008; Figueira et al. 2009), macroalgal cover of temperate reefs will likely influence recruitment success (i.e., survival of individuals from settlement to the reef environment through to maturity). Diversity in available habitats and topographic complexity, such as that associated with algal forests, can strongly influence the spatial distribution of both temperate and tropical reef fish assemblages (Choat and Ayling 1987; Curley et al. 2002; Anderson and Millar 2004; Wilson et al. 2010) by determining shelter availability (Shulman 1984, 1985), changing physical stress (Johansen et al. 2007; Johansen et al. 2008) and/or through influencing competition and predation on new recruits (Beukers and Jones 1998; Almany 2004a). We can expect then that any change in the composition and/or structure of macroalgal communities within temperate reefs may ultimately impact the recruitment success of tropical fishes. For instance, species may positively associate with the structural complexity provided by macroalgal habitats, with lower pre- and post-settlement success within areas devoid of macroalgal communities, presumably due to lower predation rates, as found for some temperate reef fishes (Connell and Jones 1991; Levin and Hay 1996). In contrast, tropical reef fish recruits may avoid reef patches dominated by macroalgae, as physical movement of such habitats associated with wave action and/or relatively low levels of structurally stability may limit the availability of suitable fine-scale microshelter for new settlers (Kingsford and Carlson 2010).

The temperate systems of both SE Australia and W Japan provide a rare opportunity to investigate how climate-change mediated macroalgae loss may structure the density, richness and diversity of range expanding tropical reef fishes. To determine the influence of temperate reef habitat structure on recruitment success of tropical fishes, the density, richness and diversity of new recruit and juvenile tropical fishes (hereafter termed ‘vagrants’) were compared between macroalgal-dominated habitat (e.g., Genera *Ecklonia*, *Phyllospora*, *Sargassum*) and non-macroalgal habitats, consisting of low-lying turfing algae (e.g., Phylum Rhodophyta and Phaeophyta) and barren rocky reef, which was comprised of rock covered in encrusting and ephemeral Rhodophyta and Phaeophyta spp., or bare rock with no algae. To examine which factors contributed to differences in recruitment of tropical fishes among non-macroalgal and macroalgal reef patches, reef structure (i.e., topographical complexity), wave exposure, temperate reef fish community (including competitors and predators) and benthic composition were also quantified. In addition, to test whether habitat selection was the direct result of larval settlement preference, rather than immigration and/or differential mortality between habitats, habitat choice experiments were conducted in laboratory aquaria to examine the degree to which juveniles of the common tropical damselfish *Pomacentrus coelestis* distinguished between macroalgal and non-macroalgal habitat at settlement.

4.2 Methods

4.2.1 Tropical fish recruits on macroalgal and non-macroalgal temperate rocky reef

Underwater visual surveys of new recruit and juvenile tropical fishes were conducted in summer and early autumn; when these fishes recruit into coastal waters of temperate, SE Australia (January - May 2011, 2012 and 2014) and W Japan (July 2013) (Booth et al. 2007; Kuiter 1993; Nakamura et al. 2013) (Fig. 4.1). We quantified the density, richness and diversity of vagrant assemblages using haphazardly placed Global Positioning System (GPS) - tracked timed swims on snorkel in 0 - 4 m water depths within partially-exposed oceanic reefs (i.e., lee-side of headlands). To allow calculation of fish densities, paths swam were tracked by GPS (Garmin^{TM}; ≤ 3 m accuracy) at 5 sec intervals to measure distances surveyed. This survey method allows more accurate detection of richness and diversity of vagrants within temperate reefs than standard belt transects, with comparable accuracy and precision of density estimates (Chapter 2; Beck et al. 2014). Six 5 min GPS-tracked swims were conducted surveying vagrants within patches of each macroalgal and non-macroalgal habitat at seven and three sites, within SE Australia and W Japan, respectively; all sites were separated by 2.5 - 40 km. These reef patches were interspersed and haphazardly selected to ensure any influence of wave exposure on fish recruitment was comparable between sites and habitats. Macroalgal habitats surveyed within SE Australia comprised *Ecklonia radiata*, *Sargassum* spp. and *Phyllospora comosa* (Figure 2; macroalgal cover of reef patches surveyed were >75%). Macroalgal habitat in W Japan was dominated by *Ecklonia cava* (i.e., this species covered > 75% of macroalgal patches surveyed). Barren reef patches were bare rock or encrusted or covered with low relief (< 10 cm height) ephemeral or turfing Rhodophyta and Phaeophyta spp. (Fig. 4.2).

Tropical fishes encountered within 1 m either side of the observer were identified to species and their total length (TL) visually estimated. To avoid wrongly assigning individuals to a habitat due to the response of a fish to an observer, only individuals found within ±0.5 m from the edge of macroalgal and non-macroalgal habitats were recorded. Individuals were classified as new recruits or juveniles based on the family specific length-age criteria (established by Booth et al. 2007), with functional group assigned according to Froese and Pauly (2014). Tropical species were defined by the latitudinal range of a species: breeding-sized individuals that are restricted generally to between the Tropics of Cancer and Capricorn; 23°27' N and S, respectively (Froese and Pauly 2014). In total, 126 and 18 surveys of juvenile tropical fishes, within both macroalgal and non-macroalgal reef patches, were conducted in SE Australia (across three years) and W Japan (one year), respectively. All surveys were conducted by one observer (HJB) between 09:00 and 17:00, when water visibility was > 5 m and swell was < 1 m.

4.2.2 Abiotic and biotic features of non-macroalgal and macroalgal temperate rocky reef

To test whether macroalgal cover *per se* influenced tropical fish recruitment to temperate reefs, the vagrant and resident temperate reef fish species richness, density of all fish functional groups (i.e., piscivores, planktivores, herbivores and benthivores;

Froese and Pauly 2014), and total abundance of these fishes, reef rugosity (i.e., structural complexity), benthic habitat composition and wave exposure (using a fetch-based index, Chapter 3) were measured in each SE Australian reef patch surveyed during 2014. Reef rugosity was measured at three haphazardly selected areas (i.e., every 10 swim kicks) within each reef patch using the ratio of surface distance to linear distance of a 5 m chain (Risk et al. 1972; n = 126 in both macroalgal and non-macroalgal habitats). Habitat composition of each reef patch was determined by recording the proportion of time each habitat was passed over during replicate surveys. Habitat was classified as 'macroalgae' (both overall and individual species; >75% of reef covered; height > 10cm), 'turfing algae' (branching algae with height < 10 cm) or 'barren' (where all branching algae was absent). Wave-exposure for each site was calculated using a fetch-based index with MicroStation^{TM} GIS. Fetch lines were constructed with 7.5° spacing around the midpoint of survey sites to a maximum of 650km (i.e., minimum fetch distance for fully developed seas to form) and divided by the sum of fetch distances by the maximum possible total; index units are dimensionless, with exposure increasing from 0 to a maximum exposure value of one (Hill et al. 2010).

4.2.3 Settlement choice of tropical fish larvae: macroalgal vs non-macroalgal habitat

To test whether the association of vagrants with different temperate reef habitats was established by settlement preference, settlement decisions of the damselfish *Pomacentrus coelestis* were tested within aquarium trials at Yokonami Beach, W Japan (Fig. 4.1). *P. coelestis* is one of the most common tropical species recruiting to SE Australian and W Japanese temperate reefs (Booth et al. 2007; Nakamura et al. 2013; Soeparno et al. 2013). *P. coelestis* was selected as the focal species due to its high abundance throughout this western Japan site (Nakamura et al. 2013). Moreover, no other tropical fish species were caught in sufficient numbers to test their settlement preference during the experiment.

P. coelestis larvae were collected using light-traps across four consecutive nights. At 21:00 on the night of collection, a single *P. coelestis* larvae was released into the middle of 85 L outdoor, rectangular aquaria (*sensu* Feary et al. 2007b) containing a distinct patch of encrusting algae covered rock and the kelp, *E. cava*; both habitats were the most common non-macroalgal and macroalgal habitats in W Japan. Habitats were placed at opposite ends of the aquarium, with both habitats covering 11.6 – 29.6% of aquaria bottom. Habitat choice of *P. coelestis* between the non-macroalgal and macroalgal habitat were recorded at sunrise ~05:30 (for 15 min), then 08:00 (for 15 min), with 'choice' considered when an individual was found ≤ 2 cm from a habitat for at least 10 min. Twenty four settlement trials were conducted, with each individual used only in a single trial. Between trials, habitats were randomly switched between ends of the aquaria to reduce any 'tank' effect.

4.2.4 Statistical analyses

As the number of survey occasions (three years in SE Australia, one year in W Japan), replicate surveys (126 in SE Australia, 18 in SE Japan) and number of sites (seven in SE Australia, three in W Japan) differed between regions, tropical fish assemblages were separately compared within SE Australia and W Japan. To determine whether temperate macroalgal cover influences recruitment of tropical fishes, we compared the total tropical fish assemblage density (i.e., total individuals per m^2) and species richness (i.e., total species per m^2), as well as the density and richness of functional groups, between macroalgal and non-macroalgal habitat (fixed), site (random) and year (SE Australia only; random), using permutation analysis of variance (PERMANOVA; Type III Sums of Squares; 9999 permutations under the reduced model) (Anderson 2001).

The species and functional diversity of tropical fish assemblages was measured and compared between habitat, site and year (SE Australia only) using *K*-dominance plots. As a diversity measure, *K*-dominance plots better account for species and functional group evenness than single value diversity indexes (Lambshead et al. 1983). *K*-dominance plots were constructed individually for replicate surveys on fourth root transformed density data (Clarke and Gorley 2006; Clarke et al. 2006), cumulatively ranking species and functional diversity, expressed as a percentage of all species, in decreasing order of their density. Fourth root transformations were used since there many low and some high fish counts within survey replicates; as recommended by Quinn and Keough (2002). Pairwise distances between *K*-dominance plots, constructed for each survey using Manhattan distance metrics, were then calculated using DOMDIS (PRIMER^{TM} v6 with PERMANOVA+ extension) (Warwick 1986; Clarke 1990; Clarke and Gorley 2006). *K*-dominance plots, both for species and functional diversity, were then compared between years (SE Australia only), habitats and amongst locations by PERMANOVA, using the same design as for richness and diversity (above). Functional groups that were important contributors to dissimilarity of fish assemblages between habitats were identified using the similarity percentages routine (SIMPER; Clarke 1993) then graphically explored by principle coordinate analysis (PCO) using Spearman's rank correlation. Analysis of similarities (ANOSIM) was used to test for differences in functional groups of vagrant fishes between habitats. We considered functional groups with % $\bar{\delta}_i$ > 10% as important contributors to overall dissimilarity between habitats; where $\bar{\delta}_i$ is the average contribution of the *i*th functional group to the overall dissimilarity [$\bar{\delta}$] between the two habitats. The densities of functional groups, found by SIMPER as important contributors to variance in fish assemblages, were then compared between years (SE Australia only), habitats and sites using PERMANOVA (as above).

All survey data were inspected for homogeneity of variance using the PERMDISP procedure (PRIMER^{TM} v6 with PERMANOVA+ extension), with data ln(X+1) transformed where required. PERMANOVA was used here as it is typically more robust to heterogeneity of variances and assumptions of data normality than parametric analyses (Underwood 1997; Anderson and Walsh 2013). Where the *p*-value of a factor was > 0.25, it was removed from the model by pooling this factor with the residual (following Underwood 1997). The Monte-Carlo *p*-value [*p*(mc)] was used when the number of unique permutations for a term within an analysis was < 100 (following Anderson 2001). Significant interactions between factors for all analyses of field parameters were explored using PERMANOVA *post-hoc* pairwise tests.

To determine the combination of environmental variables (i.e., temperate fish assemblage, reef complexity, habitat composition and/or wave exposure) that best predicted variance in vagrant assemblages between macroalgal and non-macroalgal temperate reef habitats, the best-fit distance based linear model (DistLM) procedure [PERMANOVA; 9999 permutations pertaining to the Akaike information criterion with a correction for finite sample sizes (AIC_c); with a maximum of 10 variables] was conducted using Bray-Curtis similarity measures on fourth root transformed vagrant abundance for all sites, habitats and species composing surveys during 2014 in SE Australia (Clarke and Gorley 2006). Environmental data were checked for multicollinearity and dispersion using draftsmen plots, $\ln(X+1)$ and square root transformed where required and then normalised prior to analysis. Factors best explaining variance in SE Australian vagrant communities were graphically explored by PCO and Spearman rank correlation.

To further analyse whether temperate fishes influenced habitat associations of tropical fishes, densities of planktivores, omnivores, herbivores and piscivores (the primary trophic groups detected) were compared between macroalgal and non-macroalgal reefs (fixed) and sites (random) by PERMANOVA.

To determine whether vagrant habitat choice was associated with active preference at settlement, the proportion of *P. coelestis* that settled into either the macroalgal or non-macroalgal habitat were compared using binomial tests, treating the probability of either outcome by chance as 50%. These proportional data were normalised by arcsine square root transformation prior to analysis. *A priori*, $p < 0.05$ was the set level of significance for all analyses. Field data were analysed using PRIMER$^{\text{TM}}$ v6 with PERMANOVA+ extension, whilst SPSS$^{\text{TM}}$ v20 was used to analyse settlement trial data.

4.3 Results

4.3.1 Tropical fishes recruits in non-macroalgal and macroalgal temperate rocky reef

Overall assemblages

A total of 1792 vagrant tropical fishes, encapsulating 39 species in seven families were surveyed within SE Australia (235 individuals, 29 species and six families) and W Japan (1557 individuals, 20 species and five families) (Table 4.1). There was a 34% overlap in species between countries, with Pomacentridae (damselfishes), Acanthuridae (surgeonfishes), Chaetodontidae (butterflyfishes), Labridae (wrasses) and Zanclidae (Moorish idol) observed in both SE Australia and W Japan.

Vagrant densities and overall species richness were over seven times greater in non-macroalgal than macroalgal reef habitats in both regions (PERMANOVA; $p < 0.05$ for these metrics in both countries; Table 4.2, Fig. 4.3). Vagrant species diversity was also greater within non-macroalgal than macroalgal habitats in both SE Australia and W Japan (PERMANOVA; $p < 0.05$ in both countries; Table 4.2). There were no significant interaction with habitat and all other factors within the model for overall densities, species richness and species diversity within either country (PERMANOVA; $p < 0.05$; Table 4.2).

