Habitat associations of tropical fishes across latitudes: Implications for ocean warming and species range expansion

Thesis submitted 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 at this or any other university, nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

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Abstract

Climate change is fundamentally altering the structure and functioning of terrestrial and marine ecosystems globally. In coral reefs, fishes are under increasing pressure from elevated temperatures and habitat degradation associated with climatic warming. Their ability to cope with these changing conditions will be key to species persistence and population sustainability into the future. The poleward shift in the geographic distribution of tropical fishes has also been documented in response to the warming and intensification of poleward boundary ocean currents, which strongly influence dispersal of fishes. However, high latitude reefs present novel conditions (e.g. temperature, resource availability, species interactions) which influence the ability of species to successfully colonise these areas. This thesis examines how habitat associations of tropical fishes may vary with latitude and temperature, in light of dynamic climate change impacts, including ocean warming and the poleward range expansion in species distributions. Such knowledge will be critical in managing coastal and coral reefs under pressing climate change scenarios.

Firstly, this thesis examined habitat associations of reef fishes, with particular focus on tropical species, across a latitudinal gradient. Fish assemblages were compared across four reef locations spanning 17 degrees of latitude along the east coast of Australia to determine the role that benthic complexity and composition of the receiving environment have in structuring the distribution of reef fish assemblages from tropical to temperate reef environments (Chapter 2). Total fish density was highest at the temperate location followed by the subtropical and two tropical locations. Overall, the densities of adult fishes were greater than juvenile fishes across all locations and among latitudinal affinities (i.e. tropical, subtropical and temperate fishes). The only exception was the greater abundance of tropical juvenile fishes than adults at the temperate location. There was also a clear difference in the functional groups driving the separation of fish assemblages among the temperate, subtropical and tropical locations. Benthic composition, compared to habitat complexity, best predicted differences in the distribution of total fish assemblages, and specifically tropical fish assemblages, among latitudinal locations. These results suggest species that rely on particular corals or have highly specialised habitat and/or trophic requirements (e.g. obligate corallivores) are

unlikely to successfully establish populations in temperate environments. Overall, local benthic composition is likely to play a role in determining which tropical fish species successfully colonise temperate reefs in the future.

Building on this foundation, behavioural time budgets, social group structure, feeding patterns and movement were quantified for three common tropical fishes (*Chaetodon auriga, Abudefduf sexfasciatus* and *Pomacentrus coelestis*), across three locations, spanning tropical to temperate reefs (Chapter 3). Species behavioural time budgets and social group structure varied both among latitudes and among species. Species were only observed to aggregate with conspecifics at the tropical location; however, mixed species aggregations were more common at subtropical and temperate locations. A reduction in movement and feeding at the higher latitudes may indicate the physiological constraints of temperature and/or impact of predation risk for tropical species in these locations. Resource availability (e.g. food, habitat, conspecifics) is also likely to have caused variation in the patterns of behaviour observed at the higher latitudes.

Following these latitudinal surveys, the influence of water temperature associated with ocean warming events on species habitat preferences were investigated (Chapter 5). Habitat choice experiments were conducted in the laboratory to isolate the effect of temperature on habitat preference. Prior to this, however, a suitable method needed to be established for detecting habitat preferences in species with varying levels of habitat association (*C. auriga, C. flavirostris, P. coelestis and A. sexfasciatus*) (Chapter 4). This study revealed that a commonly used observation interval (10 min) was not suitable, and that hourly measurements were better at detecting habitat preferences of species known to use a range of habitats (*C. flavirostris, P. coelestis and A. sexfasciatus*). The application of discrete choice modelling in understanding these habitat preferences was also found to be useful. Hourly measurements were then utilised to determine the influence of water temperatures (22˚C, 28°C and 31˚C) on habitat preferences of three common damselfishes (*P. moluccensis, P. coelestis* and *A. sexfasciatus*) selected for their range of habitat preferences (Chapter 5). Results showed *P. moluccensis* consistently selected its preferred complex coral habitat across all temperatures. Unexpectedly, however, *A. sexfasciatus* and *P. coelestis* who usually associate with a

range of habitats, developed strong habitat preferences (respectively for complex coral and boulder, and complex coral) as temperature increased from ambient levels. Therefore, we may be currently underestimating the impact of climate change on species that are known to associate with a range of habitats.

Overall, the findings of this thesis highlight that, in addition to temperature and larval supply, benthic composition likely plays a role in structuring the availability of suitable habitat and trophic resources, and thus may constrain the establishment of some tropical fishes while promoting others within high latitude reef environments. These results also provide evidence of differences in species behaviour across latitudes, giving us greater insight into the novel constraints of temperate environments, as well as which species are likely or unlikely to shift with ongoing climate change. Furthermore, within tropical reefs there are potential cumulative impacts of global warming, with risks associated both directly with habitat degradation (e.g. loss of complex coral) and possibly increasing resource overlap and competition between species in ways that have not previously been accounted for in climate prediction models. The shifts in habitat preferences observed in this study suggest we may also see increased pressure on species that do not currently rely on a particular habitat, indicating that climatic warming could affect ecological relationships in subtle and unexpected ways, prompting new lines of inquiry.

Chapter 1: General Introduction

Climate change is fundamentally altering the structure and functioning of terrestrial and marine ecosystems globally through changes in temperature, precipitation, occurrence of extreme weather events, and altering ocean circulation and acidification (IPCC, 2014). Over the last 100 years, the Earth's climate has warmed approximately 0.6°C and is projected to continue to rise at a rapid rate to levels as high as 6°C by 2100 (IPCC, 2014). This rise in environmental temperature presents various challenges that threaten species survival (Parmesan, 2006, Cahill *et al.*, 2013). Increasing temperatures have been shown to directly impact the physiology (metabolism, growth and reproduction), phenology and distribution of organisms (Hughes, 2000). Climate change can also affect organisms indirectly by altering species interactions and modifying the physical structure of habitats, with profound consequences for community composition and ecosystem functioning (Thomas, 2010). However, the longer term ability of species to respond to future temperature increase is not well understood. It is likely the response will be directly linked to shifts in distributions (Parmesan, 2006) as well as the persistence of population and species at existing locations (Charmantier *et al.*, 2008, Visser, 2008, Chevin *et al.*, 2010, Somero, 2010).

The ocean's thermal capacity has led to surface waters warming three times slower than air temperatures over land (IPCC, 2014). However, most marine species are ectotherms and therefore have been shown to respond more directly to climate warming in comparison to their terrestrial counterparts (Sunday *et al.*, 2012). Tropical marine ectotherms (e.g. coral reef fish) are expected to be particularly sensitive to increasing temperature as they have evolved in relatively stable thermal environments and often live at or near their upper thermal limits (Deutsch *et al.*, 2008, Tewksbury *et al.*, 2008). Whether marine organisms have the ability to cope with the rapid rise in ocean temperature is critical to understanding the probability of species persistence and population sustainability (Donner *et al.*, 2005, Brierley & Kingsford, 2009, Hofmann & Todgham, 2010).

Physiological impacts of increasing ocean temperature on reef fishes

For coral reef fish, being ectotherms means their metabolism and energy requirements are strongly influenced by the surrounding water temperature (Pörtner & Farrell, 2008). Numerous studies have reported strong physiological impacts on their activity, growth and reproduction associated with a temperature increase of only a few degrees above current summer temperatures (Donelson *et al.*, 2010, Johansen & Jones, 2011, Rummer *et al.*, 2014). While it appears that individuals have a limited capacity to acclimate to increasing temperature over a few months (Donelson *et al.*, 2010, Nilsson *et al.*, 2010), evidence suggests fish are showing localised adaptation in some wild populations and experimental findings indicate developmental and transgenerational acclimation (Donelson *et al.*, 2011, Donelson *et al.*, 2012, Sorensen *et al.*, 2014).

Behavioural responses to climate change

Increases in environmental temperature can significantly influence the behaviour of animals, affecting biological interactions (Tuomainen & Candolin, 2011). Moreover, the initial response of animals to environmental fluctuations is often a change in their behaviour (Tuomainen & Candolin, 2011). However, few studies have explored the potential behavioural consequences of changes in environmental temperature for fishes (Killen, 2014, Freitas *et al.*, 2015, Nay *et al.*, 2015). A rapid behavioural response to warming conditions could improve the performance of individuals, the viability of populations and affect genetic adaptation (Pigliucci, 2001, Price *et al.*, 2003). For example, behavioural thermoregulation may allow some species to reduce or modulate the harmful impacts of changing environmental temperatures (Ward *et al.*, 2010, Thums *et al.*, 2013, Johansen *et al.*, 2014). A recent experimental study also showed temperature preferences in the cardinalfish *Cheilodipterus quinquelineatus*, which moved to areas of optimal temperature, even after being pre-exposed to prolonged periods of higher temperatures (Nay *et al.*, 2015). Such behaviour could lead this species, and perhaps other thermally sensitive reef fish, to relocate to cooler habitats as temperatures continue to increase under ocean warming (Nay *et al.*, 2015).

Conversely, maladaptive responses may occur when organisms encounter environmental conditions they have not experienced during their evolutionary history, causing reduced fitness and decline in population viability (Badyaev, 2005, Ghalambor *et al.*, 2007). Evidence suggests that elevated ocean temperatures will negatively impact the reproductive behaviour and output of coral reef fishes as water temperature can trigger the production of hormones, gonad development and spawning (Donelson *et al.*, 2010, Pankhurst & Munday, 2011, Miller *et al.*, 2015). This may cause earlier and shortened breeding seasons for fish in tropical locations, reducing larval supply to reefs (Potts *et al.*, 2014). However, there are still many gaps in our understanding of how ocean warming influences other aspects of fish behaviour, including habitat associations, social interactions among species or behavioural time budgets. For instance, as documented in terrestrial ectotherms, rising environmental temperature causes some lizard species to spend more time sheltering at the expense of other fitness related activities including foraging and reproduction, significantly impacting species persistence (Sinervo *et al.*, 2010). Therefore, we may expect shifts in behaviour associated with elevated temperatures to influence the ability of species to cope under these conditions (Sih, 2013).

Impacts of habitat loss and degradation on species survival

In addition to the effects on physiology and behaviour, climate change can also affect organisms' indirectly by modifying the physical structure of habitats, which can have profound effects on reef fish assemblages (Graham *et al.*, 2014, Pratchett *et al.*, 2014). On coral reefs, scleractinian corals are key habitat forming organisms but are in serious decline as a result of climate related disturbances (Gardner *et al.*, 2003, Bellwood *et al.*, 2004, Hughes *et al.*, 2017). Rising sea surface temperatures increase the frequency of coral bleaching events and the severity of tropical storms, leading to global declines in coral cover, reductions in habitat complexity, changes in benthic composition and habitat fragmentation (Hoegh-Guldberg, 1999, Nyström *et al.*, 2000, Webster *et al.*, 2005, Bonin, 2011). Up to 75% of coral reef fishes experience declines in abundance following the extensive loss of live coral cover, which they rely on for settlement, food and habitat (Jones *et al.*, 2004, Pratchett *et al.*, 2011, Graham *et al.*, 2014, Williamson *et al.*, 2014). Furthermore, habitat complexity is an important predictor for patterns in the distribution and abundance of coral reef fish assemblages as it can influence predation, competition and environmental stress (Almany, 2004, Johansen *et al.*, 2008, Graham &

Nash, 2013). Therefore, the loss of structural complexity associated with the decline and degradation of live coral is also likely to negatively impact reef fish communities (Kerry & Bellwood, 2012).

As habitats degrade and temperatures continue to rise, we can expect to see increasing pressure on species that rely on a particular habitat for survival (e.g. obligate corallivores or coral habitat specialists) while those that use a range of habitats (e.g. habitat and trophic generalists) may be less impacted (Munday, 2004, Pratchett, 2005). Although species may be able to physiologically tolerate increases in environmental temperature, their ability to persist at current locations or redistribute may ultimately depend on the suitability of available habitat and whether it provides the biological and physical factors required for survival (Opdam & Wascher, 2004, Bennie *et al.*, 2013). Hence, determining the impacts of increasing temperature on the habitat associations of reef fish is essential to predict their future success with continued environmental change. While studies have shown the negative impacts of habitat degradation, including coral loss and habitat fragmentation on coral reef fish, little research has explored the effects of increasing temperature on other aspects of fish-habitat associations such as habitat preference.

Geographic range shifts in species distributions

One of the most significant biological responses to climatic warming is the geographical redistribution of species (Parmesan & Yohe, 2003). During periods of rapid climate change, range expansion and contraction of populations has been reported historically in the fossil record (Davis *et al.*, 2002, Carnaval & Moritz, 2008) and in present day taxa (Parmesan *et al.*, 1999, Thomas & Lennon, 1999, Hickling *et al.*, 2006, Burrows *et al.*, 2011). Shifts in both the latitude (poleward) and elevation (altitude or depth) of species have been documented with rising temperatures, as species move to more suitable climates (Parmesan & Yohe, 2003, Parmesan, 2006, Dulvy *et al.*, 2008, Lenoir *et al.*, 2008, Thomas, 2010). However, accurately predicting species range shifts, including those of marine fishes, in response to future climate change is currently limited by our incomplete understanding of the factors that control species distributions.

The poleward shift in the distribution of many tropical marine organisms has occurred in response to rising ocean temperatures (Seidel *et al.*, 2008, Lu *et al.*, 2009). A recent meta-analysis described how many marine organisms including invertebrates, macroalgae and fishes have shifted poleward at a significantly faster rate than terrestrial organisms (Sorte *et al.*, 2010). These range shifts are expected to increase in strength and intensity as climatic conditions continue to change (Booth *et al.*, 2011, Madin *et al.*, 2012). This rapid redistribution threatens the structure and function of receiving environments by altering ecosystem dynamics such as competition (Arrontes, 2002), predation (Zeidberg & Robison, 2007), herbivory (Ling, 2008, Verges *et al.*, 2014) and disease (Ford & Smolowitz, 2007). These modifications to ecosystem functioning also have great potential to impact the 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). However, the role of the receiving environment in organising the redistribution of marine species, including tropical fishes, remains largely unresolved (Bates *et al.*, 2014a).

The warming and intensification of poleward boundary ocean currents strongly influence the connectivity and recruitment of fishes and has been linked to the intrusion of tropical fishes into temperate ecosystems globally (e.g. Hutchins & Pearce, 1994, Booth *et al.*, 2007, Nakamura *et al.*, 2013, Kim *et al.*, 2015). Despite increasing detection of tropical fishes in temperate ecosystems and associated impacts (Verges *et al.*, 2016), our understanding of the factors controlling these poleward expansions is limited (Feary *et al.*, 2014).

Constraints to tropical fish range shifts in temperate reef environments

Temperate ecosystems present novel conditions for tropical fishes, and may be critical in influencing the ability of species to successfully colonize these environments. Certainly, at regional scales settlement success is determined by larval supply to temperate reefs. This is largely driven by physical oceanography which is known to influence larval transport and assemblage structure (Booth *et al.*, 2007, Matis *et al.*, 2014). For instance, the richness and density of tropical recruits declined along the southeastern Australian coast with increasing distance from potential larval sources, including the Great Barrier Reef, influenced by the East Australian Current (Booth *et al.*, 2007). Species traits are also likely to determine which tropical species are successfully transported and settle in temperate environments (e.g. large body size, schooling behaviour, nocturnal activity) (Luiz *et al.*, 2013). Surprisingly, pelagic larval duration, which may impact dispersal capability (Shanks, 2009), does not strongly influence recruitment of tropical fishes into temperate regions (Booth & Parkinson, 2011, Soeparno *et al.*, 2012). However, a series of bottlenecks currently exist between these early life stages and the successful establishment of tropical fish populations in high latitude reef environments (Booth *et al.*, 2007, Figueira *et al.*, 2009, Figueira & Booth, 2010). These include over winter survival, growth to maturity, and successful reproduction (Booth *et al.*, 2007, Figueira *et al.*, 2009, Figueira & Booth, 2010).

Being ectotherms, tropical fishes are likely to be particularly sensitive to cooler environmental temperatures associated with high latitude reefs (Feary *et al.*, 2014). Thus, even if tropical species are successfully supplied to temperate reefs and can access essential resources, variation in environmental temperature may drastically limit survival. For example, significant declines in the abundances of eight tropical butterflyfishes (family Chaetodontidae) and damselfishes (family Pomacentridae) were observed when ocean temperatures off southeastern Australia dropped to 17 - 18 °C (Figueira & Booth, 2010). Similarly, reductions in the diversity and richness of tropical fish assemblages were observed over winter in western Japan (Hirata *et al.*, 2011, Soeparno *et al.*, 2013). Cooler temperatures could also impair the escape capacity of tropical fishes from temperate predators, as cooler winter waters have been seen to reduce their swimming performance (Figueira *et al.*, 2009). However, it is likely that future warming trends in sea surface temperature will increase the frequency of survivable winters (Figueira & Booth, 2010).

The distribution of fishes within shallow tropical marine ecosystems has been associated with coral cover and composition (Wilson *et al.*, 2006, Feary, 2007), predation risk (Hixon & Beets, 1993), competition (Munday, 2001), habitat complexity (Graham & Nash, 2013) and food availability (Booth & Hixon, 1999), which could also influence where fish may successfully colonise in temperate ecosystems. As a result, we expect tropical range shifts to be limited by species-specific resource requirements

(Munday *et al.*, 2008, Cheung *et al.*, 2010). Based on our knowledge of tropical reefs, the absence of coral habitat in temperate environments is likely to restrict species that rely on corals for settlement, shelter or food (Munday *et al.*, 1997, Pratchett, 2005, Feary *et al.*, 2007, Pratchett *et al.*, 2008a). Moreover, habitat and food availability at settlement and within juvenile stages are thought to be important factors that may constrain the range expansion of tropical fishes (Feary *et al.*, 2014, Beck *et al.*, 2016b). Specifically, Beck *et al.* (2016b) showed that high wave exposure was a limiting factor in the distribution of tropical fishes in temperate reefs of southeastern Australia and western Japan. In addition, high latitude reefs have substantially different benthic assemblages in composition and structural complexity compared to their tropical counterparts (Ebeling & Hixon, 1991, Kingsford & Battershill, 1998). For example, shallow temperate reefs within southeastern Australia are characterised by macroalgae and rocky barren substrate (Underwood *et al.*, 1991). Previous research suggests settlement of tropical fishes in temperate environments is closely associated with rocky urchin barren habitat and fine scale crevices (Beck *et al.*, 2014). Although subtropical reefs have been proposed to act as potential refuges for tropical species during climate change (Riegl, 2003, Riegl & Piller, 2003), these coral assemblages typically comprise of generalist, stress tolerant species that exhibit less complex morphologies including massive, encrusting, plating and laminar growth forms (Sommer *et al.*, 2014). These subtropical coral assemblages may not provide the same resources (e.g. shelter quality) as those in tropical coral reefs. Hence, tropical species that specialise on live coral, for habitat or food, would be limited in their ability to utilise reef habitats outside their natal tropical range compared to species with more generalised resource use.

Other factors that present novel conditions for tropical fishes in temperate reefs include novel species interactions (e.g. novel social interactions, predation and competition) (Feary *et al.*, 2014). Native predators and/or competitors may significantly alter species behaviour and ultimately impact survival by restricting access to resources, including food and habitat (Hixon & Jones, 2005, Holt & Barfield, 2009, Beck *et al.*, 2016a). For instance, a study on the range expanding tropical damselfish, *Abudefduf vaigiensis*, showed a reduction in vertical movement of individuals away from shelter and feeding rate directly related to the presence of temperate predators (Beck *et al.*, 2016a).

However, the potential for competition or social group interactions among tropical fish and native temperate species is unknown.

Many knowledge gaps still exist in understanding the factors that may facilitate or constrain range expansions, making it difficult to accurately forecast which species are more likely to and which species are unlikely to shift (Figueira & Booth, 2010, Madin *et al.*, 2012, Feary *et al.*, 2014). A review by Feary *et al.* (2014) highlighted several key areas of research that require greater focus to better understand range shifts among tropical species. These included behavioural ecology, habitat use, physiology, predation and competition with temperate residents. Furthermore, understanding how the receiving environments may affect the distribution of fishes, not just at the species level but also at the assemblage/community level is critical for conservation and management of adverse impacts to receiving ecosystems that may result from this redistribution (Gilman *et al.*, 2010, Bates *et al.*, 2014b).

Study system

The present research was undertaken at various regional scales along the east coast of Australia (Fig. 1.1). This region is a climate change hotspot, with increasing water temperatures and changing ocean currents driving poleward range shifts of tropical fishes (Booth *et al.*, 2007, Figueira & Booth, 2010). This study utilised four locations (Cairns, One Tree Island, Solitary Islands and Sydney) spanning 17 degrees of latitude (and 6 °C), along the east coast of Australia (16°39'26.58"S to 33°48'2.26"S) to look at characteristics of fish assemblages and habitat availability (Chapter 2). These locations were selected because they encompassed a gradient of tropical (Cairns and One Tree Island), subtropical (Solitary Islands) and temperate reef environments (Sydney) connected by larval dispersal via the East Australian Current (Booth *et al.*, 2007). A focal behavioural study was also carried out on tropical fishes (known to recruit from tropical to temperate reefs each summer, Booth *et al.*, 2007) at One Tree Island, the Solitary Islands and Sydney (Chapter 3). Lastly, two experimental studies were undertaken at One Tree Island, located on the southern Great Barrier Reef, to focus on tropical fishes in their natal reef environment (Chapter 4, Chapter 5).

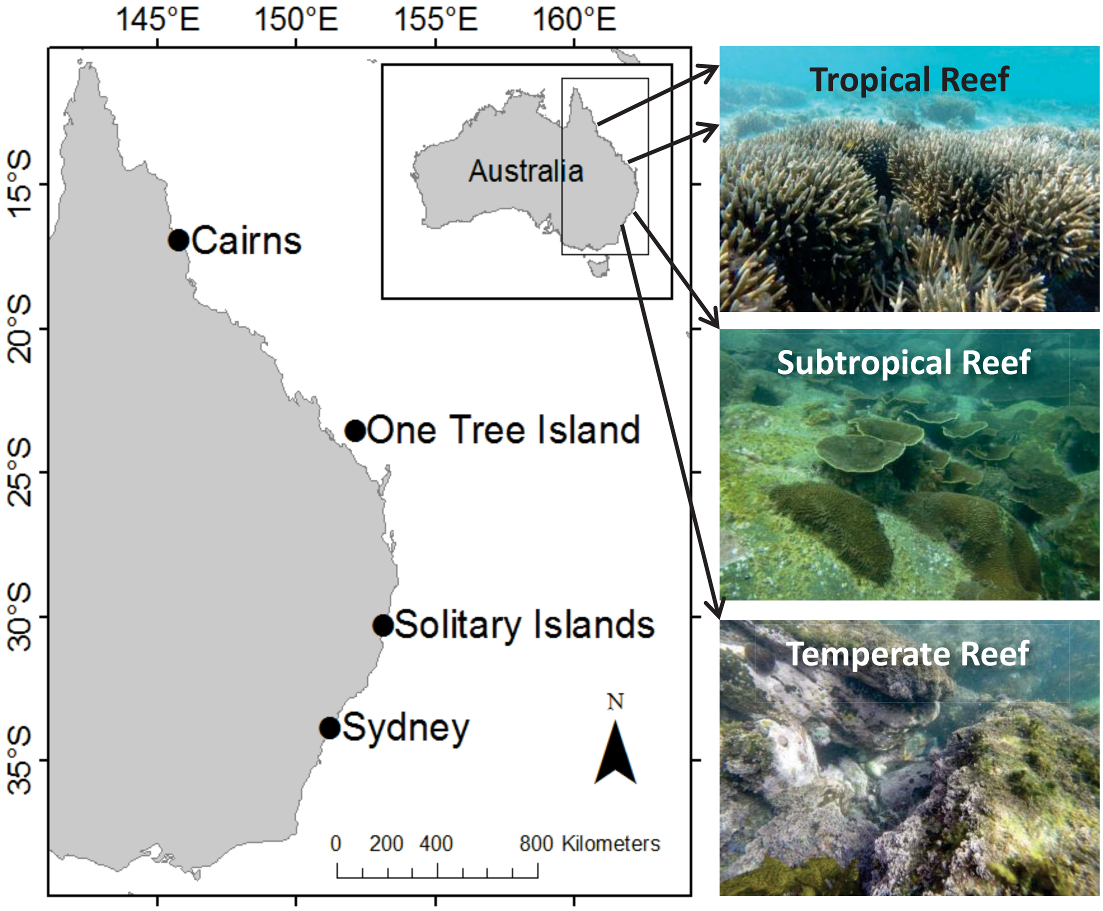


Figure 1.1. Map of eastern Australia showing the four study locations where research for this thesis was undertaken, spanning ~ 2400 km from Cairns (16°39'26.58"S, 145°59'26.09"E) in the north to Sydney (33°48'2.26"S, 151°17'49.84"E) in the south. Images show the typical reef environments at the locations of Cairns (tropical reef), One Tree Island (tropical reef), Solitary Islands (subtropical reef) and Sydney (temperate reef).