Functional assemblage and individual functional groups

Planktivores were the most common functional group within SE Australia (73%) and W Japan (64%), with each assemblage also comprising herbivores (18% in both regions), benthivores (4% Australia; 16% Japan), omnivores (6% Australia; 2% Japan) and parasite cleaners (1% Australia only). The species diversity and richness of functional groups was significantly greater in non-macroalgal than macroalgal habitats in both SE Australia and W Japan (Tables 4.1 and 4.2; $p < 0.05$). There were no significant interactions between habitat and any other variable for either metric when analysed in either country ($p \geq 0.09$ for remaining terms in models).

Functional assemblages varied significantly between non-macroalgal and macroalgal habitats along PCO axis 1, explaining 68.6% and 63% of variance in functional assemblages within SE Australia and W Japan, respectively (ANOSIM; SE Australia: $R = 0.44$, $p = 0.01\%$, W Japan: $R = 0.76$, $p = 0.01\%$; Fig. 4.4). Planktivores, herbivores and omnivores in both SE Australia and W Japan, as well as benthivores in W Japan, primarily accounted for differences in assemblages between non-macroalgal and macroalgal habitats (SIMPER; $\% \; \bar{\delta}_i > 10\%$). These functional groups were positively correlated with non-macroalgal reefs along PCO axis 1 within their respective countries (Spearman correlation; $p < 0.05$, $r_s > 0.52$; Fig. 4.4).

Of the vagrant functional groups that primarily discriminated between temperate habitats, herbivore densities were greater in non-macroalgal than macroalgal reefs in W Japan [$\mathit{Pseudo}\text{-}F_{1,\,30} = 20.33$, $p(\mathrm{mc}) = 0.04$]. In SE Australia, although there was a significant interaction between year and habitat ($\mathit{Pseudo}\text{-}F_{2,\,246} = 7.93$, $p = 0.001$), when each year was analysed separately, herbivores were always found in greater densities in non-macroalgal reef (Pairwise tests; $p < 0.005$ within all three years). Omnivores were also found in greater densities within non-macroalgal reef in W Japan [$\mathit{Pseudo}\text{-}F_{1,\,30} = 4.33$, $p(\mathrm{mc}) = 0.04$], and within SE Australia ($\mathit{PseudoF}_{1,\,238} = 35.05$, $p = 0.01$), after pooling data across years; there no difference in densities among years ($\mathit{Pseudo}\text{-}F_{2,\,210} = 0.24$, $p = 0.78$)**.** The influence of habitat type on planktivore density differed at the site level in both W Japan ($\mathit{Pseudo}\text{-}F_{2,\,30} = 7.68$, $p = 0.02$) and SE Australia ($\mathit{Pseudo}\text{-}F_{6,\,238} = 2.91$, $p = 0.008$). However, planktivores were found in greater densities within non-macroalgal than macroalgal habitats in five of six sites in SE Australia (Pairwise; $p < 0.05$ at all sites but MB), after pooling data across years – no difference in density was detected among years ($\mathit{Pseudo}\text{-}F_{2,\,210} = 1.45$, $p = 0.27$). In W Japan, planktivores were found in greater densities in non-macroalgal reef at KU and US (Pairwise tests; $p \leq 0.001$ at both sites), but not at TA (Pairwise test; $p = 0.2$). Failure to detect a significant difference in planktivore densities between habitats at MB and TA was largely due to infrequent observations of tropical fishes at these sites; densities were lowest at these sites within their respective country. In W Japan, influence of habitat type on benthivore density differed at the site level ($Pseudo\text{-}F_{2, 30} = 5.52$, $p = 0.001$) with benthivores found in greater densities in non-macroalgal reefs in TA [t = 2.76, p(mc) = 0.02] but not KU or US [p(mc) > 0.13 at both sites]. Nevertheless, lack of detected difference in benthivore densities at the latter two sites were likely due to rarity; one benthivore was observed in KU, whilst only one out of four benthivores was observed in macroalgae in US. All interactions involving 'habitat' type with site and/or year (SE Australia only) not reported here were non-significant in both countries (i.e., $p > 0.05$ for all other interactions with habitat type not reported).

4.3.2 Abiotic and biotic influences on tropical fish recruitment

Variance in vagrant assemblages amongst habitat patches was best explained by the proportion of macroalgae (11.7%) and barren reef (17%), as determined by DistLM. Vagrant assemblages were positively associated with the extent of barren reef (Spearman rank; $r_s = 0.52$, $p = 0.001$), where branching algae was absent, and negatively corresponded with the cover macroalgae (Spearman rank; $r_s = -0.39$, $p = 0.02$; Fig. 4.5). The best combination of explanatory variables also included the density of the overall temperate fish assemblage (13.7%), but this failed to explain variance in vagrant assemblages, since densities of overall temperate fish assemblages were also positively associated with non-macroalgal reefs (Fig. 4.5).

Densities of temperate planktivores were significantly greater in non-macroalgal than macroalgal reefs ($PseudoF_{1, 70} = 16.13$, $p = 0.01$), whilst no significant interaction was detected between habitat and site ($PseudoF_{6, 70} = 1.78$, $p = 0.12$). Differences in omnivore densities between habitats depended on the site ($PseudoF_{6, 70} = 3.43$, $p =$

0.006), with omnivores in greater densities in non-macroalgal than macroalgal reef at four of the seven sites, and no difference in densities between habitats at the remaining three sites (Pairwise; $p < 0.05$ four sites and $p > 0.05$ at three sites). There was no significant difference in densities of temperate herbivores, benthivores and piscivores between the two habitats, nor was there a significant interaction between habitat and site for these trophic groups (i.e., $p > 0.05$ for main test of habitat and interaction between habitat and site for each of these trophic groups).

4.3.3 Settlement choice of tropical fish larvae into macroalgal and non-macroalgal habitat

A significant proportion (87.5%) of *P. coelestis* larvae settled into the non-macroalgal habitat (Binomial Test, $p < 0.001$), while only three of the 24 individuals settled into the macroalgal habitat. No individual changed habitat choice between sunrise (~05:30) and 08:00.

4.4 Discussion

To range-shift poleward with warming oceans, tropical fishes must access habitats at higher latitudes that support their recruitment (Feary et al. 2014). But at the vanguard of range expansion, structural changes in temperate reef habitats, associated with reducing cover of temperate macroalgae with rising water temperatures (Tait and Schiel 2011; Harley et al. 2012), may influence recruitment success of these tropical fishes. Here, the overall density of assemblages, functional and taxonomic diversity and species richness of new recruit and early juvenile tropical vagrants were greater within non-macroalgal than macroalgal-dominated temperate reefs throughout both SE Australia (this pattern was found throughout all three years) and W Japan. These results suggest substantial reductions in the structure of macroalgal-dominated temperate reefs, predicted to be associated with warming coastal waters (Tait and Schiel 2011; Harley et al. 2012), should facilitate the range expansion of many tropical fishes by increasing the availability of preferred recruitment habitat, at least within shallow temperate regions with a moderate to high wave climate prior to invasion of tropical algae.

The proportion of reef covered by macroalgae appeared to best explain the density, richness, diversity and functional composition of vagrant fish assemblages among temperate reefs; vagrants were positively associated with reefs where all branching algae were absent, but mostly negatively related with reef habitats dominated by macroalgae. Despite the potential impact of temperate reef fish community structure in influencing colonisation success of vagrant fishes (Bates et al. 2013), the overall assemblage density, densities of individual functional groups and species and functional richness of temperate reef fishes failed to significantly explain such strong association of tropical fishes with non-macroalgal reefs. Such non-significant impacts on vagrant assemblage structure were apparent even though the temperate fish assemblage substantially overlapped in their ecological niche. If competition with temperate species for trophic resources led to association of vagrants with non-macroalgal reef, and avoidance of macroalgae, we may expect greater densities of temperate competitors in macroalgal reef. However, densities of individual trophic groups of temperate fishes were never greater in macroalgal than non-macroalgal reefs. For instance, temperate planktivores were in greater densities in non-macroalgal than macroalgal patches, as were omnivores at four of the seven sites. Competition for trophic resources with benthivores and herbivores also did not appear to influence habitat associations of vagrants since densities of these trophic groups were comparable between the two habitats. Moreover, predation did not appear to structure the association of vagrants with non-macroalgal reef since densities of temperate piscivores did not vary significantly between the two habitats. In addition, there was a positive association between the density of the overall temperate reef fish community and non-macroalgal habitats. Hence, despite using the same habitats in which tropical fishes were found, temperate fishes did not appear to have negatively influenced recruitment of tropical fishes into these habitats.

Although there are potentially a range of factors which favour vagrant settlement into non-macroalgal habitat patches, structural differences between areas devoid of macroalgal habitat and macroalgal reef patches may be vital in determining successful vagrant settlement. For example, there is a substantial literature showing that structurally stable tropical reef habitats, predominantly scleractinian coral communities, are an important habitat in which many tropical fishes will settle and recruit (Wilson et al. 2006; Pratchett et al. 2011). Such habitat-associated recruitment has been argued to be predominantly due to the structural stability and complexity of scleractinian-dominated communities, which provide adequate shelter for small, newly recruiting fishes from resident predators (Beukers and Jones 1998), lessen impacts of physical stressors, such as wave action (Johansen et al. 2007; Johansen et al. 2008), and mediate competition for resources between resident and newly recruiting individuals (Friedlander and Parrish 1998; Almany 2004a; Gratwicke and Speight 2005; Wilson et al. 2010). Stable reef habitats may also require less energy for marine organisms to associate with than non-stable, moving macroalgal-dominated reef, and in some cases, abrasion caused by moving kelp may even force them out of this habitat (Velimirov and Griffiths 1979; Connell 2003; Gagnon et al. 2004). Furthermore, open reef habitats (e.g., non-macroalgal temperate reef) may allow prey to more easily see and escape from predators than macroalgal patches, as shown for marine invertebrates (Konar and Estes 2003; Gagnon et al. 2003) and proposed for some tropical fishes (Hoey and Bellwood 2011; Hoey 2010).

There was a greater association of vagrants with barren reef, cleared of all branching algae, than turfing algal covered reef throughout both regions. This suggests that it is not only a reduction in macroalgae that will structure vagrant recruitment, but a change from algae covered habitat to more barren rocky habitats. Based on the strong positive association of vagrants with barren reef, we may predict that tropical fish recruitment will be best supported where all branching algae are reduced. Such changes in benthic communities are the direct result of warming waters and/or increased grazing by molluscs and urchins with climate change (Schiel et al. 2004; Ling 2008; Tait and Schiel 2011). In contrast, the lower association of vagrant fishes with turfing algae suggests colonisation success of vagrants may be less likely within areas where macroalgal communities have shifted to turfing algae. Nevertheless, independent of the specific shift in benthic temperate communities, species' range expansions, such as those of tropical fishes into temperate regions, should be notably facilitated when as little as 1% of suitable habitat is created within a new range (e.g., Hodgson et al. 2011b).

The active choice by settling *P. coelestis* larvae of non-macroalgal reef suggest that *in situ* associations of tropical vagrants with non-macroalgal reef may reflect a settlement preference, rather than higher post-recruitment mortality in macroalgal reef or post-settlement movement between habitats. Interestingly, selection of *P. coelestis* for the non-macroalgal habitat occurred despite wave action lacking from this tank experiment. Hence, studies are required to determine whether kelp movement may further influence habitat selection of tropical fishes at settlement. Moreover, this work did not examine the mechanisms that resulted in such settlement preference. However, cues that potentially guide reef fish settlement on large spatial scales, such as celestial references, magnetism and water movement (Leis et al. 2011), may be discounted since macroalgal and non-macroalgal habitats surveyed were interspersed and separated by only 10s of m. Conspecifics may also guide settlement of larvae (Jones 1987; Sweatman 1988; Booth 1992, 1995), but this was unlikely since established populations of tropical fishes are currently rare within SE Australian temperate reefs due to substantial overwinter mortality (Booth et al. 2007; Figueira and Booth 2010). In the absence of conspecifics, and on such fine spatial scales, larval fishes choosing between macroalgal and non-macroalgal habitats may be using a range of localised olfactory, auditory and/or visual cues at settlement (Kingsford et al. 2002; Lecchini et al. 2005; Wright et al. 2005). To further understand how temperate habitats organise settlement success of tropical fishes, further experiments are required to distinguish which of these cues guide larvae into non-macroalgal reef patches.

Here we report the important role that macroalgal cover has in structuring recruitment of tropical fishes within regions with high wave climates. However, macroalgae may structure recruitment of tropical fishes differently where wave energy is lower. For example, of the sites surveyed here, tropical fishes associated with macroalgae most commonly in those most sheltered (TB and SB, H. J. Beck, personal observation). Macroalgae in these sheltered sites may better support tropical fish recruitment because macroalgae are typically more structurally stable in low energy environments. For instance, macroalgae in sheltered reefs flexes less due to lower wave energy (H. J. Beck, personal observation). Nevertheless, such highly sheltered reefs are rare along the SE Australian and W Japanese coastlines; < 20% of SE Australian and W Japanese reefs are sheltered comparably to TB and SB (Chapter 3). Hence, at least along the highly exposed and energetic coastlines of SE Australian and W Japanese, reef with sufficient shelter to support potentially suitable macroalgae for tropical fishes are rare. Therefore, further study of tropical fish recruitment in regions where wave energy is lower and/or highly sheltered reefs are more abundant is required to further understand how interactions between macroalgae and wave action organise tropical fish recruitment.

This study suggests climate-driven habitat changes may control the redistribution of tropical fishes, with loss of macroalgae from temperate reefs with climate change likely to facilitate their recruitment, and thus colonisation. Hence, to accurately predict range expansions of many tropical fishes, an understanding of where and when macroalgae is lost from temperate regions is required. More broadly, these results highlight that changes in the availability of habitats that support species' recruitment at higher latitudes, which result from responses of habitat engineers to climate change, may largely impact if species can redistribute with climate change. Hence, responses of habitat formers to climate change in both marine (i.e., scleractinian coral, kelp) and terrestrial (i.e., trees) ecosystems may need to be considered before we may accurately predict where and when species will colonise with future environmental warming.

4.5 Tables

Table 4.1 Frequency of tropical vagrant fishes observed in underwater visual surveys of non-macroalgal (NM) and macroalga1 (M) reef habitats with southeastern (SE) Australia (2011 and 2012) and western (W) Japan (2013). Trophic grouping of species listed according to Froese and Pauly (2014).

Taxon	**SE Australia**		**W Japan**		**Trophic Grouping**
	NM	**M**	**NM**	**M**	
F. Acanthuridae					
Acanthurus dussumieri	27	3	17	0	Herbivore
Acanthurus lineatus	2	0	0	0	Herbivore
Acanthurus nigrofuscus	68	1	4	0	Herbivore
Acanthurus olivaceus	19	0	1	0	Herbivore
Acanthurus triosteges	62	0	0	0	Herbivore
Ctenochaetus binotatus	4	0	0	0	Herbivore
Ctenochaetus striatus	0	1	0	1	Herbivore
Naso brevirostris	1	0	0	0	Herbivore
Naso unicornus	17	12	0	0	Herbivore
Naso vlamingii	0	0	1	0	Herbivore
F. Chaetodontidae					
Chaetodon auriga	7	2	1	0	Benthivore
Chaetodon auripes	0	0	16	1	Benthivore
Chaetodon citrinellus	3	0	0	0	Herbivore
Chaetodon flavirostiris	6	0	0	0	Benthivore
Chaetodon kleinii	1	0	0	0	Benthivore
Chaetodon vagabundus	3	0	0	0	Benthivore
Heniochus accuminatus	0	0	1	0	Planktivore
F. Labridae					
Labroides dimidiatus	7	0	0	0	Parasite cleaner
Stethojulis bandanensis	1	0	0	0	Benthivore
Stethojulis interrupta	0	0	12	0	Benthivore
Thalassoma jansenii	1	0	0	0	Benthivore
Thalassoma lunare	1	0	0	0	Benthivore

F. Lutjanidae					
Lutjanus russelli	1	0	0	0	Piscivore
F. Pomacentridae					
Abudefduf bengalensis	21	0	4	0	Omnivore
Abudefduf sexfasciatus	14	0	6	0	Planktivore
Abudefduf vaigiensis	849	23	68	6	Planktivore
Abudefduf whitleyi	240	1	0	0	Planktivore
Amphiprion clarkia	0	0	1	0	Planktivore
Chromis weberi	0	0	2	0	Planktivore
Plectroglyphidodon leucozonus	8	0	0	0	Herbivore
Pomacentrus bankanensis	2	0	0	0	Omnivore
Pomacentrus australis	2	0	0	0	Herbivore
Pomacentrus coelestis	101	0	43	0	Planktivore
Pomacentrus nagasakiensis	0	0	12	0	Planktivore
Stegastes gascoynei	28	0	0	0	Omnivore
Stegastes apicalis	2	0	0	0	
F. Siganidae					
Siganus fuscescens	0	0	0	20	Herbivore
F. Tetraodontidae					
Canthigaster rivulata	0	0	11	4	Benthivore
F. Zanclidae					
Zanclus cornutus	3	0	1	0	Benthivore
Total individuals	1512	42	212	36	
Total species	29	4	18	6	

Table 4.2 Results of permutational analysis of variance testing for differences in density, richness and diversity (*K*-dominance) of tropical reef fish assemblages amongst habitats (H; macroalgal vs non-macroalgal reef patches), sites (S) and years (Y; Australia only) within temperate reefs of a) SE Australia and b) W Japan. Factors were pooled with the residual when $p > 0.25$, according to Underwood (2000). Bold *p*-values indicate a significant result of $p < 0.05$. * Denotes *p*(MC), used where unique permutations for a factor was < 100, following Anderson (2001) (i.e., Monte-Carlo simulations).

	Effects of variable								
	Habitat (H)			**Other variable's *p*-values**					
Parameter	***Pseudo-F***	**d.f.**	***p***	**S**	**S x H**	**Y**	**Y x H**	**Y x S**	**S x Y x H**
a) SE Australia									
Density	51.19	1,210	**0.001**	**0.04**	0.12	0.09	0.14	**0.01**	0.14
Species richness	41.0	1,210	**0.002**	0.07	0.09	0.07	0.10	**0.01**	0.08
Species diversity	131.6	1,210	**0.001**	**0.03**	0.45	0.15	0.44	0.09	0.35
Functional diversity	106.9	1,210	**0.001**	**0.01**	0.75	0.12	0.34	0.54	0.51
b) W Japan									
Density	95.4	1,30	**0.001***	0.12	0.75	-	-	-	-
Species richness	154.0	1,30	**0.007***	0.27	0.46	-	-	-	-
Species diversity	54.67	1,30	**0.001***	0.52	0.88	-	-	-	-
Functional diversity	6.82	1,30	**0.001***	0.45	0.99	-	-	-	-

4.6 Figures

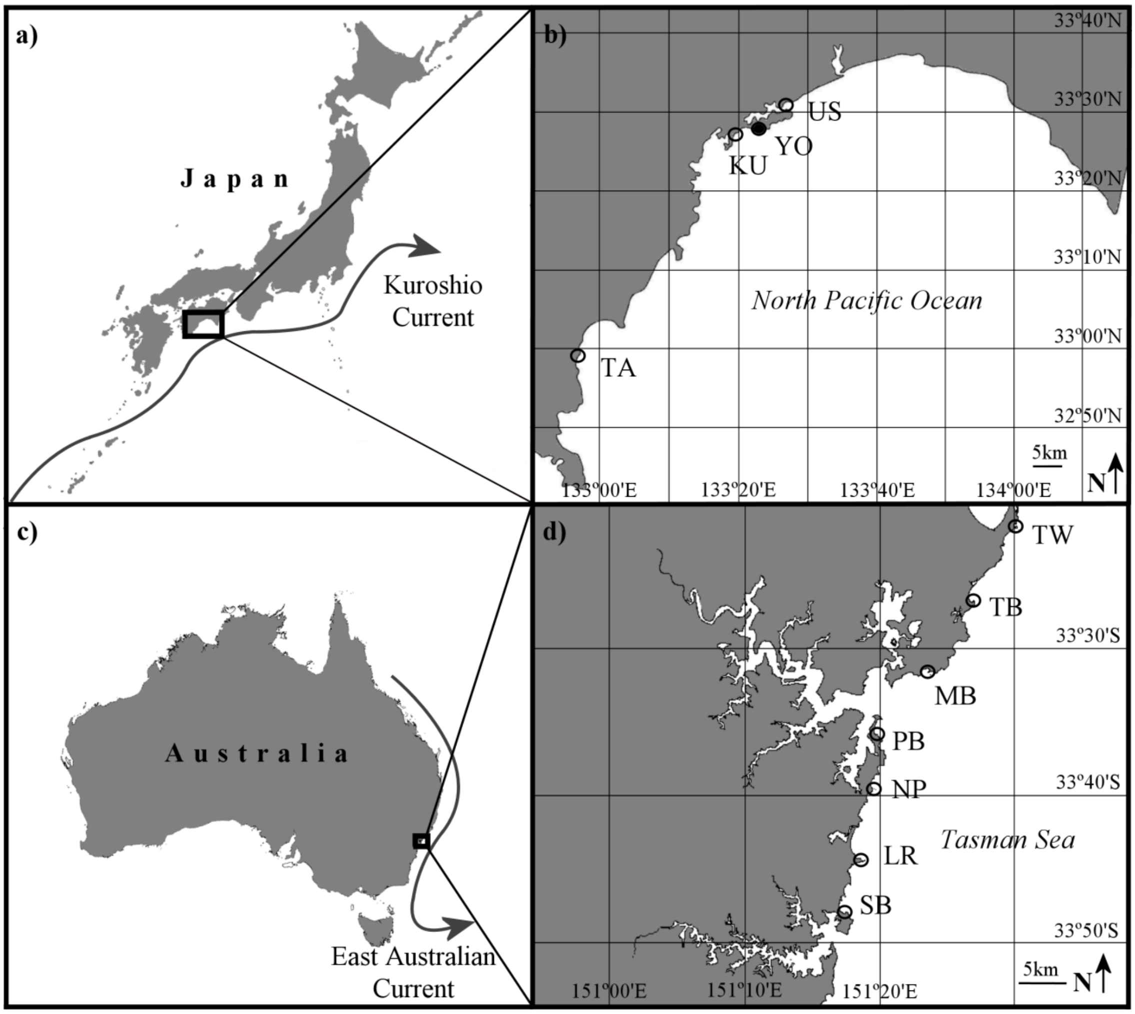

Figure 4.1 Locations of survey sites (open circles) within western Japan, insets a) and b), and southeastern Australia, insets c) and d). Tropical reef fishes are supplied to temperate latitudes as larvae from tropical sources by the a) Kuroshio Current and c) East Australian Current, where they recruit to novel reef habitats through summer within Japan and Australia, respectively. Juvenile tropical fishes were surveyed at sites by 5 min timed swims within kelp-free reef and kelp habitats, across two seasons in Australia [n = 84 per habitat; b)] and one season in Japan [n = 18 per habitat; d)]: SB = Shelly Beach; LR = Long Reef; NP = Newport; PB = Palm Beach; MB = Maitland Bay; TB = Terrigal Beach; TW = Toowoon Bay; TA = Tanoura; KU = Kutsuu and US = Usa. Settlement choice experiments were conducted at the Yokonami Rinkai Experimental Station (YO; filled circle).

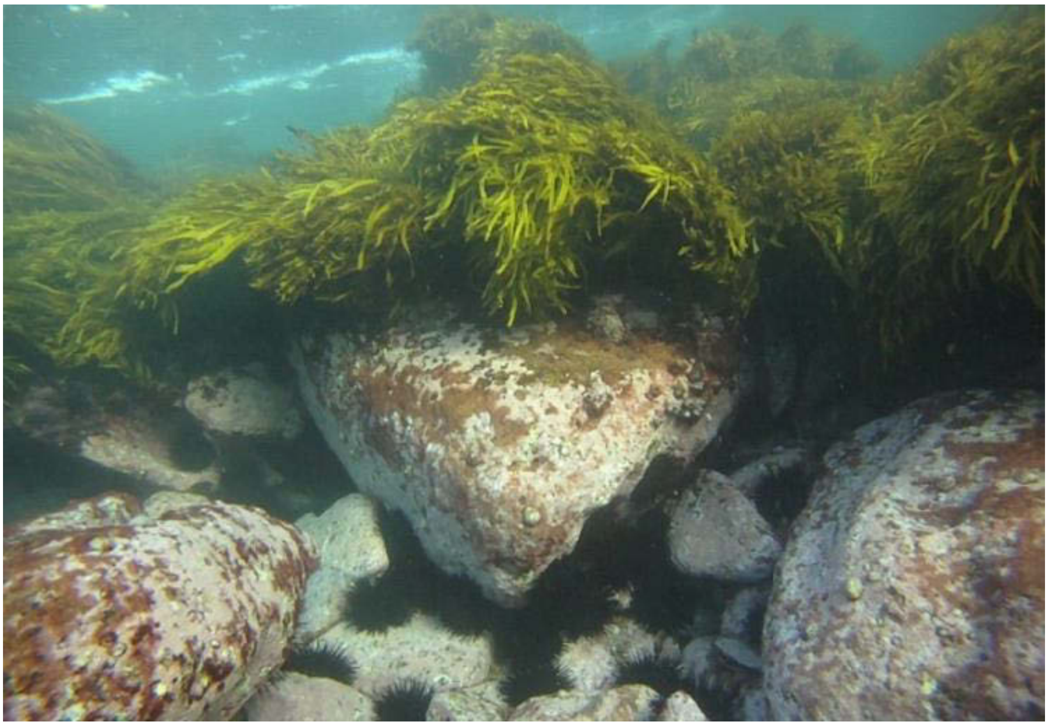

Figure 4.2 Example of macroalgal (*Phyllospora comosa*; top of image) and non-macroalgal (encrusting and low ephemeral, Phylum Rhodophyta and Phaeophyta; bottom of image) reef habitats surveyed for tropical reef fish in southeastern Australia (site = Palm Beach).

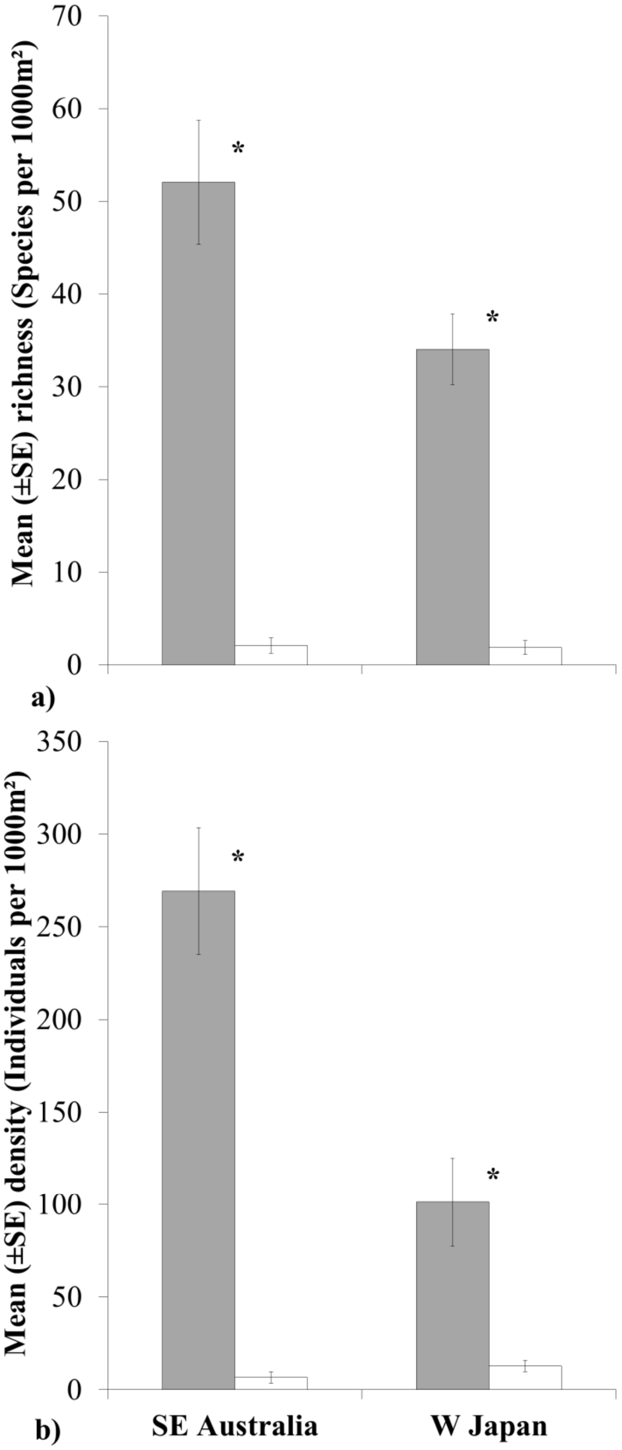

Figure 4.3 Mean (±SE) total density and species richness of tropical vagrant fishes within non-macroalga1 (grey bars) and macroalga1 reef habitats (white bars) within southeastern (SE) Australia and western (W) Japan. n = eighty-four 5 min timed swims per habitat, pooled across three years for SE Australia, and n = 18 per habitat for one recruitment season in W Japan. * Indicates a significant difference of $p < 0.05$ determined by PERMANOVA.