Aims and thesis outline

The objective of this thesis was to assess how habitat associations of tropical fishes may vary with latitude and temperature, in light of dynamic climate change impacts, including ocean warming and the poleward range expansion in species distributions. I designed my research questions from two perspectives. First, I explored habitat associations and behaviour of range expanding tropical reef fishes across a latitudinal gradient. Second, I looked at the effects of warming on habitat preferences of tropical reef fishes. I address these questions in four separate studies following the chapters outlined below.

In **Chapter 2,** I examined the role of the physical complexity and composition of benthic communities in structuring the distribution of reef fish assemblages, with a particular focus on range expanding tropical fishes, across a latitudinal gradient of tropical to temperate reefs. Despite the global increase in abundance of tropical fishes documented in temperate ecosystems, many of the factors that may facilitate or constrain such range expansions are not well understood. This knowledge gap makes it difficult to accurately forecast which species are more or less likely to shift in the future. Based on a lack of tropical corals and resources associated with tropical coral reefs, it was expected tropical fish present across all latitudinal locations would be species that do not rely on corals for survival and have more generalised habitat requirements.

Chapter 3 builds on this foundation by quantifying the behavioural time budgets, social group structure, feeding patterns and movement of three tropical fishes (*Chaetodon auriga, Abudefduf sexfasciatus* and *Pomacentrus coelestis*) found across a latitudinal gradient also spanning tropical to temperate reefs. Our knowledge of how tropical fishes behave on high-latitude reefs and how this might affect their ability to adapt to these novel environments is limited. It was anticipated that novel species interactions, resource availability and cooler temperatures associated with temperate reefs was likely to cause variation in the patterns of behaviour at the higher latitudes for all species. Specifically, I expected species movement to be restricted in temperate reefs and to observe less free swimming and more sheltering given these ectotherms have evolved in a relatively stable thermal environment. I also anticipated the lack of resources associated with tropical reefs to restrict feeding activity. The potential for novel interactions with temperate species was also predicted.

Following these latitudinal surveys, I focused on the influence of water temperature associated with ocean warming events on species habitat preferences. A laboratory experiment was used to isolate the effect of temperature on habitat preference. Prior to this, however, a suitable method needed to be established for detecting habitat preferences in species with varying levels of habitat association. In **Chapter 4,** I evaluated the usefulness of discrete choice modelling in understanding habitat preferences of individual species. I used this to study the observation period required to accurately record the habitat preferences exhibited by four common reef fishes (*C. auriga, C. flavirostris, A. sexfasciatus* and *P. coelestis*), selected for their range of habitat associations.

Based on the results of **Chapter 4**, hourly measurements were then utilised in **Chapter 5** to determine the influence of water temperature on habitat preferences of three common damselfish (*P. moluccensis, P. coelestis* and *A. sexfasciatus*), selected for their range of habitat specialisation. I expected that increased thermal stress would elicit a stronger preference in species known to associate with a particular habitat, compared to those that are known to use a wider range of habitats.

This work examines habitat associations of tropical fishes in light of their ability to cope with future climate change, including which species are likely to successfully redistribute to higher latitudes and which species may be most affected by ocean warming in natal tropical reefs. Such knowledge will be critical in managing coastal and coral reefs under pressing climate change scenarios.

Chapter 2: Habitat predicts the distribution of tropical fishes across a tropical to temperate gradient

This chapter was prepared for submission to *Marine Ecology Progress Series*

Abstract

Marine species are responding to warming oceans by shifting their distribution poleward, including the global intrusion of tropical fishes into subtropical and temperate ecosystems. While increasing water temperatures will reduce the physiological constraints for tropical fishes at higher latitudes, little is known about the importance of habitat in early establishment of such species. Here, I investigate the extent to which benthic composition and habitat characteristics can explain variation in reef fish assemblages across a tropical to temperate gradient along the east coast of Australia (16°39'26.58"S to 33°48'2.26"S). Total fish density was highest in temperate reefs of Sydney followed by subtropical reefs of the Solitary Islands, and tropical reefs of One Tree Island and Cairns. Overall, densities of tropical, subtropical and temperate adults were higher than densities of juveniles at all locations, with the exception of Sydney, where tropical juveniles were more abundant than adults. Fish assemblages at the tropical locations were characterised by obligate corallivores, omnivores, apex predators and detritivores, whereas subtropical and temperate assemblages were typified by benthic herbivores, planktivores and mesopredators. Variation in fish assemblages among latitudinal locations was closely linked with benthic composition, especially for fishes of tropical affiliation, whereas habitat complexity only played a minor role. Results suggest that generalist fish species are more likely to colonise high latitude reefs, while species that rely on particular corals or have highly specialised habitat and/or trophic requirements are less likely to successfully establish populations in temperate environments. These findings highlight that local benthic composition will likely play an important role in determining which tropical fish species successfully establish populations in temperate environments in the future.

2.1 Introduction

Climate change is altering terrestrial and marine ecosystems by causing changes in temperature, precipitation, occurrence of extreme weather events, and altering ocean circulation and acidification (IPCC, 2014). Increasing environmental temperature presents various challenges that threaten species survival (Parmesan, 2006, Cahill *et al.*, 2013) and can directly impact the physiology (metabolism, growth and reproduction), phenology and distribution of organisms (Hughes *et al.*, 2018). Tropical ectotherms are particularly at risk as they have evolved in relatively stable thermal environments and often already live near their upper thermal limits (Deutsch *et al.*, 2008, Tewksbury *et al.*, 2008). Furthermore, the long term ability of species to cope with increasing temperature relies on shifts in species distributions (Parmesan, 2006) as well as persistence at existing locations (Charmantier *et al.*, 2008, Visser, 2008, Chevin *et al.*, 2010, Somero, 2010).

During periods of rapid climate change, populations have expanded and contracted their geographical ranges both historically in the fossil record (Davis *et al.*, 2002, Carnaval & Moritz, 2008) and in present day taxa (Parmesan *et al.*, 1999, Thomas & Lennon, 1999, Hickling *et al.*, 2006, Burrows *et al.*, 2011). Species are responding to warming temperatures by moving to more suitable climates with shifts in latitude (poleward) and elevation (altitude or depth) (Parmesan & Yohe, 2003, Parmesan, 2006, Dulvy *et al.*, 2008, Lenoir *et al.*, 2008, Thomas, 2010). For example, in the northern hemisphere the sachem skipper butterfly expanded its range by 676 km north in 35 years as warmer winters increased survival at higher latitudes (Crozier, 2003, Crozier, 2004). While some species ranges have expanded, especially at the leading edges with increasing temperature, others have retracted such as the upward movement of tree lines observed in the Canadian Rocky Mountains, where temperatures have risen by 1.5°C (Luckman & Kavanagh, 2000). However, incomplete understanding of the factors that control species distributions is currently limited by our ability to accurately predict species range shifts in response to future climate warming.

Climate change can also affect organisms indirectly by modifying the physical structure of habitats, with profound consequences for community composition and ecosystem functioning (Thomas, 2010). Habitat loss and degradation pose significant risks to species that rely on specific habitats for survival (Warren *et al.*, 2001, Kadlec *et al.*, 2009). For instance, declines in sea ice have led to significant reductions in populations of arctic polar bears (Stirling *et al.*, 1999). Although species may be able to physiologically tolerate increases in environmental temperature, their ability to persist at current locations or redistribute may ultimately depend on the availability of suitable habitat and whether it provides the biological and physical factors required for survival (Opdam & Wascher, 2004, Bennie *et al.*, 2013).

Many tropical marine organisms have shifted their distribution poleward in response to increasing ocean temperatures (Seidel *et al.*, 2008, Lu *et al.*, 2009), including some of the most rapid range expansions documented for marine fishes (Sorte *et al.*, 2010). The warming and intensification of poleward boundary ocean currents strongly influence the dispersal of fishes and has been linked to the intrusion of tropical fishes into subtropical and temperate ecosystems globally (e.g. Hutchins & Pearce, 1994, Booth *et al.*, 2007, Nakamura *et al.*, 2013, Kim *et al.*, 2015). Despite increasing evidence that tropical fishes are expanding their range into high latitude ecosystems and the associated impacts (Verges *et al.*, 2016), our understanding of the factors controlling these poleward expansions is limited (Feary *et al.*, 2014).

High latitude ecosystems present novel constraints for tropical fishes, further influencing the ability of species to successfully colonise these environments. For example, at regional scales recruitment success is determined by larval supply to subtropical and temperate reefs, largely driven by physical oceanography (Booth *et al.*, 2007). Species-specific traits may also influence which tropical species are successfully transported and settle in high latitude environments (e.g. large body size, schooling behaviour, nocturnal activity) (Luiz *et al.*, 2013). However, even if tropical fishes are successfully transported and settle in high latitude reefs, being tropical ectotherms means that they are likely to be particularly sensitive to cooler environmental temperatures associated with these environments (Feary *et al.*, 2014). For instance, the abundances of eight tropical butterflyfishes (family Chaetodontidae) and damselfishes (family Pomacentridae) significantly declined when ocean temperatures off southeastern Australia dropped to 17 - 18°C over winter (Figueira & Booth, 2010). Similarly, diversity and richness of tropical fish assemblages declined over winter in western Japan (Hirata *et al.*, 2011, Soeparno *et al.*, 2013). However, future warming trends in sea surface temperature are likely to increase the frequency of survivable winters (Figueira & Booth, 2010).

While climate stressors such as rising ocean temperature can affect fishes directly, the characteristics of receiving habitats may be of critical importance, yet are rarely considered. Within shallow tropical marine ecosystems the distribution of fishes has been related to coral cover and composition (Wilson *et al.*, 2006, Feary, 2007), habitat complexity (Graham & Nash, 2013) food availability (Booth & Hixon, 1999), predation risk (Hixon & Beets, 1993) and competition (Munday, 2001), which could also influence where fish may successfully colonise in subtropical and temperate ecosystems. Consequently, tropical range shifts are likely to be limited by species-specific resource requirements (Munday *et al.*, 2008, Cheung *et al.*, 2010). Indeed, habitat and food availability at settlement and within juvenile stages have the potential to constrain the range expansion of tropical fishes (Feary *et al.*, 2014, Beck *et al.*, 2016b). High wave exposure also limits the distribution of topical fishes in temperate reefs of southeastern Australia and western Japan (Beck *et al.* (2016b). Moreover, benthic assemblages on high latitude reefs differ in composition and structural complexity compared to their tropical counterparts (Ebeling & Hixon, 1991, Kingsford & Battershill, 1998). For example, shallow temperate reefs within southeastern Australia are characterised by macroalgae and rocky barren substrate (Underwood *et al.*, 1991) and the absence of coral habitat likely restricts species that rely on corals for settlement, shelter or food (Munday *et al.*, 1997, Pratchett, 2005, Feary *et al.*, 2007, Pratchett *et al.*, 2008a). Therefore, understanding the role of habitat in structuring tropical fish assemblages in receiving subtropical and temperate environments is critical for their conservation and management, as well as determining potentially adverse impacts to native species (Gilman *et al.*, 2010, Bates *et al.*, 2014b).

Here, I investigate the links between local habitat characteristics and the distribution of reef fish assemblages across a latitudinal gradient. Using eastern Australia as a model location, I quantify aspects of fish and benthic assemblages across tropical, subtropical and temperate reef environments, to explore (1) how fish assemblage composition (species, life stage, latitudinal affiliation and trophic groups) varies with changes in habitat characteristics (benthic composition, structural complexity) across a latitudinal gradient and (2) the habitat characteristics (benthic composition, structural complexity) that predict assemblage patterns in range expanding tropical fishes among tropical, subtropical and temperate reef environments.

2.2 Methods

Study locations

This study was conducted at four reef locations (Cairns, One Tree Island, Solitary Islands and Sydney) spanning 17 degrees of latitude (and 6°C), along the east coast of Australia (16°39'26.58"S to 33°48'2.26"S) during the austral summer-autumn fish recruitment period (Doherty & Williams, 1988, Booth *et al.*, 2007), 2014 (Fig. 2.1). I selected these locations because they encompassed a gradient of tropical (Cairns and One Tree Island), subtropical (Solitary Islands) and temperate reef environments (Sydney) connected by larval dispersal via the East Australian Current (Booth *et al.*, 2007). A temperature gradient exists among these locations associated with their latitudinal distribution and the ongoing influence of the East Australian Current. Average summer (Dec - Feb) temperatures for Cairns, One Tree Island, Solitary Islands and Sydney for 2014 were 28°C, 26°C, 23°C, 22°C respectively (based on Australian Institute of Marine Science data for Agincourt Reef and One Tree Island, The New South Wales Department of Primary Industries temperature logger data for the Solitary Islands and our own temperature logger data for Sydney).

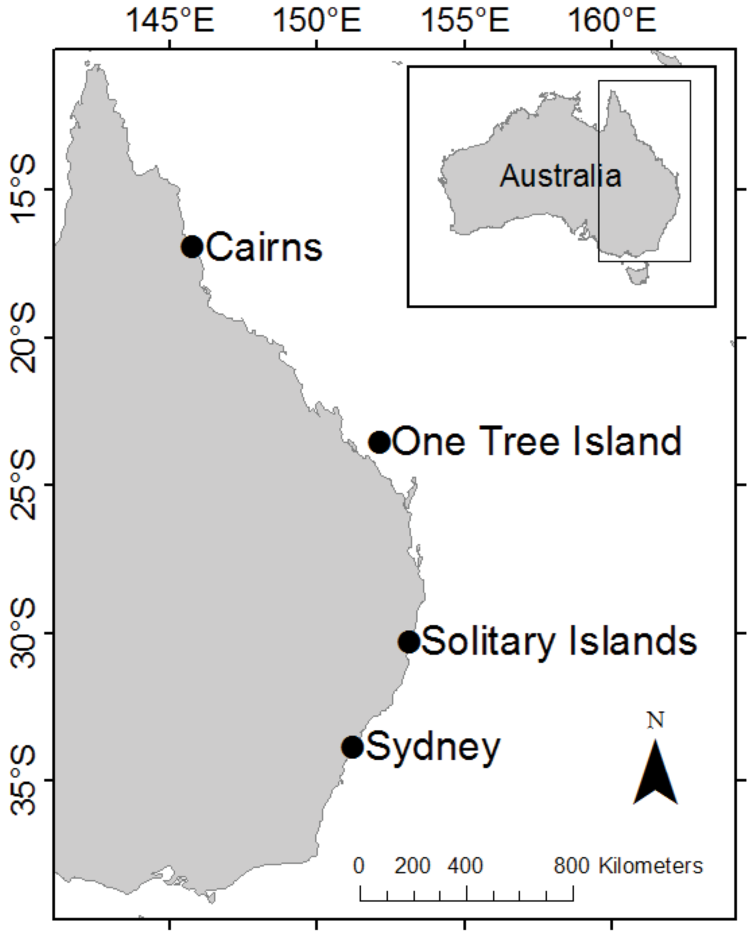


Figure 2.1. Map of eastern Australia showing the four study locations spanning ~ 2400 km from Cairns (16°39'26.58"S, 145°59'26.09"E) in the north to Sydney (33°48'2.26"S, 151°17'49.84"E) in the south. Surveys were conducted at three to four sites selected within each location.

Data collection

Three to four reef sites were sampled at each location (Cairns: Upolu reef, Vlasoff Cay, Flynn reef, Pellowe reef; One Tree Island reefs; Solitary Islands: North Solitary, South West Solitary, Split Solitary; Sydney: Shelly Beach, Little Manly, Narrabeen) based on the known occurrence of tropical fish species and logistical considerations. Sites were located on semi-protected offshore reefs and the leeward or sheltered side of islands, except Sydney where tropical fishes are only known to exist in coastal, wave-protected environments (Beck *et al.*, 2016b). Adjacent sites were separated by at least 500 m. At each site, fish and benthic assemblages were surveyed along three to four haphazardly placed 30 x 2 m replicate belt transects. A total of 52 transects were surveyed using SCUBA during daylight hours across all locations, when visibility was > 5 m and swell was < 1 m. Surveys were conducted in areas of continuous reef, with transects following the depth contour along the substrate (transect depth range overall: 1 - 8 m in depth). The species, abundance and body size (total length, to the nearest cm) of all observed non-cryptic fish species were recorded along each transect.

Benthic composition was quantified using the point-intercept method, recording the benthos directly under the transect tape at 25 cm intervals along each transect (121 points per transect). Biotic substrate was identified to the highest possible taxonomic resolution. Corals and macroalgae were identified to genus, and other invertebrates to the highest possible taxonomic groupings (anemone, ascidian colonial, ascidian solitary, asteroid, barnacle, bryozoan, echinoids (identified to species), clam, crinoid, holothurian, oyster, sponge massive, sponge encrusting, tube worm, zoanthid). Abiotic substrate types included hard substrate (bare rock, dead coral, pebble and rubble) and soft substrate (sand and sediment). To further understand the mechanisms underlying the spatial patterns of fish communities, I estimated habitat complexity or 'rugosity', directly below and perpendicular to the tape every 5 m along each transect using a standard technique, the chain link method (Luckhurst & Luckhurst, 1978). By measuring the length of a 5 m chain (18 mm links) draping the contours and crevices of the substratum needed to cover a known distance of 1 m, topography was then calculated as: total chain distance (m) divided by the known straight line distance (1 m). A score of 1 indicated the substrate was completely level, with anything over 1 indicating the substrate was more complex.

Statistical analyses

Fish assemblages

Fish species were classified by latitudinal affiliation (tropical, subtropical or temperate; determined from Randall *et al.*, 1997, Kuiter, 2000, Malcolm *et al.*, 2010), by trophic group (apex predator, mesopredator, planktivore, obligate corallivore, benthic herbivore, omnivore or detritivore; following Mora *et al.*, 2011) and as juvenile (total length < length at maturity), or adult (total length ≥ length at maturity) based on their body size (data sourced from FishBase, for some species, this information was not available, so I used parameters from other species in the same genus or family to estimate length at maturity; Froese & Pauly, 2016). Densities and species richness of fishes were compared among locations, based on latitudinal affiliation and juveniles vs. adults, using univariate permutational analysis of variance (based on Euclidean distances between sample data, Type III sums of squares, 999 permutations; Anderson, 2001). Since there were so few adult tropical fishes at the Sydney location, I combined adults and juveniles in the further analyses. Total fish (i.e. the entire fish assemblage) density data and tropical fish (i.e. fishes of tropical affiliation only) density data were fourth root transformed to meet assumptions of multivariate homogeneity and to reduce the influence of highly abundant species. Total fish assemblages and tropical fish assemblages were compared among locations (fixed) and sites (random, nested in location) using a permutational multivariate analysis of variance (PERMANOVA, Primer-E with PERMANOVA) calculated with Bray-Curtis similarity matrices (999 permutations). *Post hoc* pair-wise comparisons of locations were then carried out on unrestricted permutations of raw data. The species with the largest contribution to dissimilarity among locations were evaluated using similarity percentage analysis (SIMPER). Principal Coordinates Analysis (PCO) with overlaying vectors to summarise the main trophic groups were used to examine variation in total and tropical fish assemblage structure among locations (Anderson *et al.*, 2008).

Benthic assemblages

Benthic composition was compared among locations (fixed) and sites (random, nested in location) using PERMANOVA (Primer-E with PERMANOVA) on fourth root transformed data and calculated with Bray-Curtis similarity matrices (999 permutations). *Post hoc* pair-wise comparisons of locations were carried out on unrestricted permutations of raw data. PCO with overlaying vectors to summarise the main benthic groups was used to visualise differences in benthic composition among locations. Habitat complexity was compared among locations, using univariate permutational analysis of variance (based on Euclidean distances between sample data, Type III sums of squares, 999 permutations; Anderson, 2001).

Fish-habitat associations

A non-parametric mantel-type test (RELATE) with Spearman-rank correlation (999 permutations) was used to explore the relationship between variation in the benthic and total fish assemblages, as well as the relationship between variation in the benthic and tropical fish assemblages. PCO axes 1 and 2 of the PCO of benthic assemblages capture changes in the relative abundance of taxa across study sites. To test the extent to which benthic composition and habitat complexity could predict fish assemblage structure across study sites, I subsequently used a stepwise distance-based linear model (DistLM, 999 permutations; Anderson *et al.*, 2008), with benthic PCO axes 1 and 2 representing changes in benthic assemblages across the latitudinal gradient (PCO axis 1) and among the Solitary Islands and other locations (PCO axis 2), respectively (Fig. 2.4). Collinearity between explanatory habitat variables (habitat complexity, benthic PCO axes 1 and 2) was assessed using a draftsman plot. All variables had a correlation coefficient < 0.7 and were therefore retained for model selection (Dormann *et al.*, 2013). Explanatory variables were standardised using the “normalise” routine (Clarke & Gorley, 2006). DistLM calculates a distance-based multiple regression using permutation routines and I used the “step” procedure with Akaike Information Criterion corrected for small sample size (AICc) to identify the most parsimonious model. Results were visualised with a distance-based redundancy analysis (dbRDA; Anderson *et al.*, 2008). The same statistical procedures were then carried out to examine the influence of habitat complexity and benthic composition on variation of the tropical fish assemblage structure. I performed all analyses of fish-habitat associations using PRIMER & PERMANOVA+ v6 (Anderson *et al.*, 2008).

2.3 Results

Fish assemblages

A total of 7719 fish were recorded, belonging to 161 species and 30 families. Of these, 3215 fish (~ 42%) had a tropical affiliation, belonging to 20 families and 116 species. Unsurprisingly, fish assemblages of the two northern locations, Cairns and One Tree Island, were almost exclusively tropical species, while the two southern locations, the

Solitary Islands and Sydney had a mix of tropical, subtropical, and temperate species (Fig. 2.2).