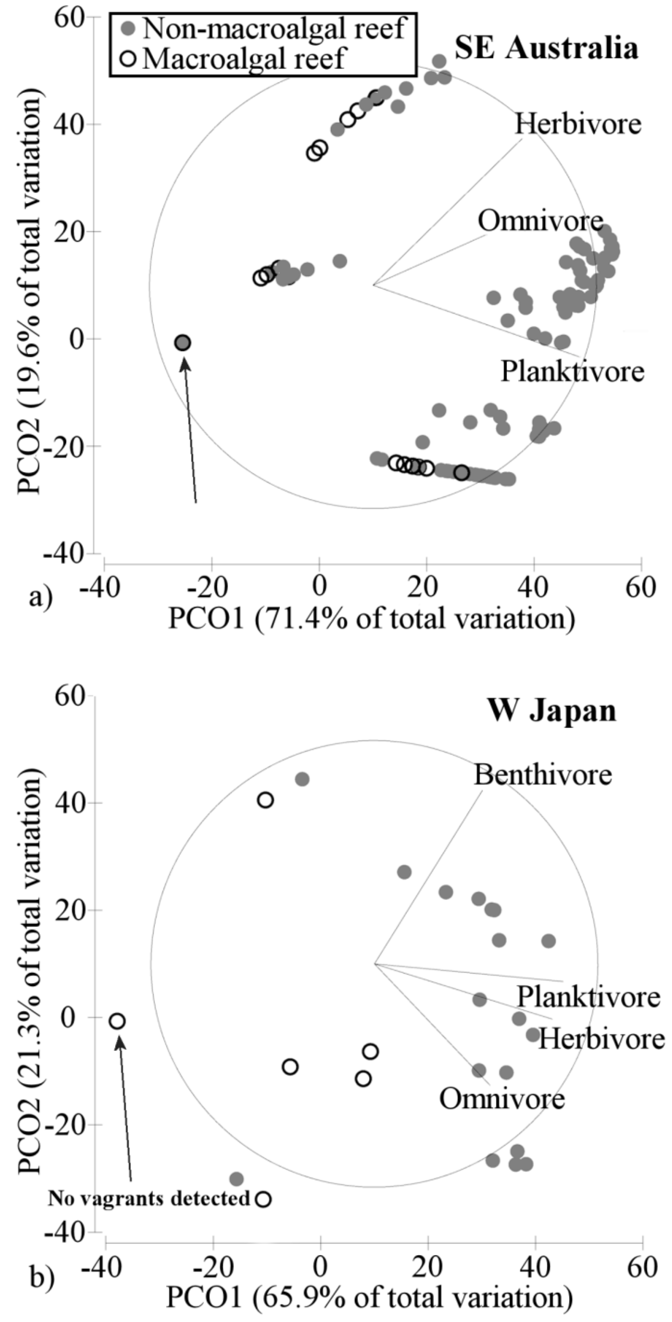

Figure 4.4 Principal co-ordinate analysis of tropical vagrant fish functional groups within macroalgal (open markers) and non-macroalgal (grey markers) reef habitats of a) SE Australia and b) W Japan. Vectors overlaid display the primary groups responsible for division of sites along PCO axis 1, determined by SIMPER analysis (result reported in text). Arrows denote replicate surveys where no vagrants were detected: n = 110 and 23 in macroalgae and non-macroalgal patches in SE Australia, respectively, and n = 13 in macroalgae in W Japan. In total, n = 126 and 18 replicate surveys were conducted in both habitats within SE Australia and W Japan, respectively. Note: grey circle with black outline are overlapping data points from the two habitats.

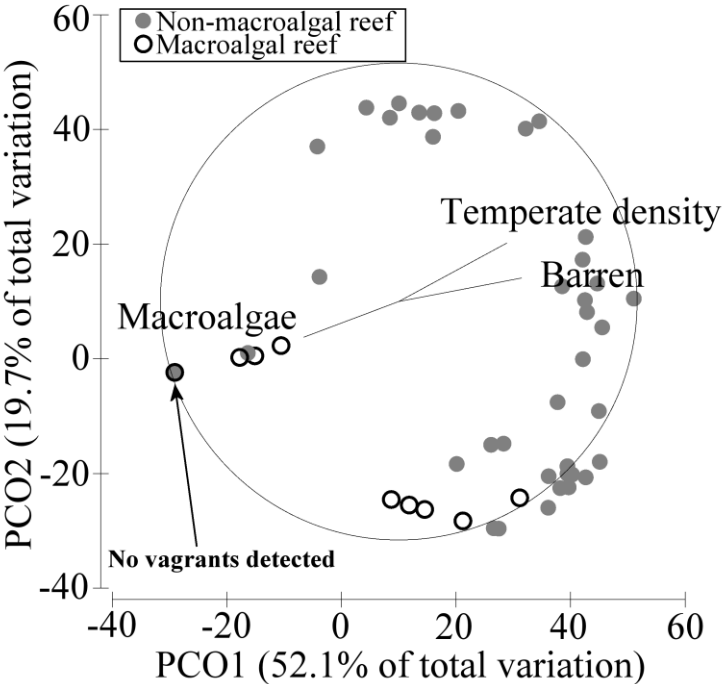

Figure 4.5 Principal co-ordinate analysis of tropical vagrant fish species within macroalgal (open markers) and non-macroalgal (grey markers) reef habitats of SE Australia during 2014, with vectors overlaid displaying the environmental correlates that best explained variance in fish assemblage data (determined by DistLM; result reported in text). Arrow denotes replicate surveys where no vagrants were detected: n = 34 and 5 in macroalgae and non-macroalgal patches, respectively. In total, n = 42 replicate surveys were conducted in both habitats. Note: grey circle with black outline are overlapping data points from the two habitats.

Chapter 5: Temperate predators and seasonal water temperatures impact feeding of a range expanding tropical fish

Beck HJ, Feary DA, Fowler AM, Madin EMP, Booth DJ (*Submitted*) Temperate predators and seasonal water temperatures impact feeding of a range expanding tropical fish. Marine Ecology Progress Series.

Abstract

Redistribution of species into higher latitudes with climate change threatens the function and composition of ecosystems globally, yet factors constraining or facilitating range expansions are poorly understood. Native predators may constrain range expansions of prey directly through consumption, or indirectly by restricting their feeding activity. However, the extent that native predators impact range-expanders will likely be structured by physiological mismatches between these groups, associated with background environmental temperature. Here we examined how temperate predators and seasonal water temperature affected foraging behaviour of the planktivorous tropical reef fish, *Abudefduf vaigiensis*, within southeastern Australian waters, an emerging new range for this species. Foraging excursions of *A. vaigiensis* were compared between predator-rich marine reserves and predator-depauperate fished reefs during summer (~22°C water) and winter (~18°C water). *A. vaigiensis* exhibited shorter foraging excursions in marine reserves than fished reefs, with foraging excursions also higher during summer than winter. An aquarium experiment isolated the effects of predation risk and water temperature on *A. vaigiensis* feeding excursions and bite rates. Groups were held at 18 or 22°C and visually exposed to three risk treatments: a temperate predator, a predator control (temperate herbivore), and no predator (an empty tank). Foraging excursions and feeding rates were reduced with exposure to predators at 22°C, but did not differ between predator and the predator control or empty tank at 18°C. Results indicate temperate predators may restrict the success of range expanding tropical reef fishes, by reducing an individuals' food intake during summer months. In contrast, winter water temperatures may limit feeding of range expanding tropical fishes, independent of predation risk. Our results suggest protection of predators from fishing should improve resistance of marine ecosystems to impacts associated with range expanding prey.

5.1 Introduction

Ongoing warming of marine and terrestrial environments is facilitating, and in some cases necessitating, the expansion of species poleward (Parmesan and Yohe 2003; Sorte et al. 2010; Poloczanska et al. 2013). This climatically-driven redistribution is changing the structure and function of ecosystems globally by displacing native fauna and modifying food webs (Harley et al. 2006). Some of the most rapid range expansions detected are those of marine fishes, due to typically high connectivity amongst populations and their great sensitivity to changes in water temperatures (Sorte et al. 2010). Despite this, there is still relatively little understanding of factors that constrain or facilitate species' geographic responses to climate change, including those of marine fishes (Li et al. 2011; Yang et al. 2011; Blois et al. 2013; Liancourt et al. 2013). Indeed, range expansions of marine fishes may be determined by the total supply of species' larvae moving into a new range (i.e., propagule pressure, Gaylord and Gaines 2000; Keith et al. 2011), the suitability and availability of local resources (i.e., food and shelter; Cheung et al. 2010), and the total variance in background environmental conditions (i.e., species climate envelope, Parmesan 2006; Parmesan and Yohe 2003; Pinsky et al. 2013). However, even if marine fishes overcome these supply, resource and abiotic filters to colonisation, the permanence of marine fish populations within a new range may still be limited by adverse interactions with native fauna (Hellmann et al. 2012; Bates et al. 2013; HilleRisLambers et al. 2013). In particular, native predators may impact the condition, growth and survival of newly arriving species (Carlsson et al. 2009; Gilman et al. 2010; Estes et al. 2011). Although empirical studies of predatory controls over range expanding species are largely lacking, we may predict from impacts of predators on invasive fishes (Sorte et al. 2010), that adverse interactions with native predators may greatly impede climate-driven range expansions of prey fishes (Baltz and Moyle 1993; DeRivera et al. 2005). If so, the diversity and abundance of native piscivore communities may mediate impacts of range expanding fishes within marine ecosystems (Bates et al. 2013).

Native piscivores may constrain the shifts of range-expanders into new habitat directly through predation-induced mortality (e.g., Ling et al. 2009; Ling and Johnson 2012), but also indirectly by restricting access to required resources (as found for invasive species; Holt and Barfield, 2009; Barrios-O'Neill et al. 2014; Dick et al. 2014). Typically, where predator abundance is high, prey fishes' movements are reduced in the presence of predators, constraining access to food of sufficient quality or quantity (Madin et al. 2010). Over time, this reduced feeding activity may have substantial consequences for the growth, condition, survival of an individual, and ultimately the stability of a population (Lima and Dill 1990; Dill et al. 2003; Preisser et al. 2005). In this sense, provided range expanding fishes recognise native predators as a threat (McCormick and Holmes 2006), avoidance behaviour within a species where predator densities are higher (i.e., increased sheltering and/or reduced movement of the species) may result in lower foraging excursions and therefore food intake (e.g., Schmitz et al. 1997; Trussell et al. 2006; Madin et al. 2010). Hence, understanding how native piscivores influence feeding behaviour of range expanding prey fishes will be vital in predicting fishes' success within expanding ranges, as well as forecasting impacts associated with their geographic redistribution into high latitude habitats (O'Gorman 2014).

Outcomes of interactions between range expanding prey fishes and native piscivores are likely to vary seasonally due to differential responses between these groups of organisms to environmental temperatures (Davis et al. 1998b; Gilman et al. 2010; Harley 2011; Grigaltchik et al. 2012; Milazzo et al. 2013; Nagelkerken and Simpson 2013). During summer months, the physiological performance of both native piscivores and range-expanders may be relatively similar, with both assemblages showing high movement and feeding activity (Pörtner and Peck 2010). Within these warm periods, feeding excursions and bite rates of range expanding fishes may be substantially structured by native predator abundance, as within their historic range (e.g., Stallings, 2008; Madin et al. 2010). However, within cooler winter months, although both assemblages will likely reduce feeding activity as a result of reduced physiological performance (Figueira et al. 2009), range-expanders may reduce their activity levels more than native species since tropical species are physiologically adapted to much warmer climates (Rijnsdorp et al. 2009; Pörtner and Peck 2010). Hence, such seasonal cooling may push range-expanders further away from their physiological optimum than natives. In effect, as environmental temperatures decrease seasonally, physiological constraints to the feeding activities of range expanding prey may outweigh those imposed by native predators, resulting in substantially reduced feeding excursions and potentially lower feeding rates independent of predator abundance (e.g., Figueira et al. 2009). Therefore, as waters within a new range cool during winter and approach the lower thermal thresholds of range-expanders, predator-induced constraints to feeding may diminish, with feeding activities likely to be more strongly suppressed by slow metabolism within range-expanders (Pörtner 2001; Pörtner and Peck 2010).

To determine the role of native piscivore abundance and environmental temperature in structuring the feeding ecology of range expanding marine fishes, we focused on juveniles of the tropical damselfish *Abudefduf vaigiensis* within temperate reefs of southeastern (SE) Australia. This species is one of six tropical damselfishes predicted to colonise temperate SE Australian waters in response to climate-driven intensification of the poleward flowing East Australian Current (EAC) (Figueira and Booth 2010). This strengthening current may facilitate range expansions of tropical fishes by increasing the frequency of thermally tolerable winters for tropical fishes in temperate reefs, whilst transporting larvae 100s to 1000s of km from tropical to temperate regions (Booth et al. 2007; Figueira and Booth 2010; Feary et al. 2014). We examined foraging excursions of juvenile *A. vaigiensis* in no-take marine parks (hereafter termed ‘reserves’) that have higher abundances of native predators and compared this with excursions of this tropical range-expander in predator-depauperate fished reefs (hereafter ‘fished reefs’), during both austral summer and winter. We hypothesised that foraging excursions of *A. vaigiensis* would be lower in reserves than fished reefs, associated with higher native predator abundance and consequently greater predation risk for *A. vaigiensis*. We also expected *A. vaigiensis* behaviour to be mediated by differences in water temperature between seasons, with greater foraging behaviour in summer and reduced foraging in winter. An aquarium experiment was then used to isolate the roles of predation risk and water temperature on foraging excursions of *A. vaigiensis*, and to test if predator-mediated suppression of foraging excursions reduced the feeding rates of *A. vaigiensis*. We predicted that foraging excursions and feeding rates of *A. vaigiensis* would be lower when exposed to a native predator than when exposed to a native non-predator (herbivore) in warm austral summer water temperatures, with feeding activities substantially reducing in cool austral winter water temperatures, independent of predation risk.

5.2 Materials and Methods

5.2.1 Study sites and focal species

Foraging behaviour of the tropical damselfish, *A. vaigiensis*, was studied in reserves and fished reefs within two regions of SE Australia (Fig. 5.1). The reserves were Shelly Beach (SB; 33°48’1’’S 151°17’50’’E) and Bushrangers Bay (BB; 34°35’50’’S 150°53’58’’E); the fished reefs were Palm Beach (PB; 33°36’0’’S 151°19’39’’E) and Bass Point (BP; 34°35’36’’S 150°53’50’’E). Protection from line- and spear-fishing within SB and BB began in 1982 and 2002, respectively. Benthic habitat within both reserves and fished reefs was primarily composed of 0.5 - 1.5 m diameter boulders (urchin barren habitat; Underwood et al. 1991), with area ranging from 1050 - 9825 m^2, and all sites being partially sheltered from the predominant south-east swell (Short and Trenaman 1992).

While tropical fishes are still relatively rare on temperate reefs in SE Australia, *A. vaigiensis* is commonly found throughout the region during summer (Booth et al. 2007) and was observed in relatively high numbers within study sites (e.g., 52.3 individuals per 1000 m^2 at SB during May, 2011; Chapter 2). Such relatively high densities of *A. vaigiensis* provided sufficient replicate observations to compare feeding behaviours between levels of fishing pressure (reserves, fished reefs) and season (summer, winter) (i.e., $n \geq 250$ individual observations demonstrated influence of predators on prey foraging by Madin et al. 2010). This species was also used because a previous study confirmed that the behaviour of *A. vaigiensis* (i.e., sheltering or flight responses) at PB and SB (reserve) was not significantly affected by observer presence (Chapter 2).

5.2.2 Predation threat and its' influence on *A. vaigiensis* in fished and reserve reefs

To confirm whether the potential predation threat for *A. vaigiensis* differed between reserves and fished reefs, densities of 11 species of common temperate predators were estimated at each site using underwater visual surveys. Predators were identified as species whose diet was at least partially composed of fishes (i.e., piscivores), as determined by Froese and Pauly (2014). Individuals of all piscivore species were counted at each site during four 30 min timed swims, conducted whilst snorkelling, during both summer and winter; n = two replicate surveys per season within each site. To standardise search effort, areas searched during timed swims were measured by towing a Global Positioning System (see details of methods in Chapter 2), which has been established as a reliable method for quantifying densities of rare reef fishes (Beck et al. 2014). Predator surveys were conducted in both summer (March - May) and winter (June - August) during 2011 (SB and PB) and 2012 (BB and BP). Water temperature was continually recorded at all four sites throughout the study period using HOBO^{TM} pendant loggers. Mean daily water temperatures ranged from 19 - 21.5°C and 16 - 18°C during summer and winter, respectively. To ensure *A. vaigiensis* recognised temperate piscivores as a threat, we compared vertical foraging excursions of *A. vaigiensis* between periods when temperate predators were visually present and visually absent. To do this we recorded the maximum distance from the substrate that individual *A. vaigiensis* were positioned at 15 sec intervals for 3 min, while simultaneously recording any piscivores that came within 3 m of the focal individual (*sensu* Madin et al. 2010). Predator presence or absence gave an estimate of the acute risk of predation faced by prey fishes: 'high risk' was when a predator was present, while 'low risk' was when a predator was absent (*sensu* Madin et al. 2010). To ensure sufficient replicate observations of the reaction of *A. vaigiensis* to temperate predators, behavioural reactions to 'high risk' and 'low risk' situations were measured within SB; this site held the highest piscivore densities (as determined by predator surveys detailed above).

5.2.3 *A. vaigiensis* feeding excursions in fished and reserve reefs during summer and winter

The distance and temporal stability of foraging excursions of *A. vaigiensis* were measured within fished and reserve reefs during the austral summer (March - May) and winter (June - August) of 2011 (SB, PB) and 2012 (BB, BP). As *A. vaigiensis* is largely site-attached during the juvenile stage, while also being primarily planktivorous in feeding (Allen et al. 2003), foraging excursions were taken as the vertical movement of individual *A. vaigiensis* away from the reef matrix, usually a low overhang or small cave. To confirm that such vertical movements were indeed foraging excursions, the number of bites that individuals made when making a vertical movement (i.e., moving into the water column) in comparison to the number of bites taken when individuals made a strictly horizontal movement (i.e., remaining on the benthos) were recorded for a subset (n = 407) of individuals. This revealed that ~95% of all bites were taken when making a vertical movement. This preference for planktivorous feeding was significantly greater than that expected by chance [X^2 (2, n = 407) = 726.58, p = 0.0001].

To measure *A. vaigiensis* foraging excursions, individuals were observed for 1 min from a distance of 3 m, after 3 min of habituation to the presence of an observer. The distance (to the nearest 10 cm) that individuals foraged above the substrate were visually estimated every 15 sec, with fish total length (TL; nearest cm) and number of conspecific individuals within the shoal recorded (*sensu* Madin et al. 2010). In total, foraging behaviours of 410 individuals were observed. Observer estimates of distances from the substrate were calibrated with a tape measure before commencing estimates of foraging excursions; mean (SE) error of distance estimates was 19 (3) cm (n = 60 estimates). To eliminate the potential confounding effect of habitat on feeding comparisons, observations were restricted to barren rocky substrata with low coralline turfing or crustose algal; *A. vaigiensis* most commonly associates with this habitat type (Chapter 2). Observations of *A. vaigiensis* and density surveys of temperate predators were made at depths less than 4 m on cloudless days between 09:00 and 16:00. Water visibility was > 10 m and swell was < 0.75 m throughout the study.

To ensure predator abundance and seasonal water temperature were the main factors driving behavioural differences of *A. vaigiensis* between reserve and fished reefs, reef complexity (contour to straight length ratio for a 5 m chain; n = 18 per site; *sensu* Risk et al. 1972), *A. vaigiensis* group sizes (recorded throughout behavioural observations above), temperate competitor densities (the abundance of temperate planktivorous fishes were estimated by surveying communities within six 5 min GPS-tracked timed swims per site; as detailed in Chapter 2), water visibility (maximum horizontal distance the substrate was observed away from the observer in surveys above) and wave energy (estimated for a 10 min period before conducting observations each sampling day) were also measured within all sites (see Table 5.1 for rational).

5.2.4 Effects of predation threat and water temperature on *A. vaigiensis* feeding behaviours

To test and compare the effect of predator presence and differing water temperature on feeding behaviour of *A. vaigiensis* (i.e., vertical foraging excursion and bite rate), high- and low temperature acclimated groups of this species were experimentally exposed to three predation threat treatments: (1) temperate predator; (2) temperate herbivore (predator control) and (3) an empty cell (tank control).

Juvenile *A. vaigiensis* were collected from coastal sites throughout Sydney by hand net, then randomly divided into 12 groups of six individuals. Groups were immediately transferred to 100 L holding tanks at the University of Technology, Sydney aquaria facilities (UTS). Six groups were acclimated for one week at mean Sydney daily summer (22 ±1°C) and winter (18 ±1°C) water temperatures (Figueira et al. 2009). Individuals were fed SpectrumGrow^{TM} marine pellets to satiation daily. The eastern red scorpionfish (*Scorpaena jacksoniensis*) and the rock blackfish (*Girella elevata*) were selected as the predator and herbivore for aquaria trials, respectively. Both species are common within shallow coastal reefs of SE Australia (Kuiter 1993), and were collected from coastal sites in Sydney and housed in 1000 L tanks at UTS. *S. jacksoniensis* and *G. elevata* were fed daily a diet of prawn and green algae to satiation, respectively. All fishes were maintained at a 12 hr light/12 hr dark cycle. 50% of water was changed per tank daily to ensure high water quality.

There was no difference in *A. vaigiensis* total lengths (TL) between temperature treatments ($T_{70} = -0.119$, $p = 0.91$). Mean (SE) TL of *A. vaigiensis* groups were 52.81 (1.419) mm. *G. elevata* and *S. jacksoniensis* ranged from 15.2 to 21.2 cm TL.

Comparing bite rates and foraging excursions

Each of the twelve groups of six individuals was exposed to the three predator treatments (i.e., predator, herbivore and empty cell) with one day breaks between subsequent trials. *A. vaigiensis* were trialled as groups rather than individuals because 87.5% of individuals observed in behavioural surveys (above) were actively shoaling. A group size of six individuals was selected because this was the mean group size observed within *in situ* surveys (see result below; 5.3.2). To ensure the order of exposure to predator treatments did not bias results, groups were exposed to the three treatments in permutated order, so that groups within each temperature were exposed to treatments in a unique order. Trial aquaria consisted of one tank split into two adjacent cells by a waterproof glass partition (each cell was 20 x 30 x 45 cm in dimension); the glass partition held a removable opaque screen, with the entire tank surrounded by a black plastic sheet, allowing visual but no olfactory connection between cells (Fig. 5.2). To habituate to the test aquaria, *A. vaigiensis* groups were moved from holding tanks to a cell adjacent to a predator, herbivore or an empty cell 12 hours prior to a trial. Trial cells contained a 12 x 6 cm terracotta shelter and temperature was maintained within ±1°C of the acclimation temperature of the group being tested. Individual predators and herbivores were transferred to cells adjacent *A. vaigiensis* when required, with individuals left for 30 min prior to trials, or until normal behaviour recommenced. All predator treatment cells held water at 18°C.

Following the habituation period, test prey groups were visually exposed to the predator treatment by lifting the opaque partition. Feeding behaviour of each *A. vaigiensis* individual (i.e., foraging excursion and bite rate) was then filmed for 5 min while food pellets were continuously administered at a consistent rate from above the tank using a syringe. To determine fish foraging excursions and feeding rates, groups were filmed using a high-definition digital video camera (GoPro^{TM}). For each individual within each group, foraging excursions above the bottom of the tank and feeding rate were then quantified against a 0.5 x 0.5 cm grid (installed behind the tank) every 10 sec across the 5 min period. Experimental tanks were washed and dried between trials to eliminate all potential chemical cues.

5.2.5 Statistical analyses

In situ predator densities were compared between protection level (fished and reserve reefs), season (summer and winter) and site using a three-factor analysis of variance (ANOVA). Protection level and season were treated as fixed factors, while site was treated as a random factor nested within protection. To verify that temperate predators posed a risk to *A. vaigiensis*, we then examined whether distance above the substrate of *A. vaigiensis* individuals differed significantly between predators' presence and absence using a one-tailed T-test, expecting foraging excursions were greater under low than high risk scenarios.

To test the impact of predator and season on foraging excursions, vertical distance of *A. vaigiensis* above the substrate were compared between protection levels, seasons and sites using analysis of covariance (ANCOVA). The design was the same as that used for predator comparisons, with the inclusion of *A. vaigiensis* length (TL) as a covariate. Fish length was included as a covariate due to the likely effect of body size on foraging excursions; excursions of prey reef fishes typically increase with increasing body size associated with reduced perceived predation risk (Gill 2003). Interactions between the main effects (protection level and season) and TL were first tested to ensure slopes were homogenous. The model was reduced after excluding non-significant interactions between factors and the covariate (protection x TL: $F_{1,330} = 0.51$, $p = 0.48$; season x TL: $F_{1,330} = 0.67$, $p = 0.41$). Significant interactions between factors in the reduced model were explored using pair-wise one-way ANCOVAs.

To test whether factors other than seasonal water temperatures and predators contributed to *in situ* variance in foraging activities of *A. vaigiensis*, wave action, visibility and group size were compared between levels of protection, seasons and sites using ANOVA (using the same design as for predator densities, see above). Temperate planktivore densities (i.e., competitors), measured during summer, were compared between levels of protection and sites by ANOVA. Densities of temperate planktivores were also compared between summer and winter within SB and PB by ANOVA (densities were only measured at these sites through winter). Benthic complexity was compared between protection levels and site by ANOVA. Significant interactions between factors were explored using one-way T-tests.

To determine the effect of predator and water temperature on feeding behaviour of *A. vaigiensis* within experimental cells, the mean vertical distance that groups moved in aquaria and bite rates were compared amongst predation risk treatments (predator, herbivore and control) and between temperatures (18 and 22°C) using a two-factor repeated-measures ANOVA. The response of *A. vaigiensis* to water temperature and predation risk was analysed as groups, and not at the individual level, since it was difficult to visually identify individuals throughout the experiment, which is necessary for repeated measures (without resorting to potentially harmful tagging methods). Temperature was a fixed factor and risk treatment a repeated measure, since each group was trialled on three occasions. To explore whether there was an interaction between temperature and predation threat, vertical distances and bite rates were compared between predation risk levels within each temperature using pair-wise comparisons, with Bonferroni adjustment for multiple comparisons. The feeding behaviour response of *A. vaigiensis* groups between temperatures (matched with seasonal temperate water temperatures for Sydney) within each of the three predation risk treatments was compared using one-tailed T-tests, expecting feeding rate and vertical distance at 22°C would be greater then at 18°C.

All data were examined for homogeneity of variance and normality, and then transformed where required prior to analysis. *A priori*, $p < 0.05$ was the set level of significance for all analyses. Analyses were conducted using SPSS $^{\mathrm{TM}}$ v20.

5.3 Results

5.3.1 Predation threat and its influence on *A. vaigiensis* in fished and reserve reefs

Predator densities were significantly greater in reserve than in fished reefs (ANOVA: $F_{1,2} = 25.60$, $p = 0.04$; Fig. 5.3), and this did not vary significantly with season or site. When foraging excursions of *A. vaigiensis* were compared between periods when temperate piscivores were present or absent within SB, foraging excursions of *A. vaigiensis* were significantly reduced in the presence of predators ($t_{46} = 3.52$, $p = 0.001$; mean ± SE foraging excursions were 101 ± 30 and 77 ± 22 cm when a predator was present and absent, respectively). Predators that *A. vaigiensis* encountered during these predator response trials included yellowfin bream *Acanthopagrus australis* (Sparidae), longfin pike *Dinolestes lewini* (Dinolestidae), tailor *Pomatomus saltatrix* (Pomatomidae), spotted wobbegong *Orectolobus maculatus* (Orectolobidae) and giant cuttlefish *Sepia apama* (Sepiidae). These five species comprised ~85% of predators observed during surveys (Table 5.2).

5.3.2 *A. vaigiensis* feeding excursions in fished and reserve reefs during summer and winter

Foraging excursions of *A. vaigiensis* were 2.09 times greater in vertical distance on fished than reserve reefs (ANCOVA: $F_{1,2} = 29.91$, $p = 0.03$; Fig. 5.4). There was a significant interaction between season and site (protection) ($F_{2,328} = 6.14$, $p = 0.002$); however, separate analyses at the site level indicated that *A. vaigiensis* foraged at significantly greater distances above the substrate during summer than winter at all sites (ANCOVA: $p \leq 0.01$ for all sites; Fig. 5.4). All other factors and interactions in the reduced model were non-significant (ANCOVA: $p > 0.05$). The mean (SE) group size observed was 6.5 (0.33) individuals. Only fish with 4 - 10 cm TL were found during both summer and winter.