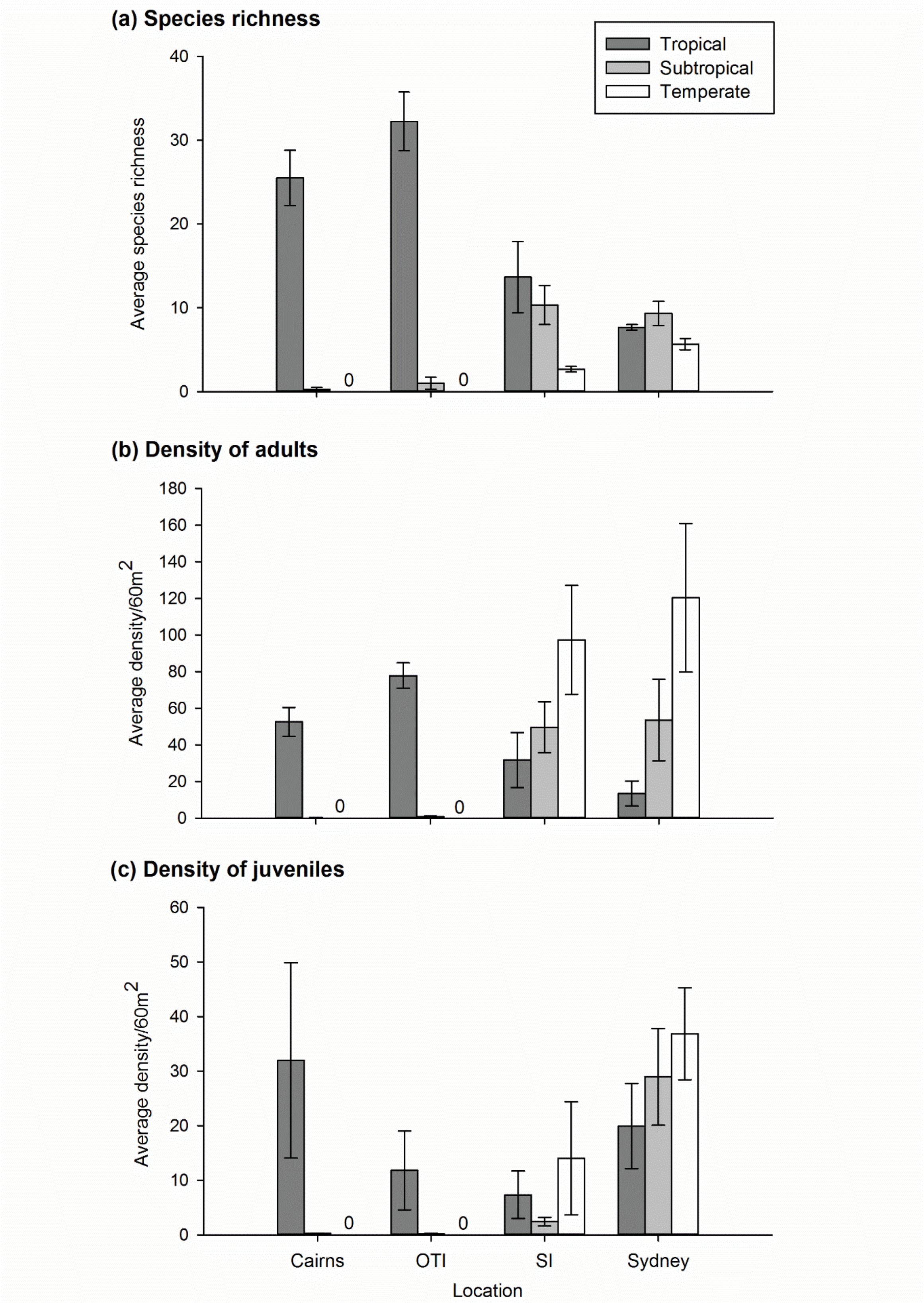


Figure 2.2. Mean (±SE) (a) species richness (b) density of adults and (c) density of juveniles, for tropical, subtropical and temperate fishes recorded across locations (Cairns, One Tree Island (OTI), Solitary Islands (SI) and Sydney).

Total fish density in Sydney was similar to the Solitary Islands ($t = 2.04$, $p > 0.05$) and significantly higher compared to One Tree Island ($t = 4.64$, $p < 0.01$) and Cairns ($t = 6.09$, $p = 0.02$) (Fig. 2.2). Densities of tropical adults were lower at Sydney compared to Cairns ($t = 3.71$, $p = 0.03$) and One Tree Island ($t = 6.48$, $p = 0.01$), and lower at the Solitary Islands compared to One Tree Island ($t = 3.04$, $p = 0.01$) (Fig. 2.2b). However, densities of tropical juveniles did not differ among locations (pseudo-F= 0.80, $p > 0.05$) (Fig. 2.2c). Densities of subtropical adults and juveniles were greater at Sydney and the Solitary Islands compared to Cairns (adults: Cairns – Solitary Islands, $t = 4.40$, $p = 0.02$; Cairns – Sydney, $t = 2.80$, $p < 0.01$; juveniles: Cairns – Solitary Islands, $t = 3.07$, $p = 0.03$; Cairns – Sydney, $t = 3.80$, $p < 0.01$) and One Tree Island (adults: One Tree Island – Solitary Islands, $t = 4.35$, $p = 0.02$; One Tree Island – Sydney, $t = 2.77$, $p < 0.01$; juveniles: One Tree Island – Solitary Islands, $t = 3.20$, $p = 0.02$; One Tree Island – Sydney, $t = 3.81$, $p < 0.01$) (Fig. 2.2b, 2.2c). Temperate adults and juveniles were only present at the Solitary Island and Sydney (Fig. 2.2b, 2.2c).

PERMANOVA results showed that fish assemblages differed significantly among locations (total assemblages: pseudo-F= 4.68, $p < 0.01$; tropical assemblages: pseudo-F= 4.41, $p < 0.01$). *Post hoc* pair-wise tests indicated that fish assemblages differed significantly between some locations but not others (Cairns – One Tree Island, $t = 1.20$, $p = 0.16$; Cairns – Solitary Islands, $t = 2.58$, $p < 0.01$; Cairns – Sydney, $t = 2.58$, $p < 0.01$; One Tree Island – Solitary Islands, $t = 2.31$, $p < 0.05$; One Tree Island – Sydney, $t = 2.11$, $p < 0.01$; Solitary Islands – Sydney, $t = 2.28$, $p = 0.08$). PCO plots supported these groupings, illustrating a clear separation of fish assemblages between Sydney, the Solitary Islands, and the two tropical locations (Cairns and One Tree), with groupings consistent for both the entire fish assemblage (Fig. 2.3) and the tropical component of the fish assemblage. The fish assemblages of Cairns and One Tree Island were characterised by obligate corallivores, omnivores, large predators and detritivores (Fig. 2.3), whereas the subtropical Solitary Islands and temperate Sydney sites were characterised by planktivores, benthic herbivores and mesopredators. The separation of tropical fish assemblages between locations corresponded with similar trophic groups.

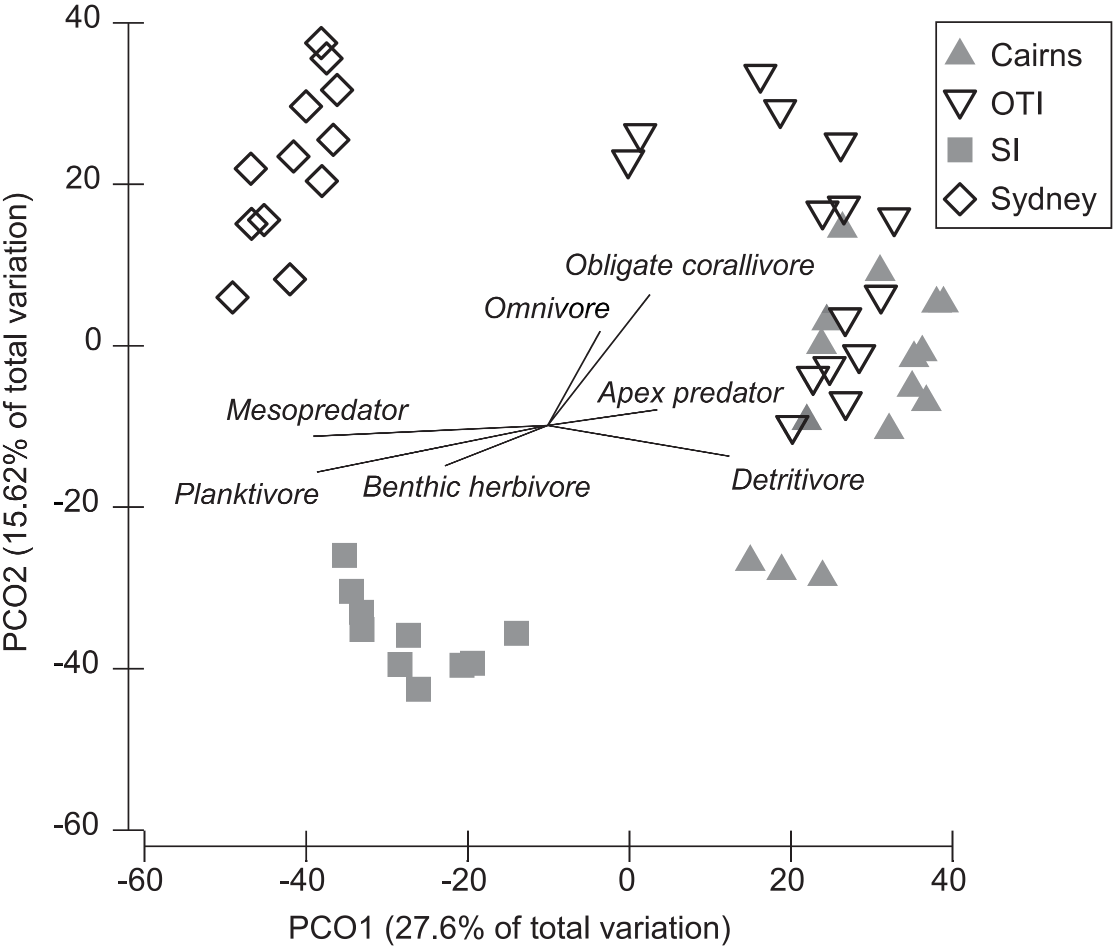


Figure 2.3. Principle coordinated ordination of total fish assemblages at each site within reef locations (Cairns, One Tree Island (OTI), Solitary Islands (SI) and Sydney). Vectors summarising the main trophic groups (apex predator, mesopredator, planktivore, obligate corallivore, benthic herbivore, omnivore, detritivore) indicate direction of the parameter effect in the ordination plot.

Similarity percentages (SIMPER) analysis indicated that a broad suite of fish taxa drove taxonomic differences among locations. At Cairns, higher densities of *Pomacentrus chrysurus, P. coelestis, P. moluccensis* and *Chromis viridis* jointly contributed > 53% of the dissimilarity in fish assemblages from other locations. At One Tree Island, higher densities of *P. moluccensis*, *P. chrysurus* and *Dascyllus aruanus* contributed > 37% of the dissimilarity between locations. Differences between the Solitary Islands and other locations were driven by higher densities of *Parma unifasciata, Trachinops taeniatus* and *P. coelestis* which jointly contributed > 45% of the dissimilarity between locations.

Differences between Sydney and other locations were driven by higher densities of *Microcanthus strigatus, Chaetodon auriga, Parupeneus signatus* and *Acanthopagrus australis* which jointly contributed > 55% of the dissimilarity between locations.

Benthic assemblages

PERMANOVA results showed that benthic assemblages differed significantly among locations (benthic assemblages: pseudo-F = 6.81, $p < 0.01$). *Post hoc* pair-wise tests showed benthic assemblages differed significantly between some locations but not others (Cairns – One Tree Island, $t = 1.23$, $p = 0.23$; Cairns – Solitary Islands, $t = 3.07$, $p < 0.05$; Cairns – Sydney, $t = 3.42$, $p < 0.05$; One Tree Island – Solitary Islands, $t = 2.37$, $p < 0.05$; One Tree Island – Sydney, $t = 2.61$, $p < 0.05$; Solitary Islands – Sydney, $t = 3.43$, $p = 0.09$). Overall the reef structure of Cairns ($t = 5.24$, $p = 0.04$) and One Tree Island ($t = 2.39$, $p = 0.03$) were more structurally complex compared to Sydney. PCO plots supported these groupings, showing a clear separation of three distinct benthic assemblages; temperate Sydney, subtropical Solitary Islands and tropical locations of Cairns and One Tree Island. The strong overlap in the benthic assemblages of Cairns and One Tree Island corresponded strongly with hard coral, soft coral and hard substrata (Fig. 2.4). The Solitary Islands benthic assemblages were characterised by ‘other invertebrates’ and corals from the Lobophylliidae, Dendrophyllidae, Siderastreidae and Merulinidae families, while Sydney had high abundance of macroalgae and soft substrata (Fig. 2.4).

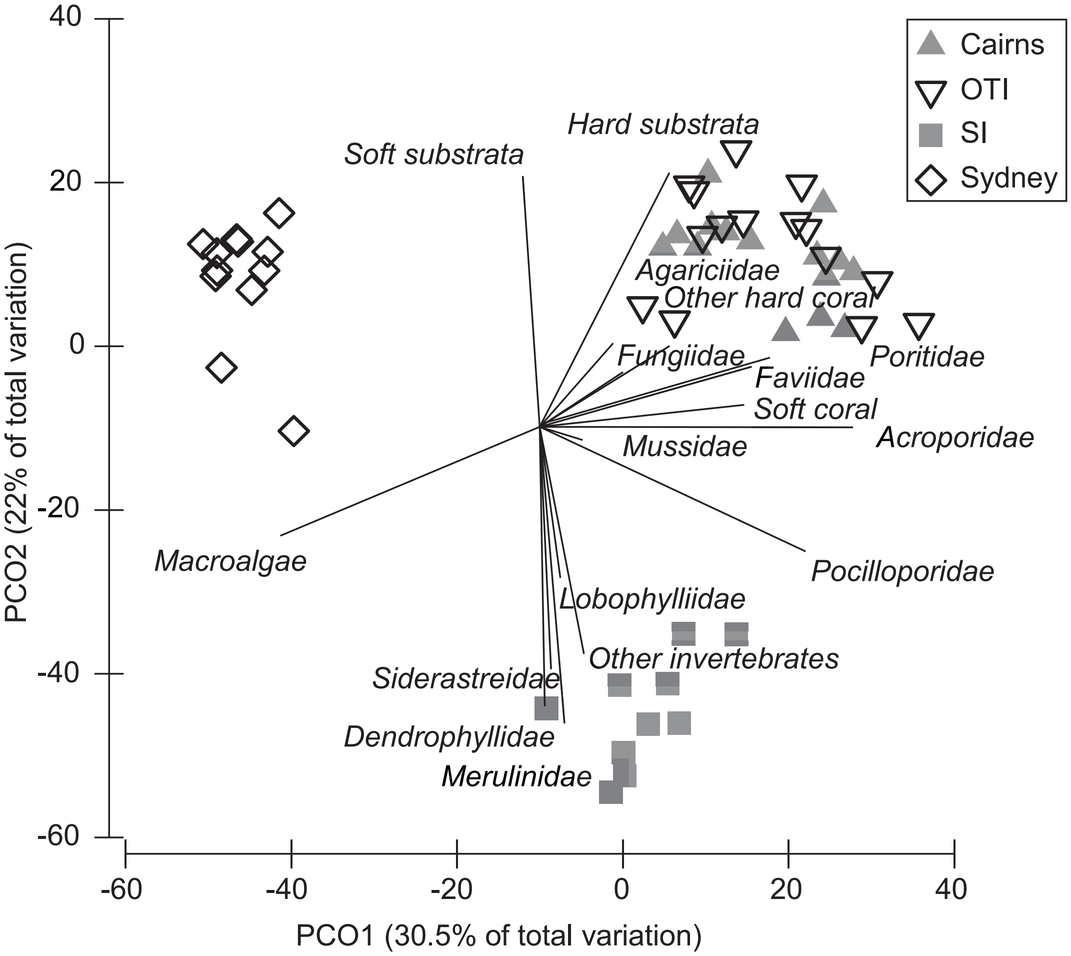


Figure 2.4. Principle coordinates analysis of benthic assemblages (detailed original ID's) at each site within reef locations (Cairns, One Tree Island (OTI), Solitary Islands (SI) and Sydney). Vectors summarising the main benthic groups (summarised at the family level) indicate direction of the parameter effect in the ordination plot.

Fish-habitat associations

Variation in benthic assemblage structure explained 69.3% of the variation in total fish assemblages across locations (RELATE; Spearman Rho = 0.693, p = 0.001) and 73.1% of the variation in tropical fish assemblages across locations (RELATE; Spearman Rho = 0.731, p = 0.001). Benthic composition explained total fish assemblages better than rugosity. According to the DistLM, ~ 38% ($R^2 = 0.383$, $p < 0.001$) of the variation in the total fish assemblages was explained by benthic composition (benthic PCO axes 1 and 2) (Table 2.1, Fig. 2.5). Habitat complexity did not improve the model fit and was eliminated by the model selection.

Table 2.1. Results of the distance-based linear model (DistLM) for total fish assemblages against explanatory variables including habitat complexity, benthic PCO axes 1 (Benthic 1) and 2 (Benthic 2). The proportion of variance in fish assemblages was explained by explanatory variables in stepwise sequential tests following AICc selection criterion. Prop. = proportion of variance explained by each single variable; res.df = residual degrees of freedom.

Sequential tests for stepwise model

Variable	AIC_c	SS (trace)	Pseudo – *F*	*P*	Prop.	Cumulative	res. df
Benthic 1	416.32	40597	14.121	< 0.001	0.220	0.220	50
Benthic 2	406.36	30092	12.974	< 0.001	0.163	0.383	49

Percentage of variation explained by individual axes

% explained variation out of fitted model			% explained variation out of total variation	
Axis	Individual	Cumulative	Individual	Cumulative
1	67.21	67.21	25.77	25.77
2	32.79	100	12.57	38.35

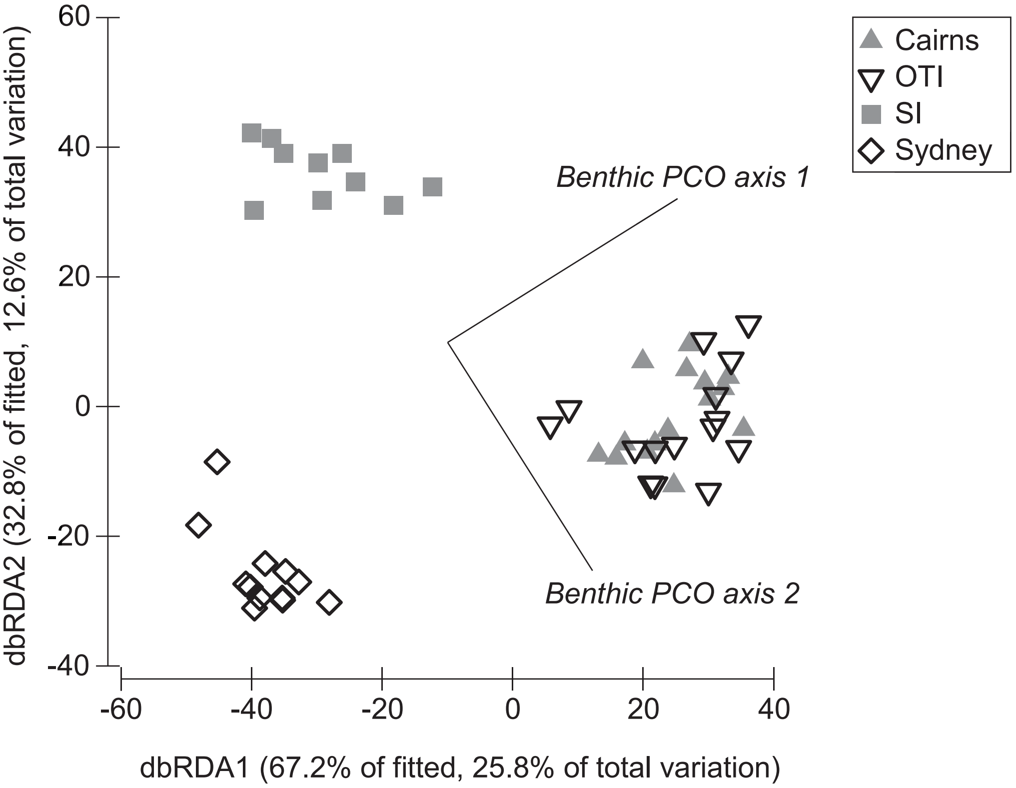


Figure 2.5. Distance-based redundancy analysis (dbRDA) plot of the DistLM based on the predictor variables (habitat complexity, benthic PCO axes 1 and 2) fitted to the variation in total fish assemblages (Table 2.1 DistLM results) at each site within reef locations (Cairns, One Tree Island (OTI), Solitary Islands (SI) and Sydney). Vectors indicate direction of the parameter effect in the ordination plot.

Similarly, benthic composition best predicted tropical fish assemblages. According to the DistLM, ~ 37% ($R^2 = 0.368$, $p < 0.001$) of the variation in tropical fish assemblages was explained by benthic composition (benthic PCO axes 1 and 2) (Table 2.2, Fig. 2.6). Habitat complexity did not improve the fit of the model and was eliminated in model selection.

Table 2.2. Results of the distance-based linear model (DistLM) for tropical fish assemblages against explanatory variables including habitat complexity, benthic PCO axes 1 (Benthic 1) and 2 (Benthic 2). The proportion of variance in fish assemblages was explained by explanatory variables in stepwise sequential tests following AICc selection criterion. Prop. = proportion of variance explained by each single variable; res.df = residual degrees of freedom.

Sequential tests for stepwise model

Variable	AIC_c	SS (trace)	Pseudo – *F*	*P*	Prop.	Cumulative	res. df
Benthic 1	416.40	40139	13.94	< 0.001	0.218	0.218	50
Benthic 2	407.55	27684	11.666	< 0.001	0.150	0.368	49

Percentage of variation explained by individual axes

% explained variation out of fitted model			% explained variation out of total variation	
Axis	Individual	Cumulative	Individual	Cumulative
1	59.24	59.24	21.82	21.82
2	40.76	100	15.02	36.84

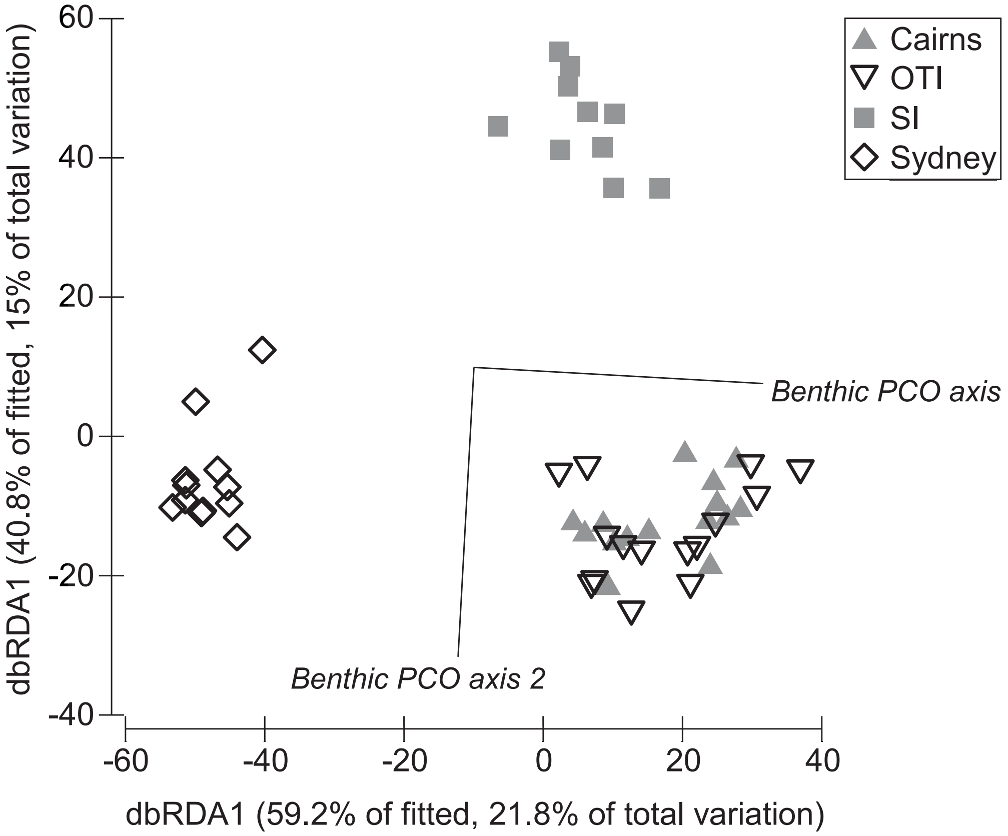


Figure 2.6. Distance-based redundancy analysis (dbRDA) plot of the DistLM based on the predictor variables (habitat complexity, benthic PCO axes 1 and 2) fitted to the variation in tropical fish assemblages (Table 2.2 DistLM results) at each site within reef locations (Cairns, One Tree Island (OTI), Solitary Islands (SI) and Sydney). Vectors indicate direction of the parameter effect in the ordination plot.

2.4 Discussion

Fish-habitat associations across latitudes

This study demonstrates a close correlation between benthic and fish assemblage structure across a tropical-to-temperate gradient along the east coast of Australia. Although larval supply and increasing water temperatures are expected to support range expansion of tropical fishes (Booth *et al.*, 2007, Figueira & Booth, 2010), the results of this study suggest that population establishment in temperate regions may also be influenced by species-specific habitat requirements.

The benthic assemblages at the tropical reef locations, Cairns and One Tree Island, differed compared to the other locations due to greater abundances of hard coral (e.g. Acroporidae and Poritidae), soft coral and hard substrata. The associated fishes driving differences among locations included *Pomacentrus chrysurus, P. coelestis, P. moluccensis* and *Chromis viridis* at Cairns, and *P. moluccensis, P. chrysurus* and *Dascyllus aruanus* at One Tree Island. These species, with the exceptions of *P. chrysurus* and *P. coelestis,* are known to rely on coral as habitat on tropical reefs (Holbrook *et al.*, 2000, Feary *et al.*, 2007). Compared to other locations, Sydney had higher abundances of subtropical species and tropical species not known to rely specifically on coral habitat for survival; *Microcanthus strigatus, Chaetodon auriga, Parupeneus signatus* and *Acanthopagrus australis* (Kuiter, 2000, Pratchett, 2005). Although corals were present in the Solitary Islands, coral assemblages differed from those in Cairns and One Tree Island. Coral assemblages on these high latitude reefs typically comprise generalist, stress tolerant species that exhibit horizontally spreading morphologies including massive, encrusting, plating and laminar growth forms (Sommer *et al.*, 2014). It is likely that these high-latitude coral assemblages do not provide the same resources (e.g. shelter quality) for *P. moluccensis, C. viridis* and *D. aruanus* as those in tropical coral reefs. Subtropical reefs have been proposed to act as potential refuges for tropical species during climate change (Riegl, 2003, Riegl & Piller, 2003). Nevertheless, our results indicate that even if fishes are successfully transported to high latitude reefs by oceanographic conditions (Booth *et al.*, 2007, Booth & Parkinson, 2011), species that rely on particular coral species or that have highly specialised habitat requirements may be limited by resource availability.

Most tropical fishes present across all reef locations were species that do not depend on corals for survival or have more generalised habitat requirements. For example, the tropical species *P. coelestis* occurred at tropical, subtropical and temperate locations, but was less abundant in temperate Sydney. However, as ocean temperatures continue to rise this species will probably become more abundant in Sydney in the future. Although *P. coelestis* does not rely on coral habitat, it is known to associate with coral rubble, which was abundant at the tropical reef locations and could reflect the greater abundances of this species in these locations (Ohman *et al.*, 1998). Similarly, in Tosa

Bay, Japan, the majority of tropical species found in both coral and rocky habitats had no strong association with live coral resources (Nakamura *et al.*, 2013). These results are consistent with the hypothesis that habitat generalists will be more likely to colonise high latitude reefs due to a limited reliance on coral habitat (Nakamura *et al.*, 2013, Feary *et al.*, 2014).

Trophic resource availability

Benthic composition influences the availability of trophic resources and therefore also indirectly affects the spatial distribution of fishes (Abrantes *et al.*, 2015). In particular, resource requirements of tropical species may be constrained by specialised dietary requirements. For example, obligate corallivores are unlikely to recruit to or survive in areas where their preferred coral species do not occur (Pratchett *et al.*, 2008a). In this study, fish assemblages at tropical locations (Cairns and One Tree Island) were characterised by obligate corallivores, omnivores, apex predators and detritivores, while assemblages at subtropical (Solitary Islands) and temperate (Sydney) locations were characterised by benthic herbivores, planktivores and mesopredators. The combination of coral and non-coral taxa present in the Solitary Islands benthic assemblage reflects the biogeographical overlap of tropical, subtropical and temperate taxa in this transition zone (Beger *et al.*, 2014) and likely provides appropriate resources to support a variety of dietary requirements including those of benthic herbivores, planktivores and mesopredators. Similarly, shallow temperate reefs within south-east Australia are characterised by macroalgae and rocky barren substrate (Underwood *et al.*, 1991) and contain the appropriate resources to support benthic herbivores, planktivores and mesopredators.

Understanding the trophic resources that support fish assemblages in different habitats is critical for their sustainable management, especially for species that participate in food webs that span several reef environments (Abrantes *et al.*, 2015). The tropical fishes present within the assemblage at temperate Sydney were non-coral or non-obligate coral feeders, including *C. auriga, Abudefduf vaigiensis, P. coelestis* among others (Kuiter, 2000, Pratchett, 2005). These results suggest that benthic composition, via its influence on trophic resource availability, probably also indirectly constrains the population establishment of trophic specialists on high latitude reefs. Moreover, recent work shows that temperate predators and seasonal water temperatures can also affect feeding behaviour of tropical fishes on temperate reefs (Beck *et al.*, 2016a). Recent work has also documented a climate-mediated increase in fish herbivory at the Solitary Islands leading to deforestation of kelp communities (Verges *et al.*, 2016). Thus, further research including focal surveys of feeding behaviour or a comparison of growth rates and body condition on a wide range of tropical fishes expanding among latitudinal reef environments is required to provide further evidence for the limitation of trophic resources at higher latitudes.

Structural complexity of reef habitat

Habitat complexity can influence predation, competition and environmental stress and plays an important role in shaping the distribution and abundance of coral reef fish assemblages (Almany, 2004, Johansen *et al.*, 2008, Graham & Nash, 2013). Surprisingly, in this study habitat complexity did not improve our models in explaining the variation in tropical nor total fish assemblages among latitudinal locations, despite a significant difference in the habitat complexity of Cairns and One Tree Island compared to Sydney. Similarly, habitat complexity did not explain differences in the tropical fish assemblages between temperate coral reefs in western Japan and temperate rocky reefs in south east Australia (Beck *et al.*, 2016b). Instead, wave exposure was shown to be an important predictor of the differences in fish assemblages between these locations (Beck *et al.*, 2016b). Habitat complexity also accounted for little spatial variation in patterns of species richness, abundance and community structure of coral reef fishes at Lizard Island on the Great Barrier Reef (Komyakova *et al.*, 2013). However, it should be noted that habitat complexity may change depending on the scale of measurement (Richardson *et al.*, 2017). This is an important consideration as animals often use their environment at spatial scales relative to their body size (Nash *et al.*, 2014). Still, structural complexity of reef habitats is inherently influenced by the composition of the underlying benthos (Richardson *et al.*, 2017). This may also explain why habitat complexity did not improve our models, with benthic composition influencing the distribution of fishes across a tropical to temperate gradient and the range expansion of tropical fishes into temperate reef environments. Future studies comparing the behavioural preferences between complex and non-complex habitats may give further insight into the importance of habitat complexity for range expanding tropical fishes at local scales.

Implications for the future success or limitation of range expansions

This is one of the few studies to compare densities of adults and juveniles among fish assemblages along a latitudinal scale. Overall, there were no difference in the density of tropical juveniles among locations, however, there were fewer tropical adults in Sydney compared to the tropical reef locations. This suggests that although temperate reefs may provide appropriate conditions for some tropical species to settle, they may lack the resources needed for growth and survival into adulthood. The low density of tropical adults recorded in Sydney supports this hypothesis. Despite the high density of tropical juveniles, this study was undertaken during the austral summer-autumn recruitment season and previous work suggests that a substantial reduction in the abundance of tropical fishes is associated with low winter-water temperatures (Booth *et al.*, 2007, Figueira & Booth, 2010). Although temperature may be a key bottleneck for survival of tropical fishes in temperate reefs at present, warming trends are likely to increase the frequency of survivable winters (Figueira & Booth, 2010). The results of this study indicate that the few adults present in the Sydney tropical fish assemblages were species considered to be more generalist and to not rely on corals as a main source of habitat or food (e.g. *Abudefduf sexfasciatus, Abudefduf vaigiensis, Chaetodon flavirostris*). A greater understanding of the factors driving differences in species distributions is needed to apprehend species range expansions into novel environments.

Climate change predictions suggest that the distributions of many marine organisms will continue to shift towards the poles at an increasing rate (Booth *et al.*, 2011, Madin *et al.*, 2012, Poloczanska *et al.*, 2013, Poloczanska *et al.*, 2016). We are already seeing altered ecosystem functioning with the expansion of various marine taxa (Ling, 2008, Verges *et al.*, 2016). As ocean temperatures continue to rise, the physiological constraints for tropical fishes at higher latitudes will likely be reduced, increasing their chances of establishing viable populations (Feary *et al.*, 2014). Moreover, some suitable tropical fish habitats (e.g. urchin barrens) are also moving poleward with climate change (Ling, 2008, Beck *et al.*, 2016a). This study highlights that, in addition to temperature and larval supply (Booth *et al.*, 2007, Figueira & Booth, 2010), benthic composition likely influences the availability of suitable habitat and trophic resources and may thus constrain the establishment of some tropical fish species while promoting others within high latitude reef environments. These findings contribute to a growing body of literature that suggest that factors including temperature, wave exposure, predation, species morphological traits, food and habitat availability may facilitate or constrain species range expansions (Figueira & Booth, 2010, Verges *et al.*, 2014, Beck *et al.*, 2016a, Beck *et al.*, 2016b, Smith *et al.*, 2016). Furthermore, research focused on key ecosystem interactions and the behavioural and physiological effects of habitat availability on range expanding tropical fishes will help us make more accurate predictions about species distributions and implement effective management plans to address potential ecosystem impacts.

Chapter 3: Latitudinal variation in behavioural patterns and social group structure of coral reef fishes

This chapter was prepared for submission to *Oecologia*

Abstract

Ocean warming is driving rapid poleward expansion of tropical marine organisms. Each summer during spawning season, the East Australian Current transports fish larvae from tropical to temperate locations in South-East Australia. Successful establishment of tropical fishes on high-latitude reefs will require appropriate behavioural responses in order to adapt to novel local organisms and habitats. Here, I investigated key behaviours related to free swimming, hovering, sheltering, foraging antagonistic interactions and movement of three common tropical fishes (*Chaetodon auriga, Abudefduf sexfasciatus* and *Pomacentrus coelestis*) across a latitudinal gradient that extends into temperate SE Australia, from the Great Barrier Reef (23°30'30"S) to Sydney (33°48′06″S). Novel social group interactions were observed at the higher latitudes, but not within their normal tropical coral-reef range. At the subtropical and temperate locations, but not in the tropical location, *C. auriga, A. sexfasciatus* and *P. coelestis* formed heterospecific groups with other tropical and temperate species. Both *C. auriga* and *A. sexfasciatus* prioritised sheltering and/or hovering over free swimming or foraging and individuals of all species moved shorter distances at the temperate location, potentially highlighting the constraints associated with high latitude reef environments (e.g. temperature, resource availability, predation and competition). The feeding rate by *C. auriga* (which could not be determined for the other two species) was quicker at the tropical reef location compared to the subtropical and temperate reef locations, which could result in slower growth rates and longer periods of vulnerability to predation at the higher latitudes. Overall, the findings of this study give us greater insight into the ability of species to modify their behaviour in response to novel environmental conditions that may ultimately influence their distribution under climate change and potential impacts to native species.

3.1 Introduction

One of the most significant ways in which species are responding to climatic warming is through rapid shifts in their geographical distributions (Parmesan & Yohe 2003; Poloczanska et al. 2013). Shifts in both the latitude (poleward) and elevation (altitude or depth) of species have been documented with rising temperatures, as species move to more suitable climates (Parmesan & Yohe, 2003, Dulvy *et al.*, 2008, Thomas, 2010, Poloczanska *et al.*, 2013, Lenoir & Svenning, 2015). The distributions of marine species, in comparison to terrestrial species, more closely follow their environmental niche and are therefore more likely to respond directly to climate warming (Sunday *et al.*, 2012). In particular, many tropical marine organisms have been shifting poleward as oceans warm (Seidel *et al.*, 2008, Lu *et al.*, 2009, Poloczanska *et al.*, 2013), with some of the most rapid range expansions documented for fishes (Sorte *et al.*, 2010).

The global intrusion of tropical fishes into subtropical and temperate ecosystems has been linked to the warming and intensification of poleward boundary ocean currents (e.g. Hutchins & Pearce, 1994, Booth *et al.*, 2007, Nakamura *et al.*, 2013, Kim *et al.*, 2015), which strongly influence the dispersal of fishes (Booth *et al.*, 2007). These poleward range shifts are expected to increase in strength and intensity with ongoing climate change (Booth *et al.*, 2011, Madin *et al.*, 2012), threatening the structure and function of receiving environments by altering ecosystem dynamics such as competition (Arrontes, 2002), predation (Zeidberg & Robison, 2007), herbivory (Ling, 2008, Verges *et al.*, 2014) and disease (Ford & Smolowitz, 2007). Therefore, predicting which species are likely to colonise high latitude reef environments will be crucial in making accurate forecasts about changes in biodiversity and ecosystem functioning that may occur under continued climate change (Figueira & Booth, 2010, Madin *et al.*, 2012, Feary *et al.*, 2014). However, for this to be possible, increased knowledge of the factors controlling these poleward range expansions is required (Feary *et al.*, 2014).

Temperate reefs have been proposed to act as potential refuges for tropical fishes during climate change, however they present novel environmental conditions which are likely to influence species' ability to adapt to these locations (Riegl, 2003, Riegl & Piller, 2003). For example, temperature strongly influences the metabolic rate of fishes and therefore influences individual growth, movement, behaviour, reproduction, survival and overall fitness (Pörtner & Farrell, 2008, Donelson *et al.*, 2010, Payne *et al.*, 2016). Thus, as tropical ectotherms, tropical fishes are likely to be particularly sensitive to cooler environmental temperatures associated with high-latitude reefs (Feary *et al.*, 2014). For instance, when ocean temperatures off southeastern Australia dropped to 17 - 18°C, significant declines in the abundances of tropical butterflyfishes (Chaetodontidae family) and damselfishes (Pomacentridae family) were observed (Figueira & Booth, 2010). Reductions in the swimming performance of tropical fishes have also been documented in association with temperate reef winter temperatures (Figueira *et al.*, 2009). Similarly, based on our knowledge of tropical reefs, the absence of coral habitat in temperate environments is likely to restrict species that rely on corals for settlement, shelter or food (Munday *et al.*, 1997, Pratchett, 2005, Feary *et al.*, 2007, Pratchett *et al.*, 2008a). Moreover, benthic assemblages within high latitude reefs differ substantially in composition and structural complexity from their tropical counterparts (Ebeling & Hixon, 1991, Kingsford & Battershill, 1998). For example, shallow temperate reefs of southeastern Australia are typically dominated by areas of macroalgae and rocky urchin barren habitat (Underwood *et al.*, 1991), and although subtropical reefs have coral assemblages, these typically comprise of generalist, stress tolerant species that exhibit less complex morphologies (Sommer *et al.*, 2014), and therefore may not provide the same resources (e.g. shelter quality) as those in tropical coral reefs. Other novel factors associated with high latitude reef environments include interactions with native species, including novel social interactions, predation and competition (Feary *et al.*, 2014). Native predators and/or competitors may significantly alter species behaviour and ultimately impact survival by restricting access to important resources, including food and habitat (Hixon & Jones, 2005, Holt & Barfield, 2009, Beck *et al.*, 2016a). However, there is still a limited understanding of how these novel conditions affect assemblage composition, habitat associations and behaviour of tropical fishes at the higher latitudes (Figueira & Booth, 2010, Madin *et al.*, 2012, Feary *et al.*, 2014).

The ability of tropical fishes to establish populations outside their normal range is likely to be determined by their ability to adapt, acclimate or acclimatise to novel environmental conditions (Feary *et al.*, 2014). For many organisms, a change in behaviour is often the initial response to environmental variation (Tuomainen & Candolin, 2011). A rapid behavioural response to environmental change may improve species' individual performance, population viability and the possibility of genetic adaptation (Pigliucci, 2001, Price *et al.*, 2003). However, behavioural responses may also be maladaptive and come at a cost to the individual (Gates & Gysel, 1978, Schlaepfer *et al.*, 2002, Robertson *et al.*, 2013, Robertson & Chalfoun, 2016). For instance, species have been shown to reduce non-essential activities, including swimming, foraging, growth and energy storage when temperatures become too hot or too cold (Pörtner, 2002, Pörtner & Peck, 2010). Therefore, it is critical to understand how novel species interactions, resource availability and cooler temperatures may affect behavioural responses of tropical fishes at the higher latitudes, which is likely to have significant implications for survival and distribution of species' outside their natal tropical reef environments (Figueira & Booth, 2010, Tuomainen & Candolin, 2011, Madin *et al.*, 2012, Feary *et al.*, 2014). A recent review also highlighted that aside from established topics of research on species traits (e.g. larval biology/ecology, post-settlement resource use), behavioural patterns is a key area of research required to better understand range shifts among tropical fishes (Feary *et al.*, 2014). Increased knowledge about how tropical fishes behave within novel environments will give us further insight into which species may be able to establish populations at the higher latitudes, as well as how they might impact local species and ecosystem functions.

Therefore, the aim of this study was to investigate potential differences in the behaviour of tropical fishes across a latitudinal gradient encompassing tropical, subtropical and temperate reef environments. I quantified aspects of behaviour for three common coral reef fishes along the east coast of Australia, to address the following three questions: (1) do key behaviours of tropical fishes differ among tropical, subtropical and temperate reef environments? (2) do these behaviours differ among tropical fish species and (3) can any differences in behaviour inform us about which species are more/less likely to succeed in colonising high latitude reefs?

3.2 Methods

Study locations

This study was undertaken during austral summer-autumn in 2015 at three locations (tropical: One Tree Island, subtropical: Coffs Harbour and temperate: Sydney) connected by larval dispersal via the East Australian Current (Booth *et al.*, 2007), spanning 10 degrees of latitude along the east coast of Australia (23°30'30"S to 33°48′06″S, Fig. 3.1). Ocean temperatures for One Tree Island, Coffs Harbour and Sydney were ~28°C, 24°C, 22°C respectively when surveys were conducted (Australian Institute of Marine Science temperature loggers for One Tree Island; http://weather.aims.gov.au/#/station/131, The New South Wales Department of Primary Industries temperature loggers for the Solitary Islands and our own temperature logger data for Sydney). Four to six reef sites were selected at each location based on the known occurrence of study species, which included semi-protected offshore reefs and coastal, wave-protected environments, separated by at least 500 m.

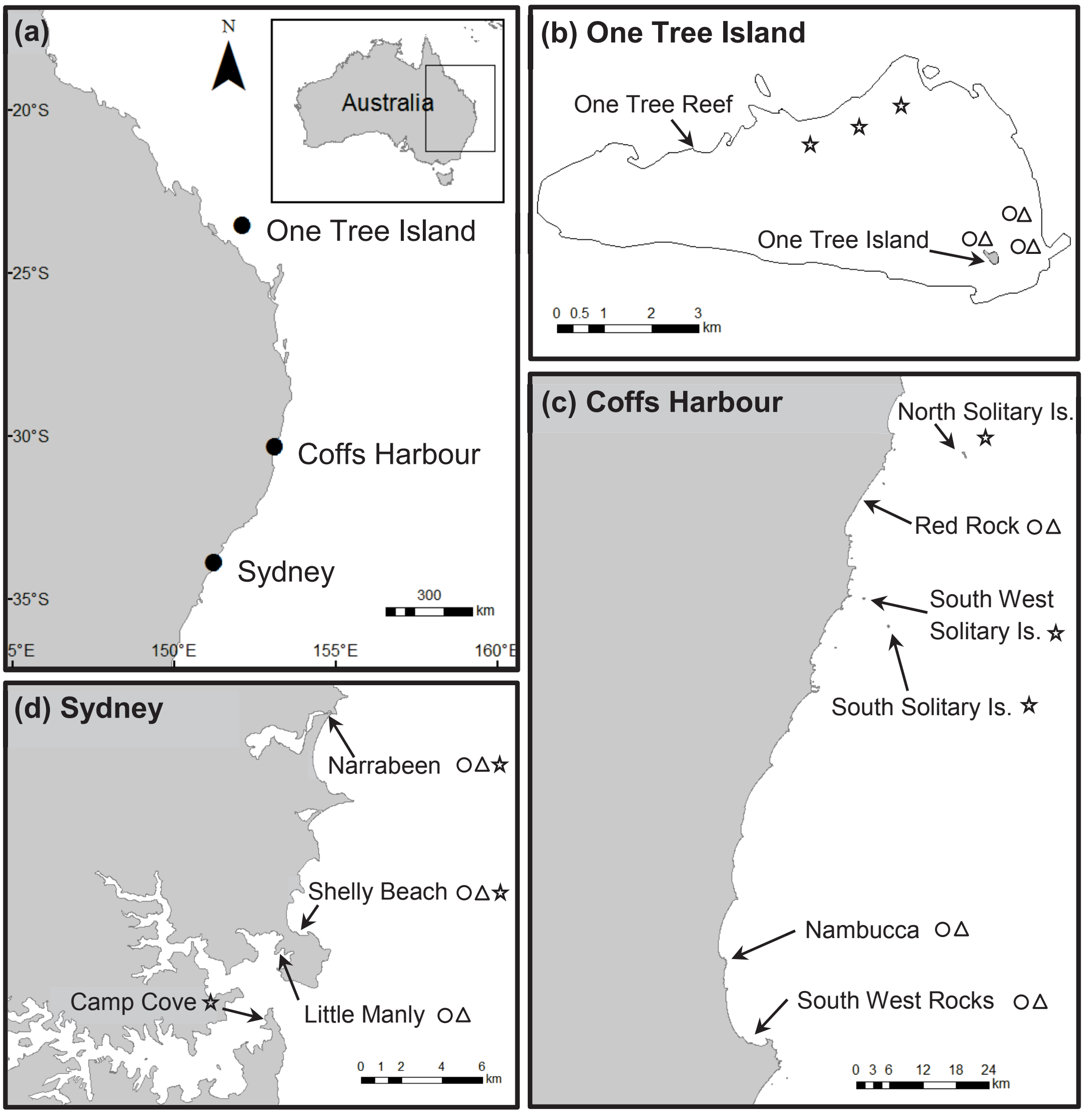


Figure 3.1. Map of eastern Australia showing (a) the geographic position of the three study locations: One Tree Island, Coffs Harbour and Sydney, and (b - d) the position of sites within each location. Focal observations of *Chaetodon auriga* (triangle), *Abudefduf sexfasciatus* (circle) and *Pomacentrus coelestis* (star) were conducted at three sites selected within each location.

Study species

This study focused on three juvenile tropical fish species; the butterflyfish *Chaetodon auriga,* and damselfishes *Abudefduf sexfasciatus* and *Pomacentrus coelestis* (species classified as tropical from Randall *et al.*, 1997, Kuiter, 2000, Malcolm *et al.*, 2010). These species were selected because they are common on tropical and subtropical reefs of Eastern Australia and are some of the most abundant tropical fishes that have been observed to consistently recruit to the temperate reefs of Sydney each summer over the past 15 years (Booth *et al.*, 2007, Feary *et al.*, 2014). *C. auriga* is known to associate with a variety of habitats ranging from rich coral reefs to rubble covered areas but as juveniles they typically inhabit lagoons and sheltered patch reefs (Pratchett *et al.*, 2008a). *C. auriga* mainly feed on coral polyps, other invertebrates and algae (Randall *et al.*, 1997, Pratchett, 2005). In contrast, *A. sexfasciatus* associates with a range of habitats at all life stages from coral reefs to rocky shorelines where they aggregate to feed on plankton and algae (Allen, 1991, Hutchins & Pearce, 1994). *P. coelestis* is also found on a broad range of habitats from coral rich to algal-dominated rocky and rubble areas, and is an omnivorous species (Randall *et al.*, 1997, Ohman *et al.*, 1998). However, as juveniles they generally aggregate on coral rubble patches (Ohman *et al.*, 1998).