5.3.3 Experimental comparison of predation threat and water temperature on *A. vaigiensis* feeding activity

There was a significant interaction between water temperature and predation risk treatments for group foraging excursion distance and bite rates (ANOVA: $F_{2,20} = 8.32$, $p = 0.002$ and $F_{2,20} = 5.75$, $p = 0.03$, respectively; Fig. 5.5). Foraging excursions and feeding rates of *A. vaigiensis* groups acclimated to 22°C water temperature were greater when exposed to the herbivore than predator (Pairwise: $p < 0.05$ for both metrics) but did not differ between the empty cell and herbivore treatments (Pairwise: $p > 0.05$ for both metrics); feeding rate was ~46% lower in the presence of a predator than herbivore. Foraging excursions of *A. vaigiensis* groups acclimated to 18°C water temperature were greater when exposed to an empty cell than the herbivore and predator (Pairwise: $p < 0.05$ for both metrics and comparisons), but there was no difference in vertical distance travelled between herbivore and predator treatments for this group (Pairwise: $p > 0.05$ for both metrics).

When comparing foraging excursions of groups acclimated to each temperature treatment, both groups showed greater foraging excursions at 22°C than 18°C within both the herbivore and predator treatments (T-tests: $p < 0.05$ within both treatments), but not when exposed to the empty cell ($p = 0.21$). Feeding rates were > 64% lower at 18°C than 22°C within each of the three risk treatments ($p < 0.05$ within all treatments). Assumptions of data sphericity were met (Machly's Tests: $p > 0.05$ for all repeated measure analyses).

5.4 Discussion

Here we report the first field-based evidence that native predators may limit of access of tropical fishes to food resources, which may constrain their range expansion. Our results suggest that for range expanding tropical prey fishes, temperate predators may substantially limit feeding activities, including the vertical movement of individuals away from shelter and the physical movement of the jaw structure to capture prey. Such reduced feeding activities mediated by native piscivores will likely impact the growth, condition and ultimately the survival and colonisation of tropical range expanding fishes in temperate environments (cf. Olyarnik et al. 2009). Therefore, although larval supply and water temperature may be suitable to support range expansions of tropical fishes into temperate reefs (Booth et al. 2007; Figueira and Booth 2010), colonisation may be highly restricted within regions that support high predator densities.

Although there are a number of biotic and abiotic factors that may structure the feeding behaviour of range expanding tropical fishes (Figueira et al. 2009; Figueira and Booth 2010; Luiz et al. 2013; Feary et al. 2014), we showed that reductions in feeding excursions of *A. vaigiensis* were directly attributed to the presence, and ultimately density, of temperate predators within coastal reefs in SE Australia. Such negative impacts of predator presence on feeding behaviour of *A. vaigiensis* were confirmed in both aquaria trials and within field sites. Within aquarium trials *A. vaigiensis* individuals negatively responded to common temperate piscivores when foraging, and significantly lower foraging excursions were apparent in reserve, compared to fished sites. Within the field study, predator density was the only factor observed to differ between fished and reserve sites, despite reef complexity, group size, temperate competitor densities, water visibility and wave energy being measured within all sites (Table 5.1). Food availability was unlikely to explain behavioural differences of *A. vaigiensis*, as reserve and fished reefs were spatially close (i.e., < 6 km), whilst shorelines of SB (reserve), PB and BP faced northeast, so plankton density (i.e., food supply for *A. vaigiensis*) was likely to be comparable regardless of protection level. The nearshore reef structure (< 25 m depth), which may influence plankton distribution on a local scale by altering water flow (Mackas et al. 1985), also did not notably vary between reserve and fished reefs, with reefs at all sites gradually sloping to a reef edge < 100 m seaward of the shoreline (Jordan et al. 2010).

The influence of native predators on feeding activity of range expanding fishes appeared to be more pronounced in summer, than in cool, winter waters in these temperate reefs. Although *in situ* feeding excursions were still greater in fished than reserve reefs through winter, foraging excursions of this tropical species were notably reduced during the winter season. Such reductions in *A. vaigiensis* foraging appeared to occur independent of any potential seasonal change in environmental factors, such as water visibility, group size, wave action and temperate competitor or predator densities (Table 5.2). Although not quantified, plankton food supply may reduce toward winter in SE Australia due to reduced primary productivity at this time (Thompson et al. 2009), thus influencing the foraging behaviour of planktivorous fishes. However, any reduction in food supply into winter would not explain the reduced foraging of *A. vaigiensis* during this period, or at winter water temperatures in the laboratory experiment, because these fish would then be expected to increase their foraging excursions in response to scarce food resources (Biro and Booth 2009). Hence, seasonal changes in water temperature, rather than food supply and/or other environmental factors, appeared to dictate differences in foraging behaviour of *A. vaigiensis* between seasons.

Aquaria trials presented further evidence that cooler waters through winter reduce the influence of temperate predators on *A. vaigensis* foraging. When the effects of predation risk and water temperature were isolated from other environmental factors in experimental trials, foraging excursions and bite rates of cool-acclimated groups of *A. vaigiensis* were reduced when exposed to both the predator and predator control. Such reduced influence of temperate predators on *A. vaigiensis* feeding in cool winter waters was likely attributable to suppressed metabolic activity of this warm-adapted tropical species within the reduced temperature water. Therefore, regardless of *in situ* predation threat, temperatures encountered through winter by *A. vaigiensis* within SE Australian reefs surveyed in this study (i.e., 17 - 18°C water) may greatly reduce the physiological performance of this species, resulting in reduced feeding rates, swimming performance and growth (Figueira et al. 2009). Hence, although temperate predators may restrict tropical fishes feeding during summer (when their performance is relatively high), these predatory constraints will likely weaken approaching winter, as cool waters suppress the metabolic performance of warm-adapted tropical fishes.

Although temperate predators may structure feeding activities of tropical fishes at the vanguard of prey fish range expansions, these constraints may diminish with further warming of temperate waters. For instance, the burst swim speed of *A. vaigiensis*, and therefore the potential of this species to escape temperate predators, increases as temperate water temperatures rise (Figueira et al. 2009). In addition, as the consumption of prey fishes by predators is limited by predator jaw size and digestive capacity (the so called “size escape”; Gill 2003), the threat posed by temperate predators to *A. vaigiensis* will also likely reduce, because warmer temperate waters allow this species to grow faster and remain for shorter time periods in small, predator-vulnerable sizes (Figueira et al. 2009). Moreover, the risk of being preyed upon by temperate predators will also reduce for range expanding prey fishes, such as *A. vaigiensis*, as predator communities in temperate reefs become dominated by tropical piscivores. For example, temperate piscivores have been largely replaced by tropical species in western Japan in response to recent and rapid warming of coastal waters (Nakamura et al. 2013). Hence, temperate predators may strongly constrain access of tropical prey fishes to necessary resources during initial stages of range expansion, but will likely reduce in importance with ongoing climate change.

We demonstrate here that temperate predators and cool winter waters restrict feeding activities of a tropical prey fish, yet the extent to which this limits the survival of range-expanders needs to be determined. However, based on the high rates of mortality reported for congeneric species where food availability matches the reduced feeding rate observed for *A. vaigiensis* in this study, we may anticipate that feeding constraints for range expanding prey in temperate reefs should substantially limit individual survival. For instance, mortality rates of the damselfish *Stegastes partitus* were doubled when juveniles were fed a one third food ration over seven days (Booth and Hixon 1999). In addition, mortality rates of *Pomacentrus moluccensis* juveniles increased fourfold when fed a one third feed ration over just five days (Booth and Beretta 2004). This dramatic increase in mortality for starved individuals was attributed to higher rates of *in situ* predation; these individuals had substantially poorer growth and condition than individuals fed a full ration, which potentially increased the likelihood of being preyed upon. Starved individuals also displayed more erratic swimming behaviours, which heightened their susceptibility to predation. Here, temperate predators reduced food intake by 46% within summer temperatures, with winter water temperatures reducing food intake of *A. vaigiensis* by 64%, independent of predation threat. Hence, assuming predators and winter water temperatures reduce feeding in the field similar to within aquaria, and that predation pressure is high enough to select against starved individuals, temperate predators and winter water temperatures may substantially limit *A. vaigiensis* survival.

Although climate-driven species range expansions may impact human societies by altering supplies of natural resources (Cardinale et al. 2012; Madin et al. 2012; Vergés et al. 2014), strategies for managing this redistribution are presently lacking. Our results suggest predator-rich habitats, such as marine reserves, offer greater resistance of native communities to species colonising with climate change by restricting access of these range-expanders to necessary resources. Hence, we may anticipate that the resilience of ecosystems to impacts associated with range expansions, such as changes to food webs and displacement of native fauna, may be improved by increasing predator densities; via habitat protection, harvest restrictions, and/or predator reintroductions. Nevertheless, the strong influence of environmental temperatures on outcomes of interactions of range-expanders with native predators suggests that the biotic resistance that native predators offer ecosystems will vary temporally. As observed here, constraints of native predators on range-expander foraging may be strongest during summer, when environmental temperatures are relatively warm. But these constraints may reduce toward winter, as sub-optimal environmental temperatures reduce the feeding rates of these warm-adapted range-expanders, irrespective of predation risk. Understanding the indirect constraints that native predators place on colonisation of prey species, as well those imposed by seasonal environmental temperatures, is crucial to reliably anticipating the future distribution of prey under climate change scenarios.

5.5 Tables

Table 5.1 Test of alternative explanations of spatiotemporal variance in *A. vaigiensis* foraging behaviour. Although predator densities and seasonal flux in water temperatures correspond with patterns of *A. vaigiensis* foraging in the current study, we cannot assume causality. Hence, there may be other alternative causes for the observed foraging patterns. Nevertheless, group size, density of temperate planktivores, benthic complexity, wave action and water visibility, which may influence foraging of reef fishes, cannot explain differences in *A. vaigiensis* foraging excursions between reserve and fished reefs, or between seasons. Below describes comparisons of alternative factors between reserves and fished reefs, including how it may influence *A. vaigiensis* foraging (rational), the expected influence on *A. vaigiensis* behaviour if it explained greater foraging in reserves and through summer (expected result) and the observed result. Statistical analyses were conducted by ANOVA as described in the main text, considering $p < 0.05$ as a significant result.

Factor	**Rational**	**Expected result**	**Observed result**
Group size	Larger groups attract less risk and incur greater competition[1]	Reserve > Fished	Reserve = Fished reef (ANOVA; $F_{2, 274} = 0.05$, $p = 0.84$)
		Summer > Winter	Summer > Winter at PB and BB (reserve) (T-tests: $p < 0.05$ for both sites), but not BP and SB (reserve) (T-tests: $p > 0.05$ for both sites). Interaction in group size between season and site (protection) (ANOVA: $F_{2, 274} =$ 4.058, $p = 0.02$

Temperate planktivores	Increased competition may increase foraging excursions[1]	Fished > Reserve	Fished = Reserve (ANOVA: $F_{1,20}$ = 0.24, p = 0.67)
		Summer > Winter	Summer = Winter at SB and PB (Seasonal comparison only available at these sites) (ANOVA: PB, $F_{1,12}$ = 8.64, p = 0.21; SB, $F_{1,12}$ = 0.27, p = 0.69)
Benthic complexity	Increased complexity lowers risk and allows greater excursions[2]	Fished > Reserve	Fished = Reserve (ANOVA: $F_{1,67}$ = 0.14, p = 0.74)
Wave action	When wave action is strong, reef fishes may reduce the distance they forage above the substrate to conserve energy[3]	Reserve > Fished	Reserves = Fished (ANOVA: $F_{1,8}$ = 2.19, p = 0.28)
		Winter > Summer	Winter = Summer (ANOVA: $F_{1,8}$ = 1.32, p = 0.37)
Water visibility	In more turbid water, predation risk for prey fishes reduces, reducing constraints predators may apply to their foraging excursions[4,5]	Reserve > Fished	Reserves = Fished (ANOVA: $F_{1,8}$ = 0.18, p = 0.72)
		Summer > Winter	Summer = Winter (ANOVA: $F_{1,8}$ = 1.99, p = 0.29)

[1] Dill and Fraser 1984, [2] Brown and Kotler 2004; [3] Johansen et al. 2008; [4] Abrahams and Kattenfeld 1997, [5] Wenger et al. 2012

Table 5.2 Comparison of mean (SE) temperate predator densities between marine reserve and fished reefs across both austral summer and winter sampling periods. Species embolden denote those that *Abudefduf vaigiensis* encountered during *in situ* predator recognition and response trials. Species ranked by order of abundance.

Species (Family)	**Marine reserves**	**Fished reefs**
***Acanthopagrus australis* (Sparidae)**	126.87 (42.75)	0
***Dinolestes lewini* (Dinolestidae)**	83.33 (36.42)	27.15 (13.44)
Aulopus purpurissatus (Aulopidae)	17.92 (7.70)	0
Seriola lalandi (Carangidae)	13.12 (8.01)	0
***Sepia apama* (Sepiidae)**	9.53 (5.91)	0
***Pomatomus saltatrix* (Pomatomidae)**	8.74 (5.34)	0
Acanthistius ocellatus (Serranidae)	2.66 (2.66)	3.63 (3.51)
Lethrinus nebulosus (Lethrinidae)	4.13 (3.86)	0
Hypoplectrodes maccullochi (Serranidae)	1.15 (0.75)	2.75 (2.63)
Pseudocaranx georgianus (Carangidae)	2.48 (2.32)	0
Platycephalus caeruleopunctatus (Platycephalidae)	0.45 (0.22)	0

5.6 Figures

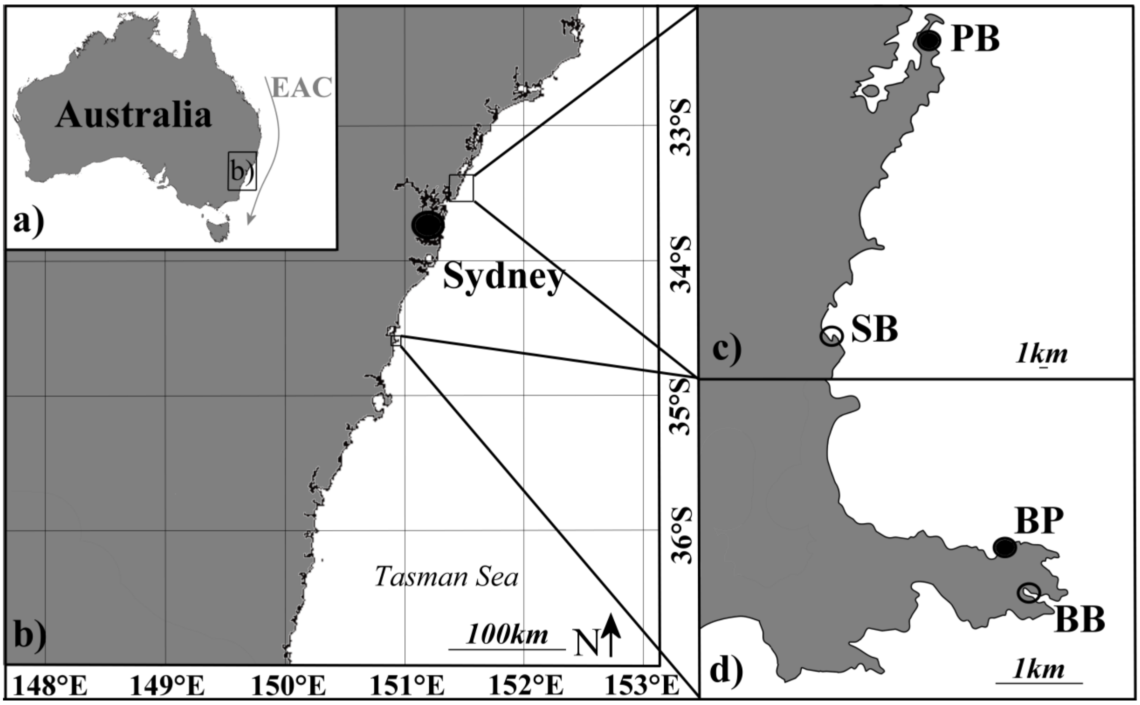

Figure 5.1 Locations of field sites within southeastern (SE) Australia. Juvenile tropical reef fishes are supplied by the East Australian Current [(EAC; inset a)] where they recruit to temperate habitats along the SE Australian coast throughout summer; inset b). Foraging behaviour of the tropical damselfish, *Abudefduf vaigiensis*, was compared between the Shelly Beach (SB) and Bushrangers Bay (BB) marine reserves (open circles), and the adjacent fished reefs (closed circles) of Palm Beach (PB) and Bass Point (BP); insets c) and d).