Behavioural observations

For each species (n = 20 individuals per location) at each location, juveniles (< 1/3 max body length for the species) of the target species were haphazardly selected by a diver for focal observation. Observations were roughly divided evenly among sites for each species. All observations were undertaken between 0800 hr and 1600 hr, when visibility was > 5 m and swell was < 1 m. Following a 3 min habituation period, fish were observed for a further 3 min where their behaviour was recorded using a hand-held video camera (GoPro Hero 3+). During the habituation period group size of the individual was recorded (if individuals were part of a group), including the number of conspecifics and heterospecifics. The observer remained at least 2 m from the focal individual at all times during the observational period. Individual observations were aborted and data discarded if the focal individual was lost or appeared to be affected by the presence of the observer. The behavioural time budget of each fish was calculated from the video recordings by quantifying the proportion of time allocated to each of the pre-specified behaviours (Table 3.1).

Table 3.1. Behaviours recorded by the observer and definitions/interpretation for focal individuals of juvenile *Chaetodon auriga, Abudefduf sexfasciatus* and *Pomacentrus coelestis.*

Free swimming	Fish mobile, exhibiting no other discernible behaviour
Hovering	Fish stationary, exhibiting no other discernible behaviour
Sheltering	Fish stationary, within a shelter site
Foraging*	Period of continuous nose down posture, with regular feeding bites (*C. auriga*) or vertical movements into the water column, away from the reef matrix (*A. sexfasciatus*) (Beck et al. 2016)
Antagonistic behaviour	Short bursts of increased swimming speed that is directed away from or at another individual

*Only recorded for *C. auriga* and *A. sexfasciatus* because foraging activity could not be distinguished for *P. coelestis.*

Feeding

The average bite rate was also calculated for *C. auriga* from the video recordings (number of bites taken per 3 min observation period), however bite rate was not recorded for *A. sexfasciatus* or *P. coelestis* as bites could not be distinguished. Feeding rate of *C. auriga* was then defined by dividing the total time spent foraging per min by the number of bites per min.

Movement

The maximum horizontal linear distance moved (to the nearest 5 cm) and vertical distance above the substrate (to the nearest 5 cm) were recorded for focal individuals in situ every 15 s (following protocols by Madin *et al.*, 2010, Beck *et al.*, 2016a). The maximum horizontal distance and the mean vertical distance were calculated from these estimates and served as the values for each individual (Madin *et al.*, 2010, Beck *et al.*, 2016a).

Statistical analyses

The average proportion of time fish allocated to free swimming, hovering, sheltering and foraging was compared among locations (One Tree Island, Coffs Harbour and Sydney) using a series of canonical discriminant analyses (CDAs). Separate analyses were conducted for each species since I was interested in the relationships between locations for individual species, rather than the relationships between species at particular locations. To meet the assumptions of CDA, behavioural variables were log-transformed. Mean group centroids were plotted for the first two canonical variates, together with 95% confidence ellipses (Krzanowski & Radley, 1989).

The number of antagonistic interactions recorded between focal individuals and other species were compared among locations using nonparametric Kruskal-Wallis tests, since data did not meet the assumptions of normality and homoscedasticity. Tests were carried out (SPSS v. 23), with *post hoc* comparisons performed using Dunn's test with Bonferroni correction (Dunn, 1964). The same statistical approach was used to compare group size, maximum straight line distance and average distance above substrate for each species among locations. Patterns in the feeding behaviour of *C. auriga* were also compared using the nonparametric Kruskal-Wallis tests with *post hoc* comparisons to analyse the differences in average bite rate and feeding rate among locations.

3.3 Results

Behavioural time budget

Behavioural patterns differed significantly for each species among the different reef locations (CDA ordination plots of group centroids; Fig. 3.2a, 3.2c, 3.2e). *C. auriga* spent more time free swimming at One Tree Island, whereas at sites of the Sydney latitude they sheltered and hovered more, driving some separation in behaviour between these locations (Fig. 3.2a, 3.2b). *C. auriga* generally spent more time foraging at the Coffs Harbour sites compared to One Tree Island and Sydney (Fig. 3.2a, 3.2b). Antagonistic interactions were only observed for *C. auriga* at One Tree Island (Kruskal-Wallis *H* test: χ^2 (2) = 41.71, $p < 0.01$, Fig. 3.3a).

A. sexfasciatus spent a greater proportion of time free swimming at the Coffs Harbour sites but spent more time hovering at sites of the Sydney latitude, driving the separation in behaviour between these locations (Fig. 3.2c, 3.2d). At Coffs Harbour *A. sexfasciatus* also foraged less compared to One Tree Island and Sydney (Fig. 3.2c, 3.2d). *A. sexfasciatus* were not observed to shelter at any location. There was also no difference in the number of antagonistic interactions involving *A. sexfasciatus* among locations (Kruskal-Wallis *H* test: χ^2 (2) = 4.25, p > 0.05, Fig. 3.3b).

P. coelestis spent more time free swimming at One Tree Island and Sydney sites compared to Coffs Harbour (Fig. 3.2e, 3.2f). In contrast, *P. coelestis* spent a greater proportion of time hovering at Coffs Harbour compared to the other locations (Fig. 3.2e, 3.2f). *P. coelestis* did not shelter at One Tree Island but spent a very small proportion of time sheltering at Coffs Harbour and Sydney (Fig. 3.2e, 3.2f). *P. coelestis* were involved in more antagonistic interactions at Sydney than One Tree Island (Kruskal-Wallis *H* test: χ^2 (2) = 6.04, p = 0.04, Fig. 3.3c).

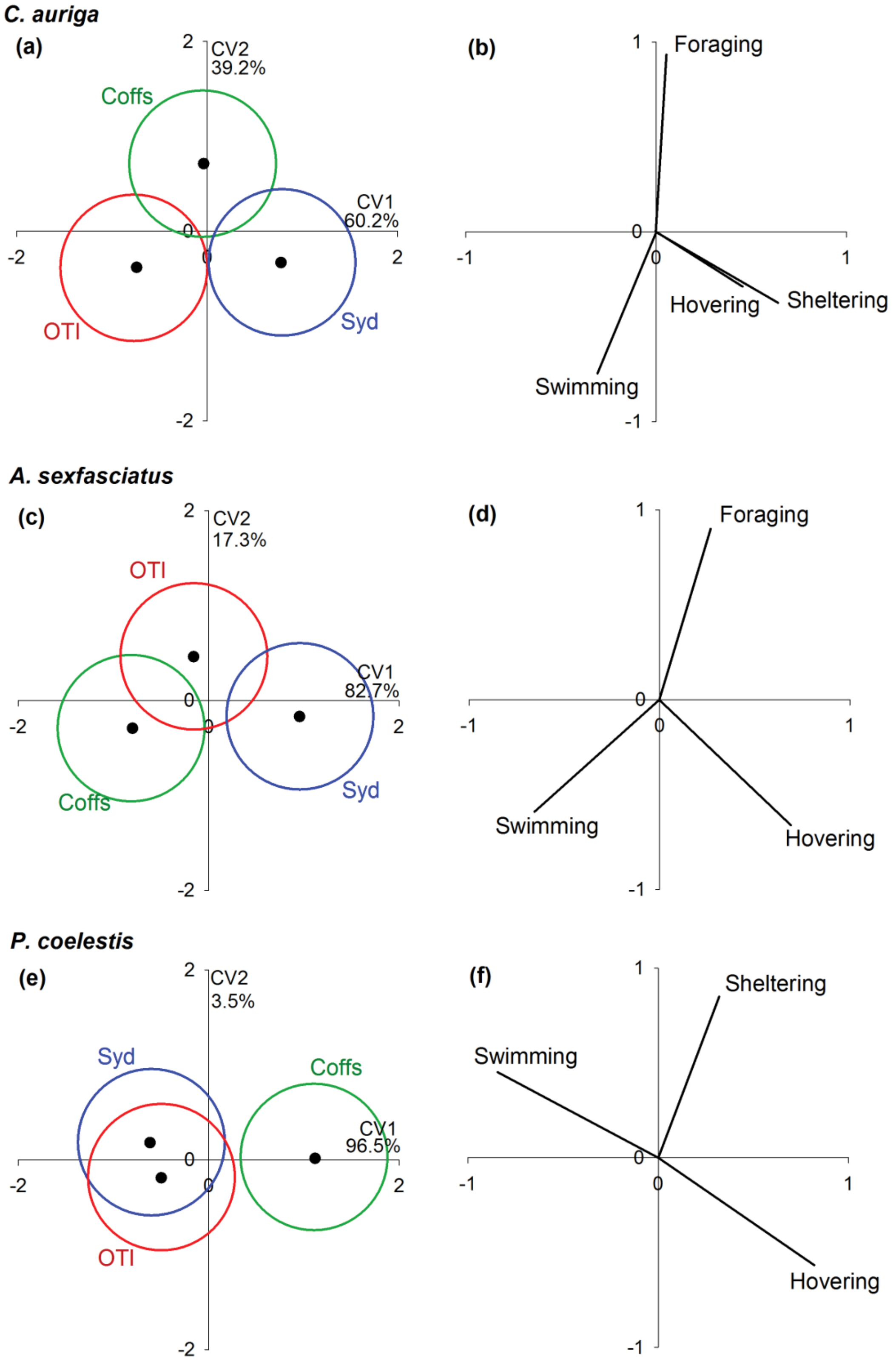
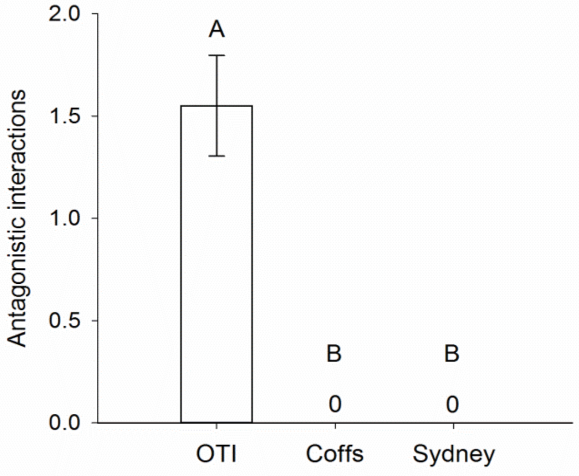


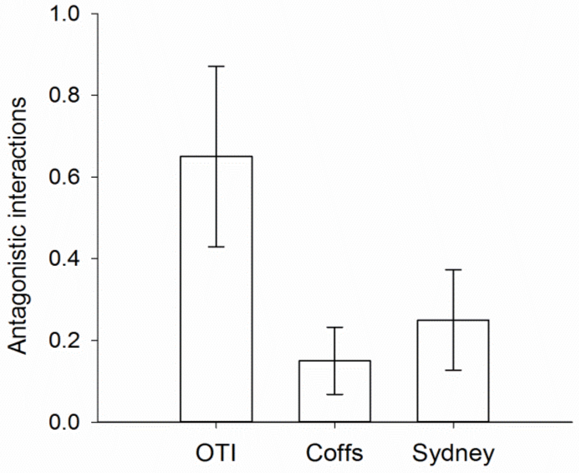
Figure 3.2. Canonical discriminant analysis (CDA) of the behaviour of *Chaetodon auriga, Abudefduf sexfasciatus* and *Pomacentrus coelestis* among the three reef locations (One Tree Island, Coffs Harbour and Sydney). Ordination plots on CV1 and CV2 of group centroids for (a) *C. auriga,* (c) *A. sexfasciatus* and (e) *P. coelestis* with

95% confidence ellipses at the locations of One Tree Island (red), Coffs Harbour (green) and Sydney (blue) and vector plots for (b) *C. auriga,* (d) *A. sexfasciatus* and (f) *P. coelestis* based on full correlations between the behavioural variables and CV1 and CV2. n = 20 per species, per location.

(a) *C. auriga*



(b) *A. sexfasciatus*



(c) *P. coelestis*

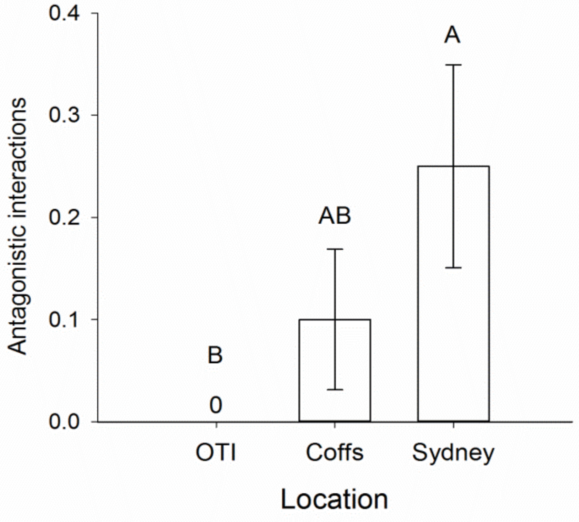


Figure 3.3. Mean (±SE) number of antagonistic interactions observed (per 3 min observation) for juvenile (a) *Chaetodon auriga*, (b) *Abudefduf sexfasciatus* and (c) *Pomacentrus coelestis* at One Tree Island (OTI), Coffs Harbour (Coffs) and Sydney.

Note: differences among locations were determined using a rank test and no significant differences were observed in (b). n = 20 per species, per location.

Group behaviour

Group behaviour for each species differed among locations, however these patterns were not consistent among species (Fig. 3.4). Group size of *C. auriga* were significantly larger at sites of the Sydney latitude compared to Coffs Harbour and One Tree Island (Kruskal-Wallis *H* test: χ^2 (2) = 27.72, $p < 0.01$, Fig. 3.4). In Sydney, *C. auriga* either formed large aggregations with heterospecifics, were alone or in conspecifics pairs (Fig. 3.4a, Table 3.2). At Coffs Harbour, *C. auriga* were generally alone but sometimes seen to form larger aggregations with heterospecifics (Fig. 3.4a, Table 3.2). In contrast, at One Tree Island all *C. auriga* were observed as solitary individuals (Fig. 3.4a). *A. sexfasciatus* varied in group size among locations (Kruskal-Wallis *H* test: χ^2 (2) = 9.41, $p < 0.01$) driven by larger group sizes at One Tree Island than in Coffs Harbour (Fig. 3.4b). Groups of *A. sexfasciatus* at One Tree Island were always composed of conspecifics, whereas in Coffs Harbour they occasionally formed small conspecific groups but generally formed larger heterospecific groups (Fig. 3.4b, Table 3.2). In contrast, *A. sexfasciatus* were only observed in heterospecific groups in Sydney (Fig. 3.4b, Table 3.2). *P. coelestis* also varied in group size among locations (Kruskal-Wallis *H* test: χ^2 (2) = 9.73, $p < 0.01$), with smaller group sizes in Sydney compared to One Tree Island and Coffs Harbour (Fig. 3.4c). *P. coelestis* were generally observed alone or in small conspecifics aggregations, but were occasionally seen in larger heterospecific aggregations in Sydney (Fig. 3.4c, Table 3.2). At Coffs Harbour, *P. coelestis* were observed in both heterospecific and conspecific groups, whereas at One Tree Island *P. coelestis* were only observed in conspecific aggregations (Fig. 3.4c, Table 3.2).

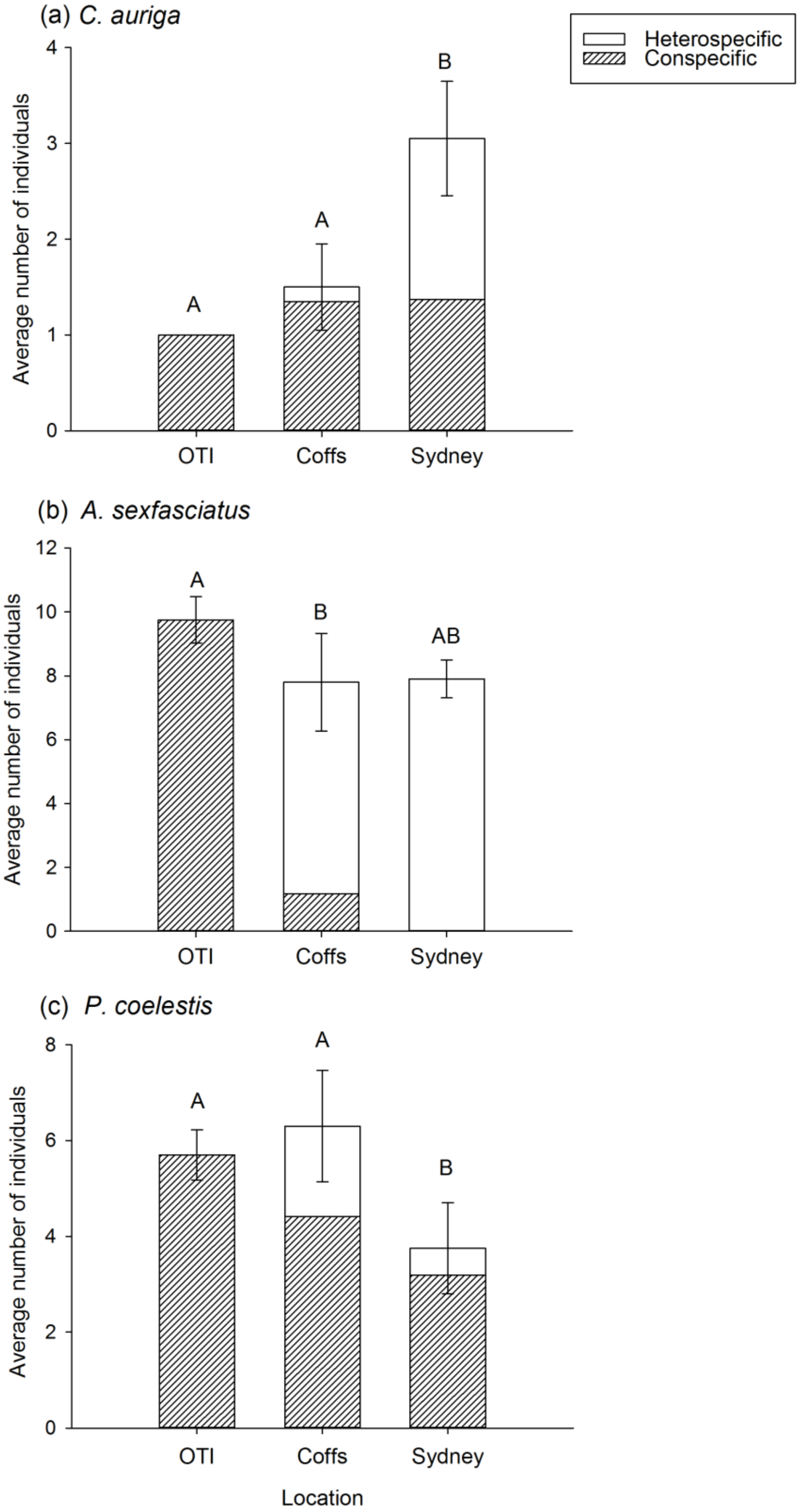


Figure 3.4. Mean (±SE) group size, including the proportion of conspecific and heterospecific groups, of juvenile (a) *Chaetodon auriga*, (b) *Abudefduf sexfasciatus* and (c) *Pomacentrus coelestis* at One Tree Island (OTI), Coffs Harbour (Coffs) and Sydney. Note: differences among locations were determined using a rank test. n = 20 per species, per location.

Table 3.2. Other species observed in social groups with focal individuals of juvenile *Chaetodon auriga, Abudefduf sexfasciatus* and *Pomacentrus coelestis* at Coffs Harbour and Sydney. Latitudinal affiliation (Lat) classified as tropical (Trop), subtropical (Sub) or temperate (Temp) (determined from Randall *et al.*, 1997, Kuiter, 2000, Malcolm *et al.*, 2010).

	Heterospecific species			
	Coffs Harbour		Sydney	
Focal species	**Species**	**Lat**	**Species**	**Lat**
C. auriga	**F. Acanthuridae**		**F. Acanthuridae**	
	Acanthurus dussumieri	Trop	*Acanthurus dussumieri*	Trop
	F. Chaetodontidae		*Acanthurus triostegus*	Trop
	Chaetodon flavirostris	Trop	**F. Chaetodontidae**	
	F. Microcanthidae		*Chaetodon flavirostris*	Trop
	Microcanthus strigatus	Sub	**F. Microcanthidae**	
			Microcanthus strigatus	Sub
			F. Mullidae	
			Parupeneus signatus	Sub
			F. Plesiopidae	
			Trachinops taeniatus	Temp
			F. Pomacentridae	
			Parma microlepis	Temp
A. sexfasciatus	**F. Pomacentridae**		**F. Acanthuridae**	
	Abudefduf bengalensis	Trop	*Acanthurus dussumieri*	Trop
	Abudefduf vaigiensis	Trop	**F. Kyphosidae**	
	Abudefduf whitleyi	Trop	*Atypichthys strigatus*	Sub
			Kyphosus sydneyanus	Temp
			F. Pomacentridae	

			Abudefduf vaigiensis	Trop
P. coelestis	**F. Plesiopidae**		**F. Mullidae**	
	Trachinops taeniatus	Temp	*Parupeneus signatus*	Sub
	F. Pomacentridae		**F. Pomacentridae**	
	Pomacentrus wardi	Trop	*Parma microlepis*	Temp

Feeding behaviour

C. auriga had a higher bite rate at One Tree Island and Coffs Harbour compared to Sydney (Kruskal-Wallis H test: χ^2 (2) = 28.55, $p < 0.01$, Fig. 3.5a). Feeding rate (i.e. time taken for the same number of bites) of *C. auriga* were faster at One Tree Island compared to Coffs Harbour and Sydney (Kruskal-Wallis H test: χ^2 (2) = 9.47, $p < 0.01$, Fig. 3.5b).

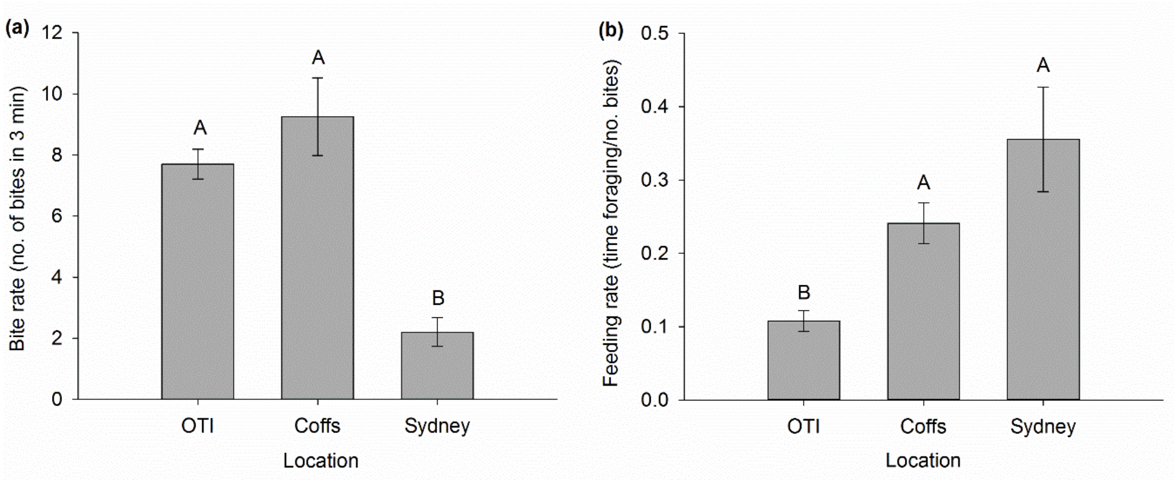


Figure 3.5. Mean (±SE) (a) bite rate (number of bites in 3 min) and (b) feeding rate (time spent foraging in a 3 min bout/number of bites taken in 3 min) of *Chaetodon auriga* at One Tree Island (OTI), Coffs Harbour (Coffs) and Sydney (n = 20 per location). Note: differences among locations were determined using a rank test.