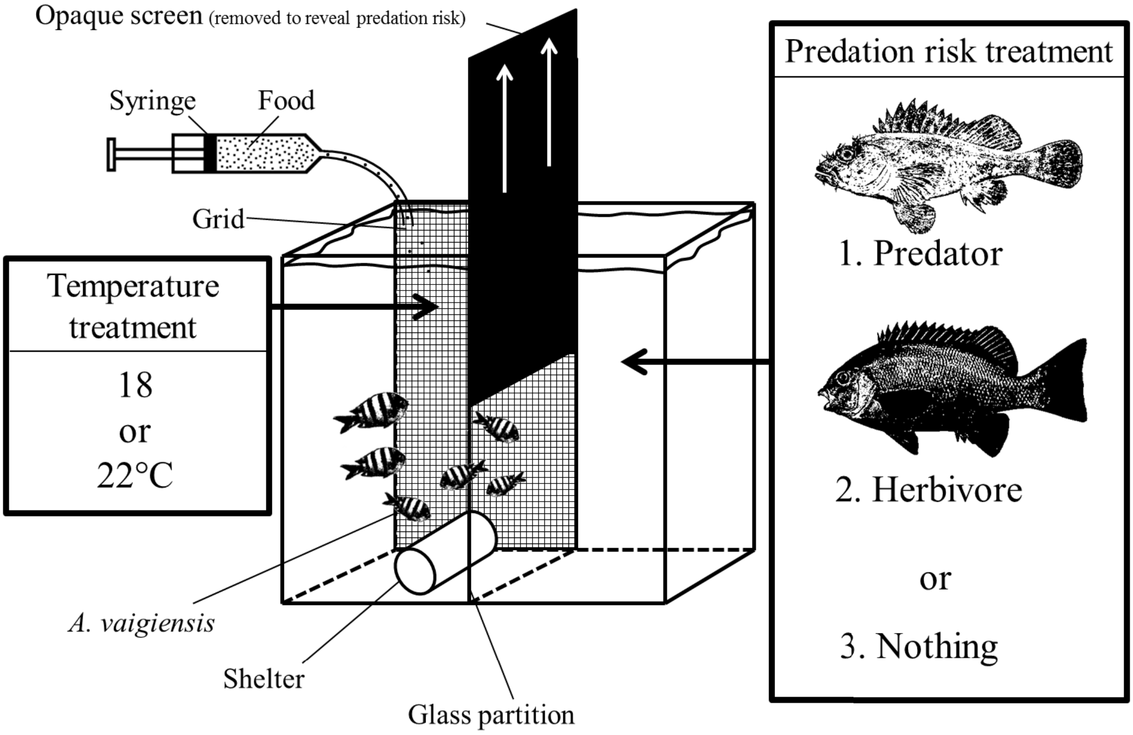

Figure 5.2 Aquaria used to test the response of *A. vaigiensis* foraging excursions to three predation risk treatments: 1) predator, 2) herbivore and 3) empty tank, at two water temperatures, 18 and 22°C. *A. vaigiensis* were physically separated from predation risk treatments by a glass partition – no movement of water occurred between experimental tanks. Groups of *A. vaigiensis* were visually exposed to a predation risk treatment by removing the opaque screen, with all behaviour then filmed against a 0.5 mm^2 gridded background for 5 min. Food was added from above at a constant rate using a syringe throughout trials.

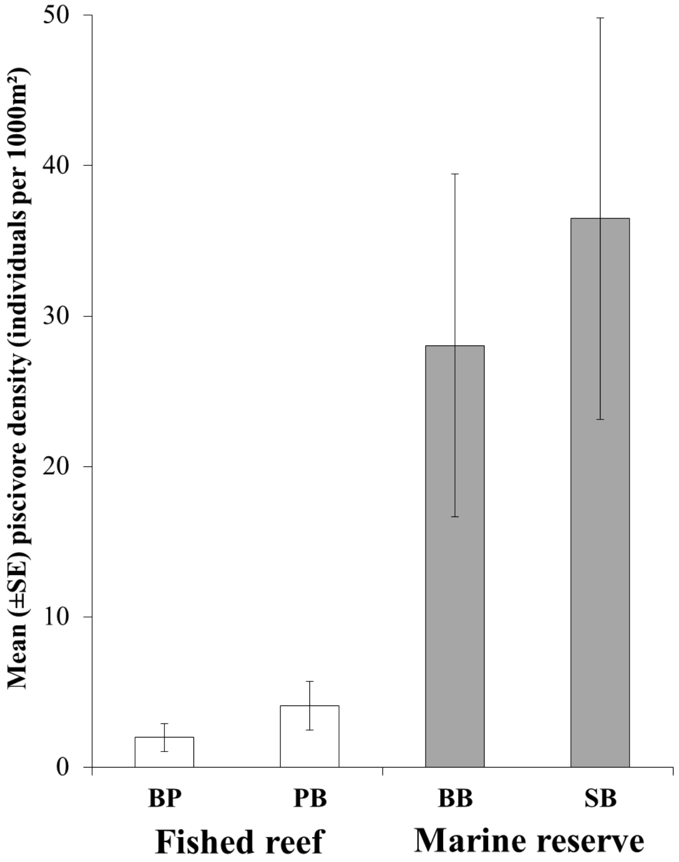

Figure 5.3 Mean (±SE) piscivore densities within fished reefs (white bars), Palm Beach (PB) and Bass Point (BP), and marine reserves (grey bars), Bushrangers Bay (BB) and Shelly Beach (SB) as determined by GPS-tracked timed-swims (n = 8 per site). Data are mean piscivore density across both austral summer and winter sampling periods. Note that heterogeneous variances were accounted for by ln(x+1) transformation prior to analysis.

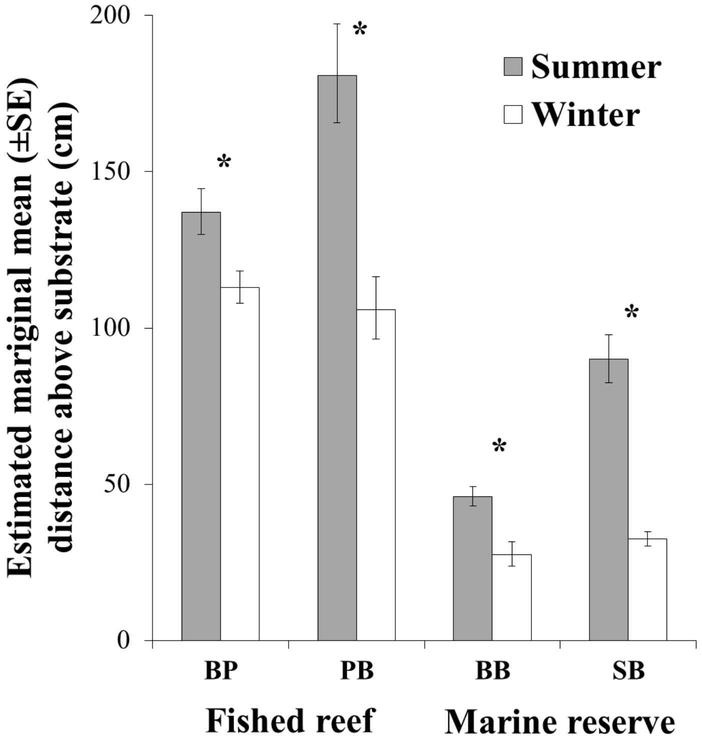

Figure 5.4 Estimated marginal mean (±SE) distance *A. vaigiensis* foraged above reef during summer (grey bars) and winter (white bars) within fished reefs, Bass Point (BP) and Palm Beach (PB), and marine reserves, Bushrangers Bay (BB) and Shelly Beach (SB). * denotes significant difference between summer and winter when distances were compared within sites by one-way ANCOVA ($p < 0.05$), with total length as covariate = 0.79.

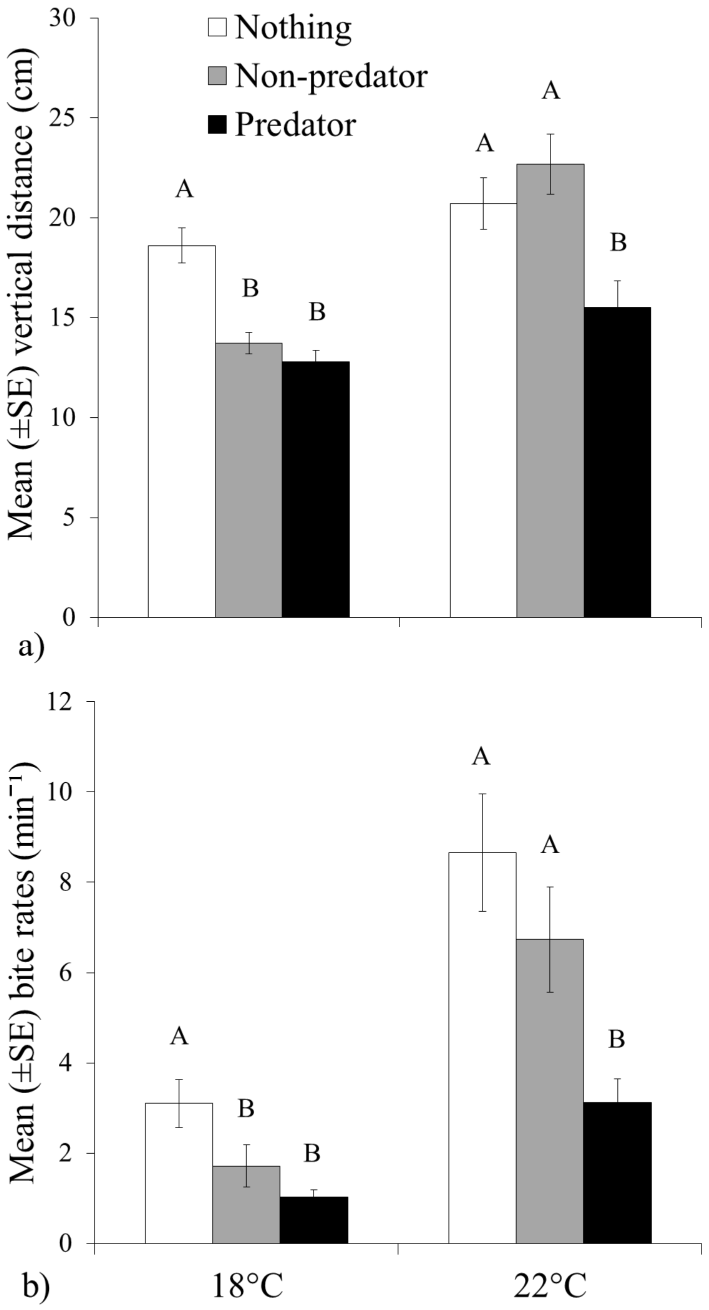

Figure 5.5 Mean (±SE) a) foraging excursions and b) feeding rates of *A. vaigiensis* groups acclimated to 18 and 22°C water, when exposed to an empty tank (nothing; white bars), temperate herbivore (*G. elevata*; grey bars) and temperate predator (*S. jacksoniensis*; black bars) within aquaria trials. Differing letters denote significant differences ($p < 0.05$) amongst treatments when group responses were compared by pairwise comparisons within each temperature (data spherical; $p > 0.05$). n = six groups of six individuals acclimated to each temperature. Maximum vertical distance = 43 cm. Food added at a constant rate from above throughout trial.

Chapter 6: General discussion

To effectively manage ecological impacts of climate change, reliable predictions of species' geographic response to warming environments are required. However, our ability to accurately predict where and when species will redistribute is commonly precluded by a limited understanding of how habitats control species' ranges (Gaston 2009; Sexton et al. 2009; Angert et al. 2013; HilleRisLambers et al. 2013). For reef-associated marine organisms, the distribution of suitable reef habitats at higher latitudes may strongly organise where they may colonise with warming waters, yet the habitat use of most range shifting species within a newly settled range are currently unknown under these novel circumstances (Sorte et al. 2010; Bates et al. 2014). Tropical reef fishes, rapidly expanding their distribution into temperate regions in response to intensifying poleward flowing boundary currents, present a unique model that shed light on this issue. In these temperate regions, tropical fishes face a diverse range of novel reef habitats, which may constrain their recruitment, and hence ultimately impact whether populations will successfully shift poleward with warming waters.

Previous work has shown that larval supply and the thermal suitability of waters at higher latitudes are important requirements for tropical fish to range-shift poleward (Booth et al. 2007; Figueira et al. 2009; Figueira and Booth 2010; Nakamura et al. 2013). Hence, considering local water temperatures and distance from tropical larval sources, tropical fish redistribution may be predicted somewhat reliably at regional spatial scales (i.e., 10 to 100s of km; Figueira and Booth 2010). Species' functional traits may also organise the temporal order that species colonise temperate latitudes, with species possessing behaviours and a morphology that reduce predation risk, as well as allowing a relatively generalised trophic use (i.e., non-obligate feeders) more likely to initially establish on temperate reefs (Luiz et al. 2013; Feary et al. 2014).