Spatial movement

Both *C. auriga* and *P. coelestis* moved significantly greater maximum linear distances at One Tree Island compared to Coffs Harbour or Sydney (*C. auriga*: Kruskal-Wallis *H* test: χ^2 (2) = 8.74, p = 0.01; *P. coelestis*: Kruskal-Wallis *H* test: χ^2 (2) = 11.51, p < 0.01; Fig. 3.6a, 3.6e). Similarly, *C. auriga* and *P. coelestis* tended to be a greater average distance above the substrate at One Tree Island compared to Coffs Harbour or Sydney (*C. auriga*: Kruskal-Wallis *H* test: χ^2 (2) = 16.90, p < 0.01; *P. coelestis*: Kruskal-Wallis *H* test: χ^2 (2) = 20.04, p < 0.01; Fig. 3.6b, 3.6f). In contrast, *A. sexfasciatus* generally moved greater maximum linear distances at Coffs Harbour than Sydney (Kruskal-Wallis *H* test: χ^2 (2) = 10.64, p < 0.01, Fig. 3.6c), however were a greater average distance above substrate at Sydney compared to Coffs Harbour (Kruskal-Wallis *H* test: χ^2 (2) = 7.80, p = 0.02, Fig. 3.6d).

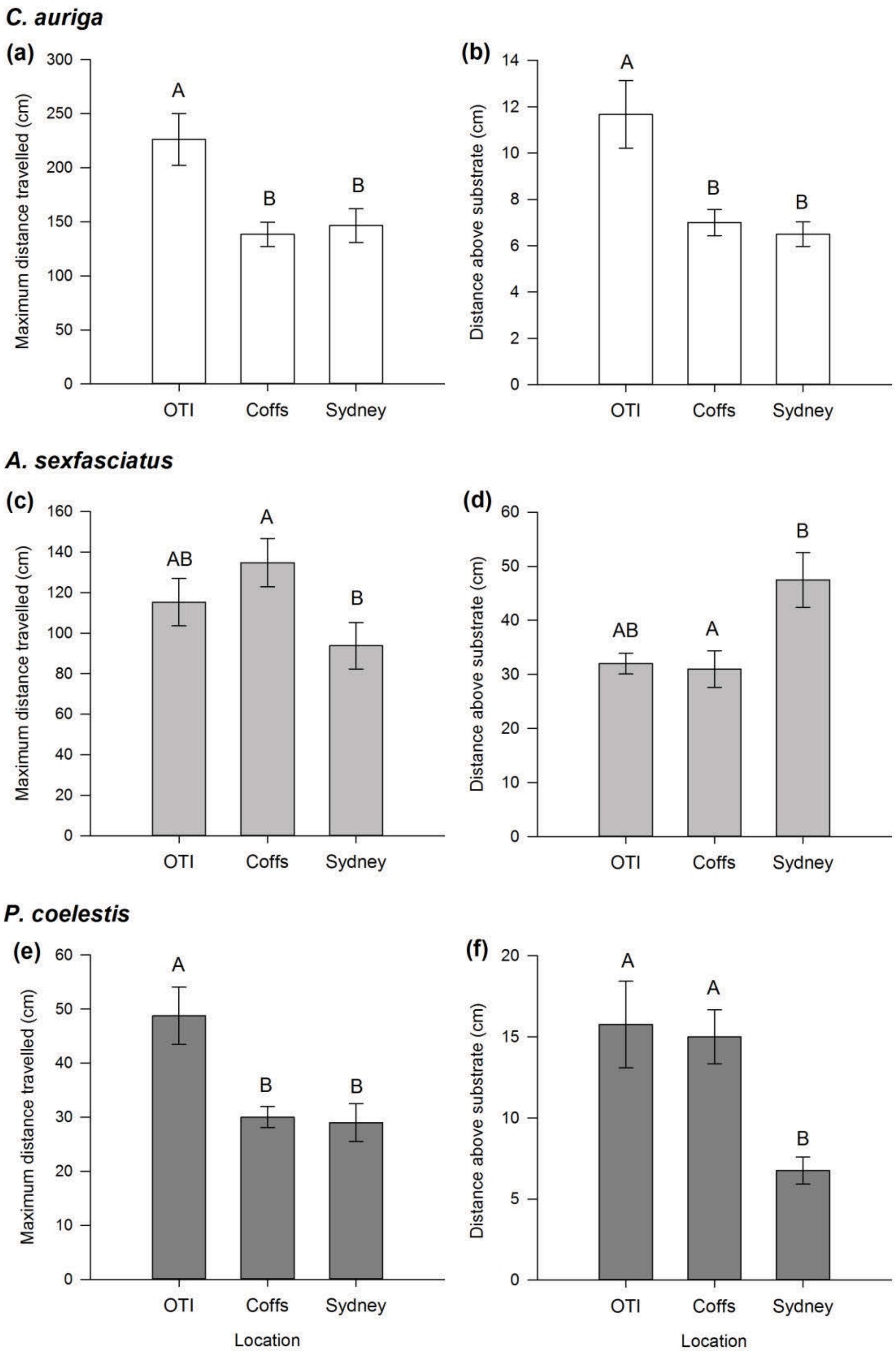


Figure 3.6. Mean (±SE) maximum linear distance moved (to the nearest 5 cm) of (a) *Chaetodon auriga*, (c) *Abudefduf sexfasciatus* and (e) *Pomacentrus coelestis*, and distance above substrate (to the nearest 5 cm) of (b) *C. auriga*, (d) *A. sexfasciatus* and

(f) *P. coelestis* among locations (One Tree Island (OTI), Coffs Harbour (Coffs) and Sydney). Note: differences among locations were determined using a rank test. n = 20 per species, per location.

3.4 Discussion

Global climate change is expected to play a central role in the distribution and diversity of species (IPCC, 2014). However, less frequently considered is that environmental variation can also produce spatial variation in species behaviour (Tuomainen & Candolin, 2011). This study demonstrates significant differences in the behavioural time budgets and spatial movement patterns of tropical fishes along a latitudinal gradient encompassing tropical, subtropical and temperate reef environments. These patterns also differed among species (*C. auriga, A. sexfasciatus, P. coelestis*). Another important finding of this study was the novel social groups observed at the higher latitude locations, where *C. auriga, A. sexfasciatus* and *P. coelestis* formed heterospecific groups with other tropical and temperate species. The fact that differences in behaviour and social structure were detected suggests that tropical reef fishes can exhibit behavioural plasticity in novel environments.

Both *C. auriga* and *A. sexfasciatus* prioritised sheltering and/or hovering over free swimming or foraging at the temperate reef sites, which may be a behavioural response to environmental conditions they experience at this location. Similarly, *C. auriga, A. sexfasciatus* and *P. coelestis* moved shorted linear distances at the Sydney latitude compared to One Tree Island. *C. auriga* and *P. coelestis* also stayed closer to the substrate in Sydney and Coffs Harbour compared to One Tree Island, and Sydney compared to One Tree Island respectively. These behaviours may be due to physiological stress associated with cooler temperatures at the higher latitudes, since these tropical ectotherms have evolved to function within a narrow range of temperatures (Hazel & Prosser, 1974, Hurst, 2007). In particular, species may make behavioural adjustments, reducing non-essential activities when temperatures become too cold, including swimming and foraging (Pörtner, 2002, Pörtner & Peck, 2010). Hence, the differences that were observed in behavioural time budgets and movement patterns of species at the higher latitudes could be a way of coping with cooler environmental temperatures (Pörtner, 2001, Pörtner & Peck, 2010). However, it is unclear whether these behaviourally plastic responses are beneficial or maladaptive and should be explored further. For example, the reduction in foraging behaviour of *C. auriga* and *A. sexfasciatus* at the temperate and subtropical locations respectively, could slow growth rates and lengthen periods of vulnerability to gape-limited predators (Sogard, 1997). However, while temperature is currently a key constraint for tropical fishes in temperate reefs, warming trends are likely to increase the frequency of survivable winters (Figueira & Booth, 2010).

The rate of antagonistic interactions observed in this study differed between locations and among species. I only observed antagonistic interactions involving *C. auriga* at One Tree Island, whereas for *A. sexfasciatus* antagonistic interactions were observed at all locations with no significant differences in the rate. In contrast, there were also significantly more antagonistic interactions involving *P. coelestis* observed at the Sydney latitude compared to One Tree Island. These results suggest that *P. coelestis* could face increased pressure from native predators and/or competitors at the higher latitudes, particularly at the temperate location where other species showed more antagonistic reactions towards them. Such interactions could have negative consequences for *P. coelestis*, whereby native predators and/or competitors may restrict their access to resources, including food and habitat (Hixon & Jones, 2005, Holt & Barfield, 2009, Beck *et al.*, 2016a). *P. coelestis* was also positioned closer to the substrate at the temperate location which may indicate threat-reducing behaviour in addition to a response to cooler temperatures (Pörtner, 2002, Hansell, 2005, Pörtner & Peck, 2010). However, *P. coelestis* spent a similar amount of time free swimming in Sydney and One Tree Island suggesting this behaviour is more likely to be linked to predator presence rather than a physiological response to temperature. In contrast, *C. auriga* may experience lower predation risk and/or competition at the higher latitudes, where antagonistic interactions were not observed. However, the greater amount of time *C. auriga* spent sheltering at the temperate location may provide protection against predation in addition to the extremes of temperature (Hansell, 2005). Although thermal constraints at the high latitudes are likely to be reduced with ongoing warming (Figueira & Booth, 2010, Feary *et al.*, 2014), predation risk and competition may still present a hurdle in the establishment of some species (Beck *et al.*, 2016a). Future studies should therefore explore potential interactions between these species and native predators/competitors to better understand the mechanisms driving these differences in behaviour across latitudes.

The behavioural and spatial movement patterns observed for all three focal species could also be driven by differences in habitat availability and composition among locations (Feary *et al.*, 2014). Post-settlement, the movement of tropical fish may be constrained to particular small areas of urchin barren habitat within temperate reefs compared to coral reefs (Beck *et al.*, 2014). While I did not enumerate the full home range of each fish, I did measured an index of movement and these patterns are likely to have important implications for the structure and abundance of populations, predator-prey interactions and individual fitness of fishes at the higher latitudes (de Roos *et al.*, 1998, Adams, 2001, Germain & Arcese, 2014). To gain further insight into the variables that may shape species distributions under climate change other aspects of movement behaviour should be investigated, including how microhabitat use and home-range size of juvenile tropical fishes vary with latitude.

This study also provided evidence for latitudinal differences in the feeding behaviour of *C. auriga,* with higher bite rates (which could not be distinguished for *P. coelestis* and *A. sexfasciatus*) observed at One Tree Island and Coffs Harbour compared to Sydney. However, when taking into account the amount of time fish spent foraging, the feeding rate at One Tree Island was much more rapid (i.e. more bites taken in shorter foraging time) compared to both high latitude locations. Although food availability was not quantified in this study, cooler water temperatures are likely to suppress feeding activity of tropical fishes in a temperate reef environment by slowing their metabolism (Pörtner, 2001, Pörtner & Peck, 2010). In addition, reduced foraging time in Sydney may also be a cost of the additional time spent sheltering and hovering at this location. Furthermore, this reduction in feeding is likely to become more extreme as temperatures cool over winter, increasing the possibility of starvation and reduction in growth rate (Eme & Bennett, 2008, Figueira *et al.*, 2009). Resource requirements of tropical fishes may be further constrained by dietary preferences (Pratchett *et al.*, 2008a). Although foraging activity of *C. auriga* did not appear to be reduced at Coffs Harbour, feeding rate was significantly slower compared to One Tree Island. Coral cover and coral species richness generally decline with increasing latitude, where benthos is frequently dominated by macroalgae, soft corals and sessile invertebrates (Harriott & Banks, 2002). Moreover, *C. auriga* is a facultative corallivore (Pratchett, 2005), and therefore patchiness or lack of preferred trophic resources is likely to impact their feeding at the subtropical location. These findings have important implications for the survival of *C. auriga* and suggest resource availability may currently constrain their ability to colonise high latitude reef environments.

Another key finding of this study was the appearance of novel social groups at the higher latitude locations. At One Tree Island and Coffs Harbour, *C. auriga* were generally observed as solitary individuals, however in Sydney they often formed heterospecific groups with other tropical and temperate species. Individuals may benefit from group behaviour in a novel environment regarding energy use, predator avoidance and enhancing foraging opportunity (Shaw, 1978, Krause & Ruxton, 2002). Thus, in a high latitude reef location, *C. auriga* could benefit from being part of a group by reducing the need for individual vigilance, since native heterospecifics may better recognise predators (Roberts, 1996, Ward *et al.*, 2011). Heterospecifics or older conspecifics could also serve as experienced guides to beneficial resources in a novel environment (Childress & Herrnkind, 2001, Leis & Carson-Ewart, 2002, Lecchini *et al.*, 2007). Moreover, group living has been shown to induce a ‘calming effect’ on individuals, reducing overall metabolic demand, while social isolation as a result of environmental change may negatively impact the physiology of gregarious species (Nadler *et al.*, 2016). It was not surprising to observe both *A. sexfasciatus* and *P. coelestis* in conspecific aggregations at the tropical location as they are known to do this on tropical reefs (Allen, 1991, Randall *et al.*, 1997). More unexpectedly, *A. sexfasciatus* commonly formed large heterospecific groups with other *Abudefduf* species at the higher latitude locations, which may be a tactic of mimicry used by *A. sexfasciatus* to confound native predators or gain access to novel resources (Randall, 2005, Pereira *et al.*, 2011). In contrast, *P. coelestis* was generally observed in conspecific groups across locations but these groups were considerably smaller at the temperate location. *P. coelestis* were also occasionally observed in larger heterospecific groups at the higher latitudes. These social behaviour patterns observed for all three species are therefore probably driven by density dependence, with fewer conspecifics with whom to form groups at the higher latitudes (Booth *et al.*, 2007), likely to change if conspecifics successfully colonise these environments in the future.

Ongoing warming will increase pressure on tropical ectotherms both physiologically and through a reduction in the quality of habitat resources available on tropical reefs (Gardner *et al.*, 2003, Bellwood *et al.*, 2004, Alvarez-Filip *et al.*, 2009). The survival of these fishes may therefore depend on their capacity to utilise environments outside their normal range. Differences in species behaviour among locations shown by this study indicate tropical fishes do have the ability to adjust their behaviour in order to cope with, or adapt to the constraints of high latitude reef environments (e.g. cooler temperatures, resource availability, predation and competition). Whether such behaviourally plastic responses are beneficial or maladaptive remains to be seen and should be the focus of future investigation. While the physiological constraints of temperature at the higher latitudes are likely to be reduced as ocean temperatures rise, the indirect impacts of predation/competition and species resource requirements (e.g. food, habitat, conspecifics) may still restrict the establishment of tropical fishes at these locations (Figueira & Booth, 2010). Furthermore, the novel species interactions between tropical and local fishes should be further considered to better understand the costs and benefits of living in mixed groups to both invader and native species.

Chapter 4: Applying discrete choice models to habitat preference studies of coral reef fishes

This chapter was prepared for submission to the *Journal of Experimental Marine Biology and Ecology*

Abstract

Investigating species' habitat preferences is critical in understanding the likely impacts of environmental change. However, statistical approaches applied to the analysis of animal preference data are diverse across studies. This study uses the framework of discrete choice models to investigate the effects of experimental temporal sampling protocol (10 min – 14 h sampling period) on the ability to detect habitat preferences of organisms with varying levels of habitat associations. To do this I conducted habitat choice trials in aquaria for four different species of coral reef fish (*Chaetodon auriga*, *Chaetodon flavirostris*, *Pomacentrus coelestis* and *Abudefduf sexfasciatus)* selected for their range of habitat associations. Multinomial logistic models were used to predict habitat preference based on observations of the individual's position during the first 10 min, then across a 14 h period. The butterflyfish *C. auriga,* known to associate with sheltered coral reefs, particularly during their early life stage, showed a strong and repeatable preference for coral within the first 10 min. In contrast, hourly measurements were required to detect habitat preferences of the butterflyfish *C. flavirostris* and the damselfish *P. coelestis*. However, the first 10 min in addition to hourly observations was optimal to detect habitat preferences of the most generalist species, *A. sexfasciatus*. These results highlight the usefulness of discrete choice modelling in understanding habitat preferences of coral reef fishes. Furthermore, this modelling technique could be applied to data collected from the field. It is also recommend that the length of observation time be considered a critical factor in the design of habitat preference experiments.

4.1 Introduction

Species' habitat selection can determine acquisition of critical resources including food (MacArthur *et al.*, 1966, Willson, 1974, Rotenberry & Wiens, 1998), shelter from predators (Leber, 1985, Kotler *et al.*, 1991, Heithaus & Dill, 2002, Eggers *et al.*, 2005) and ultimately influence the distribution and abundance of organisms in nature (Boyce & McDonald, 1999). Under natural conditions, species' habitat preferences are shaped by various factors (location, habitat type, habitat structure and the presence of conspecifics and/or heterospecifics), that impact fitness (Hildén, 1965, Jaenike & Holt, 1991, Orians & Wittenberger, 1991, Martin, 1998). Understanding the habitat preferences of individual taxa is therefore crucial in making accurate forecasts about changes in biodiversity and ecosystem functioning that may occur with continued environmental change (Pearman *et al.*, 2008, Ehrlén & Morris, 2015). Furthermore, the degree to which species' are impacted is likely to be influenced by their level of habitat specialisation (Colles *et al.*, 2009). As habitats degrade and climates continue to warm, we may see increasing pressure on species that rely on particular habitats for survival, while those that utilise a range of habitats may be less impacted (Munday, 2004, Pratchett, 2005). Thus, quantifying animal preferences is fundamental to identify important habitat and species that may be most impacted by ongoing environmental change (Chalfoun & Martin, 2007).

Animal preference is used to explore a range of ecological questions and applications, including identification of population size (Allen *et al.*, 2008), drivers of geographical range (Aldridge *et al.*, 2008), home range (Mladenoff *et al.*, 1995), habitat use within home ranges (Roever *et al.*, 2008), spatial intra and inter specific interactions among species (Hebblewhite *et al.*, 2005, Fortin *et al.*, 2009), mechanistic movement models (Fortin *et al.*, 2005) and improving design of corridors (Chetkiewicz *et al.*, 2006). However, quantifying and interpreting animal preferences is not straightforward and results can vary among studies often driven by biological processes, including variation among the behaviour of individuals (Dingemanse & Reale, 2005). For example, field-based behavioural observations provide useful information about animal preferences, but results may be difficult to interpret due to the influence of multiple confounding factors (e.g. competition, predation, resource availability and the presence of conspecifics and/or heterospecifics) (Bruno *et al.*, 2003, Hansen *et al.*, 2009, Hebblewhite & Merrill, 2009). For this reason, many studies use laboratory experiments to examine animal preferences. Although laboratory-based experiments cannot fully replicate all factors involved in habitat selection in the wild, they are useful in isolating or controlling factors of interest (such as competition, predation, resource availability and priori effects), likely to influence behavioural preferences. The design of such experiments has been examined in terms of the effects of experimental venue (Skelly, 2002), the methods required to demonstrate preference in the laboratory (Olabarria *et al.*, 2002, Underwood *et al.*, 2004, Underwood & Clarke, 2005), the number of options that animals can assess (Raffa *et al.*, 2002), and how the type of media used to present cues may affect responses (Hale *et al.*, 2009). However, other aspects of experimental design, such as the timing of observation protocols can confound biological inferences and reduce predictability of models (Beyer *et al.*, 2010), yet few studies have attempted to look further into this important issue.

In the laboratory, animal preferences are generally tested by providing two or more options and observing the individual's behaviour and choice over a set period of time. Such an approach has been adopted for a wide range of taxa, including birds (Cueto *et al.*, 2013, Lovell *et al.*, 2013), lizards (Cooper & Sherbrooke, 2012, Marshall *et al.*, 2016), frogs (Wente & Phillips, 2005), bats (Boyles *et al.*, 2007, Reckardt & Kerth, 2007), fish (Ohman *et al.*, 1998, Feary *et al.*, 2007, Pratchett *et al.*, 2008a, Brooker *et al.*, 2013, Schram *et al.*, 2013), snakes (Blouin-Demers & Weatherhead, 2001), snails (Crowe & Underwood, 1998) and tortoise (Nafus *et al.*, 2015). However, differences exist in the observation protocols used in such experiments. For instance, the timing of observation protocols used in habitat preference experiments of coral reef fish range from a few minutes (Lecchini *et al.*, 2005, Igulu *et al.*, 2011, Brooker *et al.*, 2013, Soeparno *et al.*, 2013) to several hours (Ohman *et al.*, 1998, Dahlgren & Eggleston, 2000, Feary *et al.*, 2007, Pratchett *et al.*, 2008a). Therefore, devising appropriate observation time is important in capturing information about a particular animal's habitat preferences, with the possibility that vital information is otherwise lost.

Statistical approaches applied to the analysis of animal preference data are equally diverse across studies. Due to the nominal categorical nature of habitat selection, simple hypothesis testing methods that typically assume data are continuous such as t-tests and rank tests are not appropriate in this context. A number of other analyses, including logistic regression can be used to explore presence/absence data, such as radiolocations within the home range or study area (Posillico *et al.*, 2004). However, this method is restricted to the analysis of one or two habitat types and also assumes choices are made from a set of resource units available. Alternatively, multinomial logit or discrete choice models, widely used in transportation (Greene & Hensher, 2003), market research (Revelt & Train, 1998) and health economics (Norman *et al.*, 2013), would allow simultaneous analysis of a number of habitat types, automatically taking into account dependence in the selection process. Furthermore, this approach could be particularly useful to model changes in habitat availability by changing the composition of choice sets and estimate the probability of a particular habitat being selected during one choice rather than at least once after multiple choices (McDonald *et al.*, 2006). Despite evidence demonstrating the utility of discrete choice models (Street & Burgess, 2007, Train, 2009), they are rarely used in the context of resource selection in animals (McCracken *et al.*, 1998, Cooper & Millspaugh, 1999, McDonald *et al.*, 2006, Carter *et al.*, 2010, George *et al.*, 2017). Moreover, the use of discrete choice models in the study of species' preference behaviour should be further explored.

Here I use discrete choice models to consider how the length of observation time used in experiments of coral reef fishes influences the ability to identify habitat preferences. Specifically, I explore the effectiveness of 10 min versus hourly observations in determining habitat preferences of four species of coral reef fish, with different levels of habitat association. I hypothesised that the species known to naturally associate with a smaller range of habitats would be quicker to show habitat preferences than the species known to associate with a wider range of habitat types. Preferences were also expected to be more accurately determined with the inclusion of hourly observations for all species. Therefore, I expected to observe a settling-in period of exploration, followed by behaviour associated with habitat selection and the expression of habitat choice.

4.2 Methods

Study species

This study focused on four species of coral-reef fishes, selected for their range of habitat association within the reef environment: the threadfin butterflyfish, *Chaetodon auriga* (n = 13), the dusky butterflyfish, *Chaetodon flavirostris* (n = 7), the neon damselfish, *Pomacentrus coelestis* (n = 11) and the scissortail sergeant, *Abudefduf sexfasciatus* (n = 17). *C. auriga* is known to associate with a variety of habitats ranging from rich coral growth to rubble covered areas but as juveniles they typically inhabit lagoons and sheltered patch reefs (Pratchett *et al.*, 2008a). *C. auriga* is also a facultative corallivore feeding on coral polyps, other invertebrates and algae (Randall *et al.*, 1997, Pratchett, 2005). Similarly, *C. flavirostris* inhabit areas of rich coral growth on outer and more sheltered inner reefs, but are occasionally found in estuaries or algal-covered rocky reefs (Randall *et al.*, 1997, Booth *et al.*, 2007). However, as juveniles they generally inhabit protected inner reef areas (Pratchett *et al.*, 2008a). *C. flavirostris* is also a facultative corallivore feeding on live coral, algae and other small benthic invertebrates (Cole *et al.*, 2008). In contrast, *P. coelestis* is found on a broad range of habitats from coral rich to algal-dominated rocky and rubble areas, and is an omnivorous species (Randall *et al.*, 1997, Ohman *et al.*, 1998, Booth *et al.*, 2007). As juveniles *P. coelestis* typically aggregate on coral rubble patches (Ohman *et al.*, 1998). Similarly, *A. sexfasciatus* associates with a range of habitats at all life stages from coral reefs to rocky shorelines where they aggregate to feed on plankton and algae (Allen, 1991, Hutchins & Pearce, 1994, Booth *et al.*, 2007).

Microhabitat choice experiments

This study was undertaken in February 2014, at One Tree Island, southern Great Barrier Reef, Australia (23°30′30″S 152°05′30″E). New recruits of *C. auriga* (standard length: 1.98-2.42 cm), *C. flavirostris* (standard length: 2.03-2.49 cm), *P. coelestis* (standard length: 1.31-1.50 cm) and *A. sexfasciatus* (standard length: 1.24-1.50 cm) were collected from reefs around One Tree Island and transferred to the laboratory. Fish were housed in small groups in aquaria, with constant aeration and sea water flow. All fish were kept for 48 hr prior to experimentation to acclimatise to laboratory conditions. During this time fish were provided with short lengths of PVC piping (approximately 10 cm in length) for shelter and fed once daily with live brine shrimp nauplii *Artemia* spp.

Habitat choice trials were conducted for individual fish (*Chaetodon auriga*: n = 13, *Chaetodon flavirostris*: n = 7, *Pomacentrus coelestis*: n = 11, *Abudefduf sexfasciatus*: n = 17) in a testing room with evenly distributed lighting and minimal noise from the outside environment. Individual fish were introduced to the centre of a rectangular testing arena (64 cm x 41 cm x 27 cm) containing two habitat choices: coral (*Pocillopora damicornis*), and rocky boulder, of approximately equal size (10 cm diameter), positioned at opposite ends of the arena. These habitats were chosen as all four species are known to inhabit both coral-dominated and rocky reefs (Allen, 1991, Hutchins & Pearce, 1994, Randall *et al.*, 1997, Ohman *et al.*, 1998, Booth *et al.*, 2007, Pratchett *et al.*, 2008a). *P. damicornis* was the species of coral selected for the experiment because it was frequently used by several of the species and is abundant on reefs around One Tree Island. The positions of the two habitats within the aquaria were randomised between trials. Coral health was monitored throughout trials and corals did not show any sign of stress throughout the experiments.

To start each trial, an individual fish was placed in the centre of the tank in a holding tube (10 cm in diameter) to acclimate for 5 min (Pratchett *et al.*, 2008a), and then released into the testing arena by slowly lifting the tube. Fish were considered to have selected a habitat when they were no greater than a body length in distance from the habitat, otherwise fish were considered to have made no selection. All trials commenced 4 h prior to sunset and concluded the following morning. Fish were observed and recorded continuously (every second) for the first 10 min to see how much information could be collected about their habitat preferences from a short continuous observation period. Then single observations were made on the hour for 3 consecutive hours (in daylight) to see if any additional information about habitat preferences could be collected from hourly observations, and once again the following morning (14 hr after the commencement of the trial) to determine if preferences remained consistent the following day.

Statistical analyses

All statistical tests were performed using R version 3.1.0 (R Development Core Team, 2008). To compare differences in habitat selection of fish observed in the first 10 min, Wilcoxon tests with a Benjamin-Hockberg correction (Benjamini & Hochberg, 1995) were used to make pairwise comparisons for each species. A multinomial logit model was fitted for each species to estimate differences in the proportions of selections for each habitat in the hourly measurements. This model included only an intercept term. To determine whether the information collected in the first 10 min was good at predicting behaviour collected in the hourly observations, I fitted additional multinomial logit models with the hourly measurements as the response and variables calculated from the first 10 min as predictive variables. Due to the unbalanced nature of the dataset it was not appropriate to fit a model with interaction terms so each species was analysed separately. All multinomial logistic regressions were fitted using the *vglm* function in the VGAM package (Yee & Wild, 1996, Yee, 2010).

The Multinomial Logistic Regression model (Theil, 1969) is a multivariate extension of the Logistic Regression model that allows for more than two alternatives in a categorical response variable. In this case, these were the habitat preferences recorded for each individual, with three levels: 'coral', 'rock' and 'no selection' (coral nor rock). I constructed linear regression functions related to the selection of all but one of the response levels, with the remaining level being treated as a baseline. Each of these linear regression functions were then related to the probability that an alternative was chosen through a link function. I constructed a model of habitat preference based on the proportion of time spent at coral in the first 10 min (*PC*) and the proportion of time spent at rock in the first 10 min (*PR*) and chose 'no selection' as the baseline, to construct linear regression functions for coral and rock:

$$\eta_{Coral,i} = \beta_{0,C} + \beta_{Prop\ Coral,C} \times PC_i + \beta_{Prop\ Rock,C} \times PR,$$

$$\eta_{Rock,i} = \beta_{0,R} + \beta_{Prop\ Coral,R} \times PC_i + \beta_{Prop\ Rock,R} \times PR_i.$$

The probabilities that each of the alternatives were selected for particular values of PC and PR was then given by:

$$Prob(Y_i = Coral) = \frac{\exp(\eta_{Coral,i})}{\exp(\eta_{Coral,i}) + \exp(\eta_{Rock,i}) + 1},$$

$$Prob(Y_i = Rock) = \frac{\exp(\eta_{Rock,i})}{\exp(\eta_{Coral,i}) + \exp(\eta_{Rock,i}) + 1},$$

$$Prob(Y_i = No\ selection) = \frac{1}{\exp(\eta_{Coral,i}) + \exp(\eta_{Rock,i}) + 1}.$$

Standard errors of the estimated parameters were examined to confirm the overall stability of the model estimates.

Multinomial logistic models were then used to predict habitat preference for each of the four fish species (McCullagh & Nelder, 1989, Johnson & Wichern, 2007). This was done by using the best fitting model of the form above to calculate the probability a particular fish would choose either of the two habitats or no selection, and predicting that the fish will go to the habitat with the highest probability. Model selection was performed using the Akaike Information Criterion (AIC) (Akaike, 1973), where the model with the lowest AIC value is deemed to have the best balance of goodness of fit and parsimony in parameterisation. Since I wanted to determine whether the first 10 min of observations could be used to predict hourly observations, I developed a model to relate the data obtained from the first 10 min with observations thereafter.

To determine the ability of each species' model to predict longer term habitat preferences from data collected within the first 10 min, I constructed a table to compare predicted choices based on the models with observed choices. I also compared correlations between proportions of time observed at each location in the first 10 min with the proportions recorded in the hourly observations (a correlation close to 0 indicating no linear relationship between the two sets of measurements and a correlation close to 1 or -1 indicating a strong relationship between the two sets of measurements, in the same or opposite directions respectively).

4.3 Results

Habitat preferences

Of the four species examined, *A. sexfasciatus* spent the greatest proportion of time making no selection and preferred no selection (W = 19, $P < 0.001$) and coral (W = 237.5, $P = 0.030$) over rock in the first 10 min (Fig. 4.1a). *A. sexfasciatus* spent the greatest proportion of time at coral across the hourly observations, with coral (W = 6805.5, $P = 0.001$) and no selection (W = 666, $P < 0.001$) also preferred over rock (Fig.

4.1b). In contrast, *C. auriga* showed a strong preference for coral compared to rock (W = 169, *P* < 0.001) and no selection (W = 169, *P* < 0.001), and preferred no selection over rock (W = 20, *P* = 0.003) in the first 10 min (Fig. 4.1a). However, in the hourly observations *C. auriga* spent 100% of the time at coral (Fig. 4.1b). Similarly, *C. flavirostris* preferred coral over rock (W = 2401, *P* = 0.004) and no selection (W = 1225, *P* = 0.023) in the first 10 min (Fig. 4.1a). During hourly observations *C. flavirostris* also preferred coral over rock (W = 49, *P* = 0.001) and no selection (W = 44, *P* = 0.001), with a greater proportion of time spent at coral across the hourly observations compared to the first 10 min (Fig. 4.1b). *P. coelestis* preferred rock (W = 28, *P* = 0.004) and no selection (W = 20.5, *P* = 0.015) over coral during the first 10 min (Fig. 4.1a). However, *P. coelestis* showed no preference between coral and rock habitat (W = 1372, *P* > 0.050) in hourly observations, but preferred rock over no selection (W = 2016, *P* = 0.002; Fig. 4.1b).

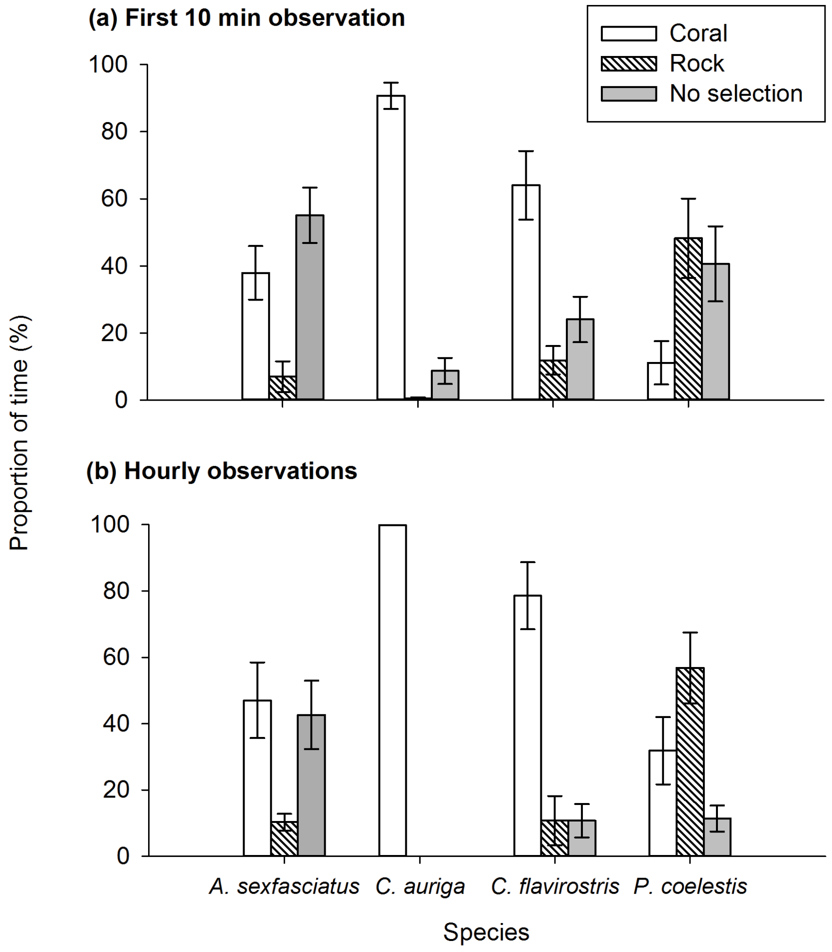


Figure 4.1. Mean (± SE) proportion of habitat preferences (based on equal availability of coral and rock) observed in the (a) first 10 min and across (b) hourly observations for *Abudefduf sexfasciatus, Chaetodon auriga, Chaetodon flavirostris, and Pomacentrus coelestis*.

Predictive modelling

Since *C. auriga* was only observed at the coral habitat within the choice trials it was not possible to model the preferences of this species. For the remaining three species, *A. sexfasciatus*, *C. flavirostris* and *P. coelestis,* models that included proportions of the first 10 min at each habitat (coral, rock or no selection) were stable and could be used to predict the hourly measurements (Table 4.1). None of the variables measured in the first 10 min were significantly related to the hourly measurements for *C. flavirostris* and *P. coelestis* (Table 4.1). In contrast, the proportion of time spent at coral in the first 10 min was related to the hourly measurements for *A. sexfasciatus*. Fish that spent more time at coral in the first 10 min were more likely to be observed at a habitat, either coral or rock, in the hourly observations than fish that spent less time at coral in the first 10 min (Table 4.1).

Table 4.1. Model estimates for three multinomial logistic regression models of *Abudefduf sexfasciatus, Chaetodon flavirostris, and Pomacentrus coelestis* hourly location based on data collected in first 10 min. Model 1 contains only intercept terms (hourly observations) and Model 2 contains intercept terms as well as the proportion of time spent at both locations in the first 10 min. Since there are three outcomes, each factor has a parameter describing the effect of the factor on the likelihood that a fish chooses coral rather than making no selection and another describing the effect of the factor on the likelihood that the fish chooses rock instead of making no selection, denoted by ":Coral" and ":Rock" respectively. The models for each species with the lowest Akaike Information Criterion (AIC) scores are indicated in bold.

Species	Model	Variable	Estimate	Std. Error	z value	Pr(>|z|)	AIC
A. sexfasciatus	Model 1:	(Intercept):Coral	-0.160	0.284	-0.565	0.572	101.512
	Intercept Only	(Intercept):Rock	-1.910	0.536	-3.564	>0.001	
	Model 2:	(Intercept):Coral	-1.414	0.522	-2.710	0.007	**96.845**
	Proportions	(Intercept):Rock	-3.272	1.101	-2.973	0.003	
		Proportion Coral:Coral	3.527	1.165	3.029	0.002	
		Proportion Coral:Rock	3.597	1.998	1.800	0.072	
		Proportion Rock:Coral	1.845	2.058	0.896	0.370	
		Proportion Rock:Rock	2.963	2.932	1.011	0.312	
C. flavirostris	**Model 1:**	(Intercept):Coral	1.992	0.616	3.237	0.001	**41.414**
	Intercept Only	(Intercept):Rock	>0.001	0.817	>0.001	1.000	
		(Intercept):Coral	4.107	5.508	0.746	0.456	44.739

	Model 2: Proportions	(Intercept):Rock	11.205	9.437	1.187	0.235	
		Proportion Coral:Coral	-2.567	5.849	-0.439	0.661	
		Proportion Coral:Rock	-15.713	12.536	-1.253	0.210	
		Proportion Rock:Coral	-3.105	14.006	-0.222	0.825	
		Proportion Rock:Rock	-19.078	22.463	-0.849	0.396	
P. coelestis	**Model 1: Intercept Only**	(Intercept):Coral	0.847	0.488	1.736	0.082	**89.067**
		(Intercept):Rock	1.386	0.456	3.037	0.002	
	Model 2: Proportions	(Intercept):Coral	2.007	1.110	1.809	0.071	90.647
		(Intercept):Rock	1.889	1.104	1.711	0.087	
		Proportion Coral:Coral	-3.432	2.293	-1.497	0.135	
		Proportion Coral:Rock	-3.791	2.234	-1.697	0.090	
		Proportion Rock:Coral	-1.314	1.615	-0.813	0.416	
		Proportion Rock:Rock	0.171	1.542	0.111	0.912	

The species-specific models with the smallest AICs correctly predicted the hourly location of fish on 67% of occasions for *A. sexfasciatus*, 79% of occasions for *C. flavirostris* and 55% of occasions for *P. coelestis* (Table 4.2). The intercept-only model for *C. flavirostris* and *P. coelestis* always predicted fish at coral and rock habitats respectively. However, for *A. sexfasciatus* the intercept-only model always predicted that individuals of this species would make no selection, which was correct in 43% of observed cases. The proportions model which included observations from the first 10 min was the best fitting model, however only slightly improved this for *A. sexfasciatus.* The model also never predicted *A. sexfasciatus* to be associated with rock habitat, despite there being observations at rock in the hourly measurements.

Table 4.2. Comparison of the predicted locations based on the multinomial logit model with the lowest Akaike Information Criterion (AIC) scores to the observed locations for *Abudefduf sexfasciatus, Chaetodon flavirostris, and Pomacentrus coelestis.* These proportions may overestimate for the ability of the model to predict behaviour after 10 min, as these proportions are calculated from predictions for the data that was also used to construct the model.

		Actual Location		
	Predicted Location	Coral	Rock	No selection
A. sexfasciatus	Coral	15	3	6
	Rock	0	0	0
	No selection	8	1	21
C. flavirostris	Coral	22	3	3
	Rock	0	0	0
	No selection	0	0	0
P. coelestis	Coral	0	0	0
	Rock	14	24	6
	No selection	0	0	0

The correlation between the proportion of time spent at coral during the first 10 min and for the hourly measurements was 0.44 for *A. sexfasciatus*, 0.23 for *C. flavirostris* and 0.01 for *P. coelestis*. Only the correlation for *A. sexfasciatus* was significant (*P* =

0.038), but the overall value of 0.44 indicated only a weak relationship between the measurements taken during the first 10 min and those taken hourly.

The correlation between the proportions of time spent at rock during the first 10 min and for the hourly measurements was 0.07 for *A. sexfasciatus*, 0.38 for *C. flavirostris* and 0.35 for *P. coelestis* and all were non-significant (no correlations were calculated for *C. auriga*, as all hourly observations for this species were at coral).

4.4 Discussion

Quantifying habitat preferences is critical in identify potential impacts of ongoing environmental change on species' (Chalfoun & Martin, 2007). This study further demonstrates the flexible nature of discrete choice modelling in the application of animal preference studies. Specifically, this study shows how this novel modelling framework can be used to evaluate behavioural preferences of coral reef fishes in an experimental setting. The use of the multinomial logit model recognises that the outcome being measured is categorical rather than a continuous measurement, in this case a selection from two habitats or no habitat selection. The factors used in this study were a mixture of continuous factors, such as proportions. Furthermore, this modelling technique could be applied to data collected from the field. For instance, this type of modelling approach would allow for testing whether a categorical variable was related to habitat association and could be applied to research questions aimed at predicting the effects of coral bleaching on the habitat selection of coral reef fishes (although care should be taken to ensure that the model explains a sufficient amount of the variation in habitat choice) (Johnson & Wichern, 2007).

The results of this study suggest that an accurate understanding of particular species' habitat preferences will be conditional on devising experimental protocols that take into account their initial level of habitat association. In general, species known to associate with a smaller range of habitats required less time to select a particular habitat than those that associate with a wide variety of habitats. For example, *C. auriga,* known to associate with sheltered coral patch reefs, particularly during their early life stage (Pratchett *et al.*, 2008a), showed a strong preference for coral in the first 10 min of observations with a very small proportion of time spent making no selection. Although the hourly observations slightly improved this with 100% of observations at coral, I was still able to detect this strong trend in the first 10 min suggesting short temporal periods are useful in detecting habitat preferences of more specialised species. In contrast, hourly measurements were better in detecting habitat preferences of *C. flavirostris* and *P. coelestis*. A comparison of the models constructed for these species provided evidence that behavioural observations needed to be longer to accurately describe their habitat preferences. The predictions obtained from the multinomial logit models of the first 10 min of observations did not predict long term measurements well, highlighting the fact that data collected in the first 10 min was not sufficient to predict the long term behaviour recorded in our hourly observations. For both *C. flavirostris* and *P. coelestis,* preferences were clearer with greater selection for coral and rock habitat respectively in the hourly observations. However, for the most generalist species, *A. sexfasciatus*, the first 10 min did provide some information to detect habitat preferences. Observations taken over just the first 10 min for *A. sexfasciatus* would have led to the conclusion that neither habitat was preferred as the greatest proportion of time was spent making no selection. Moreover, *A. sexfasciatus* is generally observed up in the water column in the wild, as it is a planktivorous species (Allen, 1991, Hutchins & Pearce, 1994, Booth *et al.*, 2007). However, with the addition of the hourly observations and observation the following day (post 14 h), I was able to detect the selection of coral habitat by this particular species. Thus, including the hourly observations for *A. sexfasciatus* gives us a better understanding of their occasional use of coral habitat, in addition to the large amount of no habitat selection. Studies that compare habitat preferences across species with differing levels of habitat associations therefore need to take into account those initial differences via selection of experimental protocols that can capture an accurate measure of habitat “choice”.

Although I adopted a continuous observation protocol for the first 10 min, while hourly measurements were only taken as discrete observations on the hour, a higher number of switches were detected for all species during the first 10 min of trials compared to later hourly measurements. These results may suggest habitat exploration preceding selection, which is a well-recognised behaviour in many organisms (Stamps & Krishnan, 1995, Leis & Carson-Ewart, 2002, Feary *et al.*, 2007). Such exploration allows animals to examine available habitats and identify where fitness will be greatest (Leis & Carson-Ewart, 2002). Similarly, Feary et al. (2007) observed high levels of movement in coral reef fish between habitats within the first temporal period of laboratory preference experiments. Moreover, in this study the proportion of no selection in the first 10 min was greatest for *A. sexfasciatus,* but was very low for *C. auriga,* considered to have stronger habitat associations during their early life history compared to *A. sexfasciatus* (Allen, 1991, Randall *et al.*, 1997, Pratchett, 2005, Booth *et al.*, 2007, Pratchett *et al.*, 2008a). The proportion of no selection observed across species suggests in experimental studies the minutes after fish are presented with habitat choices is often an initial period of exploration, where if taken in isolation may lead to incorrect assumptions about the strength of species' preferences. Studies using short (less than 30 min) periods of observations to establish an individual's choice may therefore observe exploration rather than an actual preferences, particularly for habitat generalists. Based on the proportion of time fish spent making no selection versus selecting a habitat and the observation of high levels of movement between habitat options in the first 10 min for our more generalist species, I recommend that longer (i.e. a number of hours) observation periods be preferred over short (10 min) periods in experimental habitat preference studies of coral reef fish. Furthermore, discrete choice modelling can be useful in developing appropriate observation protocols for testing habitat preferences in particular species in future laboratory or field studies.

Chapter 5: Temperature influences habitat preference of coral reef fishes: Will generalists become more specialised in a warming ocean?

This chapter is in revision at *Global Change Biology*

Abstract

Climate change is expected to pose a significant risk to species that exhibit strong behavioural preferences for specific habitat types, with generalist species assumed to be less vulnerable. In this study, habitat choice experiments were conducted to determine how water temperature influences habitat preference for three common species of coral reef damselfish (Pomacentridae) that differ in their levels of habitat specialisation. The lemon damselfish *Pomacentrus moluccensis*, a habitat specialist, consistently selected complex coral habitat across all temperature treatments (ambient winter 22˚C; ambient summer 28°C; and elevated 31˚C). Unexpectedly, the neon damselfish *Pomacentrus coelestis* and scissortail sergeant *Abudefduf sexfasciatus*, both of which have more generalist habitat associations, developed strong habitat preferences (for complex coral and boulder habitat, respectively) at the elevated temperature treatment (31˚C) compared to no single preferred habitat at 22°C or 28°C. The observed shifts in habitat preference with temperature suggest that we may be currently underestimating the vulnerability of some habitat generalists to climate change and highlight that the ongoing loss of complex live coral through coral bleaching could further exacerbate resource overlap and species competition in ways not currently considered in climate change models.

5.1 Introduction

When environmental conditions remain relatively stable, species with specialised ecological niches are often more effective at competing with generalists for given resources, such as food or habitat (Schoener, 1971, Sorensen *et al.*, 2004). However, as environmental conditions change, the flexible nature of generalist species may be advantageous, particularly when the resources that specialists rely on are lost or degraded (McKinney, 1997, Julliard *et al.*, 2004, Biesmeijer *et al.*, 2006). Loss of or reduction in availability of preferred resources for specialist species can lead to declines in performance (e.g. locomotion, growth and reproductive output) and consequently mortality if they cannot exhibit flexibility in resource use (reviewed in Clavel *et al.*, 2011). Alternatively, if species exhibit flexibility through more generalist resource use or switch to an alternative resource they can face increased competition with other species for less preferred resources, especially when resources diminish (Clavel *et al.*, 2011). Such competitive interactions are likely to involve costs and benefits to performance and survival (Munday, 2001). However, a trade-off between competitive ability and fitness associated with using alternative habitats may provide a mechanism of coexistence for competing species (Rosenzweig & Abramsky, 1997). Patterns of habitat use consistent with this trade-off have been observed among many species and ecosystems (Schoener, 1974, Colwell & Fuentes, 1975, Martin & Martin, 2001).

It has been proposed that specialist species could be used as ecological indicators for impacts of climate change at the community level (Devictor & Robert, 2009, Clavel *et al.*, 2011), just as they have in the monitoring of sustainable development (Gregory *et al.*, 2005). Thus it is of major concern that declines in population numbers of specialist species have been observed over the last decade, from a broad range of taxa, including plants (Rooney *et al.*, 2004), mammals (Fisher *et al.*, 2003), birds (Julliard *et al.*, 2004), insects (Stefanescu *et al.*, 2011) and coral reef fishes (Munday, 2004, Pratchett *et al.*, 2008b). Predicting the “winners” and “losers” within assemblages is crucial in making accurate forecasts about changes in biodiversity and ecosystem functioning that may occur with continued climate change (Pearman *et al.*, 2008, Ehrlén & Morris, 2015). However for this to be possible, increased knowledge of species’ ecological requirements (e.g. habitat) and the impacts of environmental change are required, particularly in aquatic ecosystems (Freitas *et al.*, 2015).