This thesis finds that even if tropical fishes are advected into temperate latitudes where they may theoretically tolerate local water temperatures and access necessary resources

(Eme and Bennett 2008; Figueira et al. 2009; Feary et al. 2014), the structure of temperate reef habitats may strongly limit where they may successfully recruit, and thus ultimately colonise. Specifically, this thesis shows that the exposure of temperate reefs to wave action (Chapter 3), the biogenic structure of temperate algal reef habitats (Chapters 4), combined with the potential for poor feeding that may result from limited access to food by both temperate predators and seasonably cool waters (Chapter 5), may strongly determine where tropical fishes recruit at the vanguard of their range expansion. This new knowledge will facilitate more accurate predictions of where and when tropical fishes will colonise with ongoing climate change, as well as identify temperate marine ecosystems at risk from impacts associated with these redistributing fishes.

Here, recruitment of tropical fishes to temperate reefs was organised at multiple spatial scales, with factors explaining differences in the abundance, diversity and richness of new recruit and juvenile fishes among reefs (100s of m to kms) differing to that among reef patches (10s of m). To determine habitat requirements for the early life success of tropical fish at temperate latitudes, field surveys of vagrant fishes were conducted using GPS-tracked roaming surveys; this method allowed greater detection and more reliable density estimates of these sparsely-distributed fishes than traditional belt transects (Chapter 2). This roaming survey method was used to reveal that among temperate reefs, separated by 100s of metres to kilometres along the temperate SE Australian and W Japanese coastlines, the density and richness of new recruit and juvenile tropical fishes monotonically decreased with increasing exposure to wave action. On such broad spatial scales, changes in wave exposure between sites was more highly associated with variance in vagrant recruitment than water temperature, latitude, reef complexity, distance from nearest river mouth (i.e., freshwater and tidal influence), and presence of temperate habitat engineers or predators (Chapter 3) – all factors found to spatially organise recruitment of reef fishes elsewhere (Connell and Jones 1991; Almany and Webster 2006; Wenger et al. 2012; Johansen and Jones 2013; Wenger et al. 2013; Bates et al. 2014). However, among reef habitats separated by only 10s of metres, with comparable wave exposure, tropical fish settlement and recruitment was strongly influenced by macroalgal cover (Chapter 4). This work found that the density, richness and diversity of new recruits and juveniles were greater in non-macroalgal than macroalgal-dominated reef patches in W Japan across a single year and SE Australia across multiple years. Using an aquarium experiment, tropical larvae (*Pomacentrus coelestis*) also consistently chose non-macroalgae reef over macroalgae at settlement. Hence, this work showed that spatial variance in the physical structure of temperate reefs, due to the shape of the coastline at a broad extent, and composition of biogenic habitats at finer spatial scales, may strongly organise settlement and recruitment success of tropical fishes, and thus likely influence where populations may establish.

Even if tropical fishes access suitably structured reef habitat, adverse interactions with native predators and cool winter water temperatures (i.e., 17 - 18°C water) may limit access to necessary resources, further challenging species persistence in temperate regions. Although temperate predator densities and minimum, maximum and mean water temperatures did not appear to drive differences in the richness or density of tropical fish recruits among temperate reefs (Chapters 3 and 4), native predators and winter water temperatures may ultimately limit their survival at later stages of recruitment. In the presence of a high threat of predation, such as within predator-rich marine reserves, this thesis found that temperate predators can substantially reduce the feeding activities of juvenile tropical fishes, such as *A. vaigiensis* (Chapter 5). Furthermore, independent of predation risk, ambient winter water temperatures may further suppress feeding of warm-adapted tropical species, potentially due to reductions in metabolism associated with cooler water temperatures (Chapter 5). Although the consequences of reduced feeding, including potentially lower growth rates and poorer condition, still needs to be assessed *in situ*, such reduced feeding, mediated by native piscivores and cool temperatures, will likely impact the growth, condition and ultimately survival and colonisation of tropical range expanding fishes in temperate environments (cf. Olyarnik et al. 2009). For instance, substantial *in situ* mortality of congeneric species resulting from low fed rations (Booth and Hixon 1999; Booth and Beretta 2004), which is comparable to the lowered feeding rate observed for *A. vaigiensis* when exposed to a temperate predator and acclimated to winter water temperatures within the present study (Chapter 5), suggests native predators and winter water temperatures may strongly constrain survival of tropical fishes in temperate reefs.

Based on the range of factors that have been observed to influence recruitment of tropical fishes (both published and within the present thesis), human activities that alter temperate reef habitats may facilitate or restrict colonisation of tropical fishes in temperate regions (Table 6.1). For instance, tropical fish populations may establish where reefs have been artificially sheltered from ocean swell (Chapter 3). For example, ~70% of embayed reefs in W Japan (i.e., exposure index < 0.1, Hill et al. 2010) are afforded by harbour, groyne, jetty and offshore breakwall development (Walker and Mossa 1986). Such artificial protection of reefs from wave energy may offer great potential to support tropical fish recruitment by both reducing hydrodynamic stress, as well as allowing structurally elaborate branching corals to establish (Iwas 2004) - a suitable habitat for many obligate-coral feeding fishes (Chapter 3). Widespread loss of macroalgae within temperate reefs, as a result of anthropogenic warming of temperate waters (e.g., Nagai et al. 2011; Tanaka et al. 2012), water pollution (Steneck et al. 2002), and fishing-induced changes in grazing pressure (Tegner and Dayton 2000), may also facilitate the colonisation of tropical fishes in temperate regions due to the high association of tropical fishes with non-macroalgal habitats (Chapter 4). Moreover, reductions of temperate predators, associated with fishing pressure, may improve the chances of recruitment success for tropical fishes by reducing predation risk whilst they forage, and thus improving access to trophic resources (Chapter 5). However, particular human activities may also reduce suitable habitat for tropical fishes. For instance, human-driven climate change may increase wave energy in many temperate regions (Young et al. 2011), which may reduce protection that temperate coastlines afford recruiting tropical fishes from wave action. Moreover, protection of temperate reefs from fishing, through installing marine reserves, may reduce survival of tropical fishes by enhancing their risk of predation, which is a key determinant of access to resources (Chapter 5). Hence, anthropogenic modification of temperate reef ecosystems may have complex, opposing and even synergistic influences on recruitment success of tropical fishes in temperate regions, with outcomes for tropical fish colonisation depending on the strength and types of human impacts on temperate ecosystems and reef structure.

To anticipate the extent temperate habitats limit or facilitate range expansions of tropical fishes, a full understanding of the extent that habitats limit recruitment success in their historic range, as well as their newly formed temperate range, is required. For instance, if more suitable reef habitat is available for tropical fishes within temperate regions than natal tropical waters, temperate reefs may not obstruct these species shifting poleward with warming waters. But in the reverse situation, range expansions of tropical fishes may be constrained if suitable habitats are less available for them in adjacent temperate regions. It is difficult to ascertain the extent that temperate macroalgae and predators restrict range expansions of tropical fishes since both factors are unique to temperate ecosystems (Chapters 4 and 5). However, we may anticipate that increasing wave exposure of reefs poleward may substantially limit the redistribution of many tropical fishes, at least within SE Australia and W Japan. Less than 20% of nearshore reefs in these temperate regions were found to support recruitment of many species, based on wave exposure alone (Chapter 3). In contrast, embayed habitats are highly abundant throughout the natal range for tropical fishes that are expanding into SE Australia and W Japan. For example, in eastern Australia, ~80% of mid- and inner-shelf reefs composing the Great Barrier Reef (GBR), a primary natal habitat for tropical reef fishes in this region (Allen et al. 2003), are blocked from direct ocean swell (Lewis 2001). Similarly, within the natal range for tropical fishes that are supplied to W Japan (Allen et al. 2003; Soeparno et al. 2012), the island chain extending between the Philippines and Ryukyu Islands also offer considerable protection for recruiting tropical fishes from wave action since approximately half of these islands' coastlines face west, away from the dominant easterly ocean swells (Barstow et al. 2009). Moreover, based on a positive relationship between recruitment success of tropical fishes and protection of reefs from wave action (Chapter 3), we may predict that embayed reef availability may be less of a constraint to tropical fish recruitment where wave energy reduces poleward. However, the opposite is more likely in eastern Australia since wave climate generally reduces northward in this region, so that the wave regime is lowest along the east coast of Australia within the mid- and northern-sections of the GBR (Hughes and Heap 2010). Wave energy in W Japan is also comparable to that in the Ryukyu Islands (Barstow et al. 2009). Hence, increasing wave exposure of the coastline to ocean swell, resulting from the coastline shape interacting with the dominant swell direction, suggests the availability of embayed reef habitat may provide substantial constraints for fishes shifting poleward with warming waters in these regions.

Due to the concentration of colonising tropical fishes in specific temperate reef habitats, impacts of this redistribution on temperate marine ecosystems will likely be spatially uneven. For instance, impacts associated with colonising tropical fishes should be mostly in suitable habitats, such as embayed reefs and non-macroalgae reef patches. Tropical fishes may compete with native organisms to access necessary resources, including food, shelter and living space. For instance, based on the trophic groups observed here, colonising tropical fishes may impact access of temperate species to food resources where the dietary requirements of these two groups of organisms overlap, such as those that prey on plankton, macroalgae, fishes and invertebrates (Chapters 3 and 4). High densities of herbivorous vagrant fishes on embayed reef may also concentrate grazing pressure on macroalgae, which may greatly deplete temperate macroalgae, and subsequently impact the availability of food resources for macroalgae-dependant temperate fish species (Vergés et al. 2014). Furthermore, predatory tropical fishes, including piscivores and benthivores, may also be capable of preying upon small fishes and benthic invertebrates native to temperate regions, particularly where these range expanding predators are in high abundance, such as on embayed and non-macroalgal reef. Although negative impacts of range expanding tropical fishes on temperate competitors and prey may be initially weak, due to the small size and rarity of these colonising tropical fishes, such impacts may increase as warming temperate waters allow them a wider range of prey (i.e., jaw-sized limitations to predation reduces), greater digestive capacities and an increased appetite, due to a higher metabolic rate (Figueira et al. 2009). Continued warming should also increase the ecological competitiveness of tropical fishes in temperate regions because these warm-adapted tropical species will likely gain a physiological advantage over cool-adapted temperate species (Figueira et al. 2009), as well as numerically dominate fish assemblages at temperate latitudes (e.g., Nakamura et al. 2013). Hence, colonising tropical fishes may adversely impact specific temperate ecosystems, with tropical fishes potentially preying on and/or competing for resources with temperate species, with the strength of these adverse impacts likely to increase with ongoing climate change.

This study explored roles of shallow water habitats in temperate regions with moderate to high wave energy in structuring recruitment of tropical fishes, but reef habitats may structure range expansions differently where wave action is lower, in deeper reefs and/or at different stages of redistribution. Although shallow, embayed reefs were important recruitment sinks in SE Australia and W Japan, tropical fishes may sometimes use deeper reefs to avoid hydrodynamic stress (Fulton and Bellwood 2004), whilst the availability of embayed reefs may not limit redistribution of tropical fishes into temperate regions where the local wave climate is low. Moreover, this study focused on the initial stages of range expansion, while factors influencing later stages may differ. For example, the swimming performance of tropical fishes, and therefore their potential to escape temperate predators and tolerate hydrodynamic stress, increases as temperate water temperatures rise (Figueira et al. 2009). In addition, since the consumption of prey fishes by temperate predators is limited by predator jaw size and digestive capacity (Gill 2003), constraints temperate predators place on range expanding tropical fishes may reduce with warming waters. The threat posed by temperate predators may reduce for range expanding tropical fishes with climate change since warmer conditions may result in warm-adapted tropical species growing faster than previously possible in temperate waters (provided food is available to support enhanced growth) and so they may remain for shorter periods at small, predator-vulnerable sizes (Figueira et al. 2009). Risk of being preyed upon by temperate predators may also reduce for range expanding tropical fishes as communities of these native predators diminish in temperate reefs (e.g., Nakamura et al. 2013). Nevertheless, as tropical piscivore communities shift poleward, these range-expanding predators may increasingly constrain recruitment of tropical prey fishes at temperate latitudes. Resource requirements of tropical fishes may also change between early and later life stages, leading to shifts in the use of temperate reef resources. For example, individuals may shift from sheltered estuarine and back-reef nursery habitats to more exposed, offshore reefs in response to dietary changes, reduced predation risk, and greater physiological performance (Nagelkerken et al. 2000; Adams et al. 2006). Nevertheless, a range of mature-sized individuals, belonging to Pomacentridae, Labridae and Chaetodontidae, were observed in similar habitats as they were found recruiting here, both in W Japan and SE Australia (H. J. Beck, unpublished data), so habitat requirements may be similar at temperate latitudes at least for some species. For reproductively viable populations to establish in temperate regions, the final stage of range expansions, suitable spawning habitats, both benthic and pelagic, as well as an energetically sufficient food supply, which may support gametogenesis, also need to be available (e.g., Ling et al. 2008). Moreover, once reproductive populations of tropical fishes have established, later generations may become better adapted to temperate habitats, due to an evolutionary response to stressors within these novel temperate reef environments, with some tropical fishes capable of rapid adaptation to pressures of climate change (Donelson et al. 2012; Munday et al. 2013). Hence, although this study provides a foundation for understanding how temperate reefs may structure range expansions of tropical fishes, to more accurately anticipate how tropical fishes will geographically respond to warming oceans, we also need to understand how these novel environments impact all their life stages and evolution, including influences of varying regional wave regimes and all potential temperate habitats.

6.1 Tables

Table 6.1 Established environmental constraints for tropical fishes colonising temperate regions with climate change, including the spatial-scale, potential mechanism of limitation and human activities that may modify the availability of suitable habitats. Emboldened box indicates the contribution of this thesis.

Spatial scale	Environmental constraints	Potential limiting factor	Anthropogenic modifiers (+ or –)	References
10s to 100s km	Oceanographic (ocean currents, distance from larval source, predation)	Larval supply	Intensifying poleward flowing currents (+) Warming waters speed larval development (-)	1, 2, 3
10s to 100s km	Water temperature	Physiological stress	Increasing with climate change (+)	4, 5
100s m to kms	Wave exposure	Physiological stress/ Benthic resources (coral)	Constructing wave barriers (+) Increasing wave energy with climate change (-)	Chapter 3
10s to 100s m	Benthic habitats (macroalgae)	Benthic resources	Loss of macroalgae with climate change and pollution (+)	Chapter 4
<10s m	Native predators	Food resources	Removal of piscivores by fishing (+) Marine reserves (-)	Chapter 5

[1] Booth et al. 2007, [2] Feary et al. 2013, [3] Luiz et al. 2013, [4] Figueira et al. 2009, [5] Figueira and Booth 2010

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