The first response of individuals to altered environmental conditions is often a change in their behaviour (Tuomainen & Candolin, 2011). Behavioural responses may provide a means to rapidly react to environmental change, allowing improvement or maintenance of individual performance and ultimately population viability (Pigliucci, 2001, Price *et al.*, 2003). For instance, some species have adjusted the timing of breeding or migration in response to environmental warming (Gordo & Sanz, 2005, Charmantier *et al.*, 2008, Merila & Hendry, 2014, Kuczynski *et al.*, 2017). However, not all behavioural responses to climate change will be adaptive, especially as environmental conditions shift beyond what has been experienced during the species' evolutionary history (Gates & Gysel, 1978, Schlaepfer *et al.*, 2002, Robertson *et al.*, 2013, Robertson & Chalfoun, 2016). For example, with increasing environmental temperature some lizard species have been observed to spend more time sheltering at the expense of other fitness related activities including foraging and reproduction, significantly impacting species persistence (Sinervo *et al.*, 2010). Thus, it is expected that behaviour will play an important role in how species respond to human-induced rapid environmental change (Tuomainen & Candolin, 2011). At present greater knowledge about the effects of temperature on species behaviour is required to gain insight into how species will be impacted by ongoing climate change.

Behavioural responses of individuals to environmental conditions are driven in part by their underlying physiology. Due to the lack of internal thermal regulation in ectotherms, changes in the ambient thermal conditions result in metabolic and cellular physiological impacts (Fry, 1967, Pörtner, 2002). Moreover, tropical ectotherms are expected to be disproportionally effected by climatic warming as they have evolved in relatively stable thermal environments resulting in narrow thermal performance windows as well as tending to live closer to their thermal maxima (Deutsch *et al.*, 2008, Tewksbury *et al.*, 2008, Donelson *et al.*, 2010). The physiological performance of tropical ectotherms can be significantly reduced when temperatures approach the edges of their optimal thermal ranges and species may make behavioural adjustments if they cannot compensate physiologically (Pörtner, 2001, Angilletta *et al.*, 2002). For example, when temperatures reached the upper or lower thermal limits in tropical fishes this has been shown to affect behavioural traits including levels of aggression (Warren *et al.*, 2016), boldness (Biro *et al.*, 2010) and foraging rates (Eme & Bennett, 2008, Nowicki *et al.*, 2012). Variation in the underlying physiology and thermal sensitivity of animals occupying different ecological niches is therefore likely to be a critical factor in the behavioural responses of specialists and generalists to climate warming (Martin *et al.*, 2015).

Climate change also creates pressure on ectothermic species via indirect effects due to reduction or loss of resources. An ecosystem where this is especially evident is coral reefs with recent increases in the incidence and severity of coral bleaching events (Hughes *et al.*, 2017) and the severity of tropical storms (Knutson *et al.*, 2008, Knutson *et al.*, 2010) leading to global declines in coral cover, reductions in habitat complexity, changes in benthic composition and habitat fragmentation (Hoegh-Guldberg, 1999, Nyström *et al.*, 2000, Webster *et al.*, 2005, Bonin, 2011). While studies have shown the negative impacts of habitat degradation on coral reef fishes (Munday, 2004, Pratchett *et al.*, 2011, Kerry & Bellwood, 2012, Pratchett *et al.*, 2012), little research has explored the effects of increasing temperature directly on habitat preference. As ocean temperatures continue to rise and habitats degrade, we can expect to see increasing pressure on species that rely on a particular habitat for survival (e.g. coral habitat specialisation), while those that use a range of habitats (e.g. habitat generalists) may be less impacted (Munday, 2004, Pratchett, 2005). Thus, determining how environmental temperature may influence species' habitat associations will aid our ability to predict which coral reef fishes are likely to be most impacted by future warming and ongoing habitat degradation.

The aim of this study was to investigate the effect of water temperature on habitat preferences of species of coral reef fishes, which differed in habitat specialisation. To do this, choice experiments were conducted to quantify habitat preferences of three model species from the family Pomacentridae (damselfishes). Specifically, the following questions were addressed: (1) do habitat preferences of coral reef fishes vary among current-day seasonal, and elevated environmental temperatures? (2) how does the response of habitat preference to water temperature differ between habitat specialists compared to generalists?

5.2 Methods

Study Species

This study focused on three species of coral-reef damselfish (Pomacentridae): the lemon damselfish, *Pomacentrus moluccensis*, the neon damselfish, *Pomacentrus coelestis* and the scissortail sergeant, *Abudefduf sexfasciatus*. These species were selected because they could be classified as known habitat generalists or specialists, and could be found in abundance at the study location. *P. moluccensis* is a habitat specialist, exclusively found in small aggregations on live coral, where it primarily occupies branching growth forms, and occasionally in the water column feeding on plankton and algae (Allen, 1991, Pratchett *et al.*, 2012, Coker *et al.*, 2014). *P. coelestis* is a habitat generalist, found on a broad range of habitats from coral rich to algal-dominated rocky and rubble areas, and is an omnivorous species (Randall *et al.*, 1997, Ohman *et al.*, 1998). *A. sexfasciatus* is also a habitat generalist, associating with a range of habitats from coral reefs to rocky shorelines where they aggregate to feed on plankton and algae (Allen, 1991).

Microhabitat choice experiments

This study was undertaken at One Tree Island, southern Great Barrier Reef, Australia (23°30′30″S, 152°05′30″E). Experimental fish were collected from reefs around One Tree Island daily using clove oil and hand nets. The smallest juvenile fish present were targeted to minimise post-settlement experience, which can influence habitat preference (Pratchett et al 2008a). Fish were transported to the laboratory within 1 hr of capture and housed in small groups in aquaria, with constant aeration and sea water flow. Fish were provided with short lengths of PVC piping (approximately 10 cm in length) for shelter and fed live brine shrimp nauplii *Artemia* spp. once daily.

To determine the effects of ocean temperatures on habitat preference, a total of 172 individuals were randomly allocated to one of three temperature treatments: ambient winter (22˚C: *P. moluccensis*, n = 12, *P. coelestis*, n = 9, *A. sexfasciatus,* n = 10), ambient summer (28˚C: *P. moluccensis*, n = 12, *P. coelestis*, n = 8, *A. sexfasciatus*, n = 10), and elevated, ambient summer + 3˚C (31˚C: *P. moluccensis*, n = 12, *P. coelestis*, n = 8, *A. sexfasciatus*, n = 10). These temperature treatments were chosen based on the average seasonal range of temperatures naturally experienced at this location (temperature loggers; http://weather.aims.gov.au/#/station/131) and to reflect projected ocean warming of up to + 3˚C likely to be experienced by fishes at this location by 2100 (Lough, 2007, Hobday & Lough, 2011, Collins *et al.*, 2013). Fish were acclimatised from ambient temperature conditions (~ 28˚C during the collection period) to the temperature treatments by ± 0.5˚C per day until the test temperature was reached, which was within the natural daily temperature change experienced in situ (Australian Institute of Marine temperature loggers; http://weather.aims.gov.au/#/station/131).

Habitat choice trials (two habitats presented per trial) were carried out to assess the habitat preferences of the three species. An individual fish was introduced to the centre of a rectangular testing arena (64 cm x 41 cm x 27 cm) containing two similar sized (10 cm length) but distinct habitats, positioned at opposite ends of the arena (Fig. 5.1). Positions of the two habitats were randomised using paired combinations of the following: complex coral (*Pocillopora damicornis*), noncomplex coral (*Porites lobata*), coral rubble and rocky boulder, within the arena between trials. Coral health was monitored throughout trials, with corals not exhibiting any signs of stress throughout the experiments. Experimentation was conducted in a testing room with minimal noise from the outside environment and with evenly-distributed lighting. To start each trial, fish were placed in a PVC holding tube (10 cm in diameter) for 5 min prior to being released into the testing arena (Fig. 5.1; Pratchett *et al.*, 2008a).

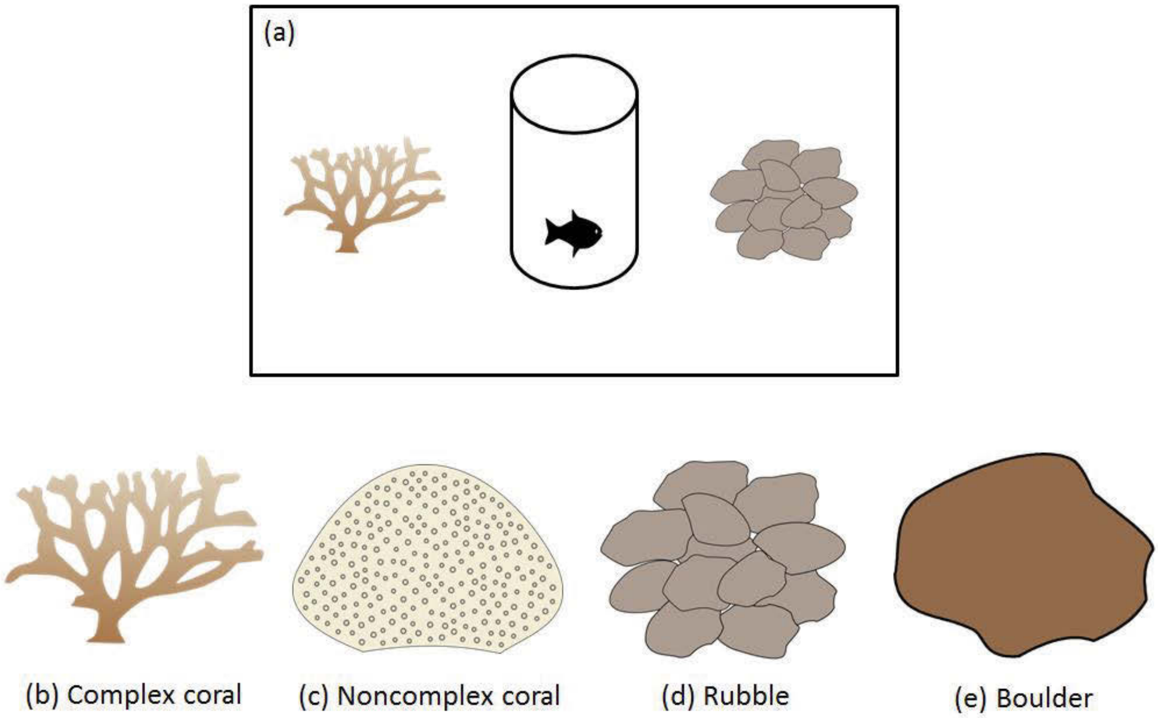


Figure 5.1. Example experimental tank set up prior to the start of a habitat-choice trial (a). Habitat preferences were assessed for juvenile *Pomacentrus moluccensis, Pomacentrus coelestis* and *Abudefduf sexfasciatus* at 22°C, 28°C and 31°C for all possible combinations using paired combinations of the following: (b) complex coral, (c) noncomplex coral, (d) coral rubble and (e) rocky boulder.

Each individual fish was run through experimentation of every 2 x 2 habitat combination in a random order. Trials were undertaken between 0800 hr and 1600 hr. Trials lasted 3 hr, which had previously been found to be the optimum time period for determining habitat preference (Matis unpublished data), and an individual's habitat choice was recorded every 15 min (total of 12 observations per trial). Fish were considered to have selected a habitat when they were no greater than a body length in distance from the habitat, otherwise the fish was considered to have made no selection.

Statistical analyses

Due to the categorical nature of habitat selection, simple hypothesis testing methods that typically assume that data are continuous such as t-tests and rank tests were not appropriate in this context. Data were therefore modelled using the framework of discrete choice experiments (Street & Burgess, 2007, Train, 2009), which are widely used in transportation (Greene & Hensher, 2003), market research (Revelt & Train, 1998), health economics (Norman *et al.*, 2013), and habitat selection behaviour (McDonald *et al.*, 2006, Carter *et al.*, 2010). This statistical approach allows simultaneous analysis of a number of habitat types, automatically taking into account dependence in the selection process. It can model changes in habitat availability by changing the composition of choice sets and can estimate the probability of a particular habitat unit being selected during one choice rather than at least once after multiple choices. The discrete choice analysis was performed in version 3.2.1 of the R programming language (R Core Team, 2015). The mlogit function from the *mlogit* package was used to build the models (Croissant, 2013). Information from each trial, including all habitat combinations, was combined into a model to allow us to estimate the overall habitat preference of each species at each temperature.

To incorporate the species and temperature information into the model, a mixed logit model was used, where the available habitats were defined at the trial level but species and temperature were defined at the level of an individual fish, since temperature and species were constant for a particular fish. In order to summarise the preference of different habitats, or no selection, across species and temperatures, the model was used to calculate the probability that a particular species would choose a particular habitat at a particular temperature. This allowed the effect of temperature on habitat preferences to be determined and establish the significance of these differences using two-proportion z-tests.

5.3 Results

Water temperature had a significant effect on habitat choice and differed among the three damselfish species (Fig. 5.2, Appendix A; likelihood ratio test, $p < 0.001$). The habitat specialist *P. moluccensis* exhibited the most consistency in habitat choice across temperatures, choosing complex coral over all other habitats at all temperatures (Fig. 5.2a, Table 5.1a). Although the dominant preference of *P. moluccensis* remained stable across temperatures, there were slight differences in the ranking of subsequent habitat choices. Individuals of this species preferred rubble over remaining habitat choices (boulder, non-complex coral and no selection) at 22°C, but preferred rubble and boulder over non-complex coral and no selection at 28°C and 31°C (Fig. 5.2a, Table 5.1a,b).

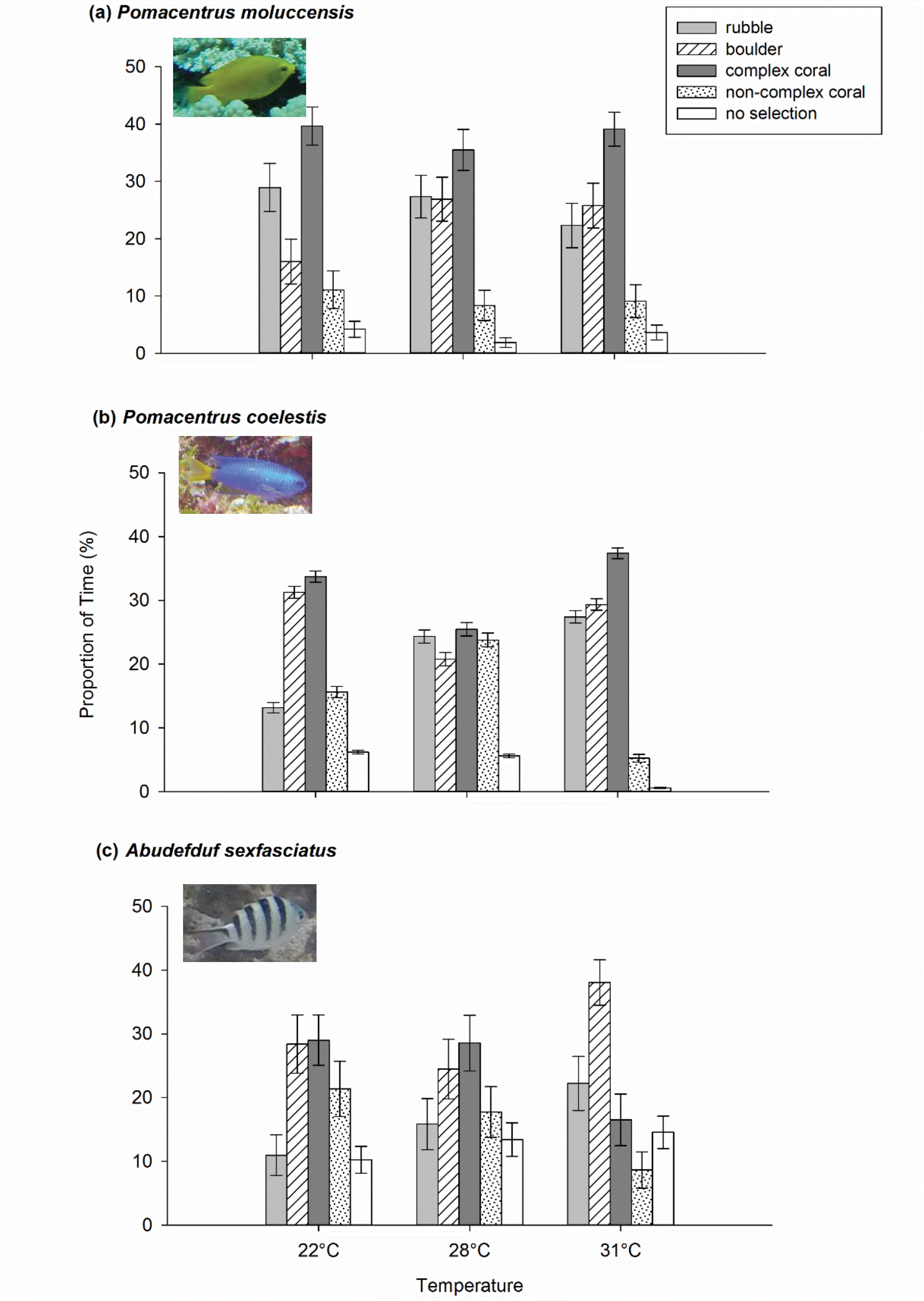


Figure 5.2. Percentage of time (mean ± SE) spent at each of four experimental habitat types, (based on the option of no selection and equal availability of habitat types) for

juvenile individuals of the species (a) *Pomacentrus moluccensis* (b) *Pomacentrus coelestis* and (c) *Abudefduf sexfasciatus* observed at 22°C, 28°C and 31°C.

Table 5.1. Comparisons of habitat preferences (p-values) of juvenile *Pomacentrus moluccensis, Pomacentrus coelestis* and *Abudefduf sexfasciatus* between (a) habitats (rubble, boulder, complex coral, non-complex coral and no selection) (b) temperatures (22°C, 28°C, 31°C) and (c) species.

(a)

Habitat Comparison	Temperature	Species		
		P. moluccensis	*P. coelestis*	*A. sexfasciatus*
Rubble v Boulder	22°C	***< 0.001***	***< 0.001***	***< 0.001***
	28°C	*>0.999*	*0.602*	***0.004***
	31°C	*0.750*	*>0.999*	***< 0.001***
Rubble v Complex	22°C	***< 0.001***	***< 0.001***	***< 0.001***
	28°C	***< 0.001***	*0.516*	***< 0.001***
	31°C	***< 0.001***	***< 0.001***	*0.208*
Rubble v Non-Complex	22°C	***< 0.001***	*>0.999*	***0.002***
	28°C	***< 0.001***	*>0.999*	*>0.999*
	31°C	***< 0.001***	***< 0.001***	***< 0.001***
Rubble v No selection	22°C	***< 0.001***	***< 0.001***	*>0.999*
	28°C	***< 0.001***	***< 0.001***	*>0.999*
	31°C	***< 0.001***	***< 0.001***	***0.024***
Boulder v Complex	22°C	***< 0.001***	*0.637*	*>0.999*
	28°C	***< 0.001***	***0.006***	*0.334*
	31°C	***< 0.001***	***< 0.001***	***< 0.001***
Boulder v Non-Complex	22°C	*0.587*	***< 0.001***	***0.023***
	28°C	***< 0.001***	*0.964*	***0.035***
	31°C	***< 0.001***	***< 0.001***	***< 0.001***
Boulder v No selection	22°C	***< 0.001***	***< 0.001***	***< 0.001***
	28°C	***< 0.001***	***< 0.001***	***< 0.001***
	31°C	***< 0.001***	***< 0.001***	***< 0.001***
Complex v Non-Complex	22°C	***< 0.001***	***< 0.001***	***0.012***

	28°C	***< 0.001***	*0.290*	***< 0.001***
	31°C	***< 0.001***	***< 0.001***	***0.049***
Complex v No selection	22°C	***< 0.001***	***< 0.001***	***< 0.001***
	28°C	***< 0.001***	***< 0.001***	***< 0.001***
	31°C	***< 0.001***	***< 0.001***	*>0.999*
Non-Complex v No selection	22°C	*0.051*	***< 0.001***	***< 0.001***
	28°C	***0.001***	***< 0.001***	*0.863*
	31°C	*0.124*	***< 0.001***	*0.058*

(b)

Temperature Comparison	Habitat Preference	Species		
		P. moluccensis	*P. coelestis*	*A. sexfasciatus*
22°C v 28°C	Rubble	*>0.999*	***< 0.001***	*0.370*
	Boulder	***< 0.001***	***< 0.001***	*0.855*
	Complex	***0.035***	*0.108*	*>0.999*
	Non-Complex	*>0.999*	***0.003***	*>0.999*
	No selection	*0.392*	*>0.999*	*0.574*
28°C v 31°C	Rubble	*0.060*	*>0.999*	*0.613*
	Boulder	*>0.999*	*0.108*	***< 0.001***
	Complex	*0.067*	***< 0.001***	***< 0.001***
	Non-Complex	*>0.999*	***< 0.001***	***0.001***
	No selection	*0.700*	***< 0.001***	*>0.999*
22°C v 31°C	Rubble	***0.042***	***0.002***	***0.005***
	Boulder	***< 0.001***	*0.546*	***< 0.001***
	Complex	*>0.999*	***0.022***	***< 0.001***
	Non-Complex	*>0.999*	***< 0.001***	***< 0.001***
	No selection	*>0.999*	***< 0.001***	*>0.999*

(c)

Species Comparison	Habitat Preference	Temperature		
		22°C	28°C	31°C
P. moluccensis v A. sexfasciatus	Rubble	***< 0.001***	***0.004***	*>0.999*
	Boulder	***< 0.001***	*>0.999*	***< 0.001***

	Complex	***< 0.001***	***0.021***	***< 0.001***
	Non-Complex	***< 0.001***	***< 0.001***	*>0.999*
	No selection	***< 0.001***	***< 0.001***	***< 0.001***
P. moluccensis v P. coelestis	Rubble	***< 0.001***	*>0.999*	*0.248*
	Boulder	***< 0.001***	*0.485*	*0.593*
	Complex	***< 0.001***	***< 0.001***	*0.593*
	Non-Complex	***0.031***	***< 0.001***	*0.516*
	No selection	*0.248*	***0.001***	***< 0.001***
A. sexfasciatus v P. coelestis	Rubble	*0.593*	***0.010***	*>0.999*
	Boulder	*>0.999*	*0.323*	***< 0.001***
	Complex	*0.637*	*>0.999*	***< 0.001***
	Non-Complex	*0.142*	*0.154*	*0.516*
	No selection	***0.021***	***< 0.001***	***< 0.001***

The habitat generalist, *P. coelestis*, did not exhibit consistent preferences for the same habitat across temperatures (Fig. 5.2b, Table 5.1). At 28°C, the only habitat preferences observed were that complex coral was significantly preferred to boulder and all habitats were preferred to making no habitat selection (Table 5.1a). In contrast, complex coral and boulder were equally preferred at 22°C, while at 31°C a strong preference for complex coral was observed with lower preferences for boulder and rubble (Fig. 5.2b, Table 5.1a). Additionally, the proportion of time no selection was made significantly reduced at 31°C compared to 28°C and 22°C (Fig. 5.2b, Table 5.1b).

Preferences of the habitat generalist, *A. sexfasciatus* were similar at 22°C and 28°C, with boulder and complex coral preferred over all other available habitats (Fig. 5.2c, Table 5.1a). However, at 31°C a strong preference for boulder emerged over all other available habitats, with a decline in preference for complex coral (Fig. 5.2c, Table 5.1a).

Differences observed between species were primarily driven by the consistency in habitat preferences shown by *P. moluccensis* across all temperatures compared to the more variable habitat preferences of *P. coelestis* and *A. sexfasciatus* across temperatures (Fig. 5.2, Table 5.1c). Distinctions in habitat preferences between *P. moluccensis* and the other species were greatest at 22°C (Fig. 5.2, Table 5.1c) due to the lack of strong preference for one specific habitat by both *P. coelestis* and *A. sexfasciatus* at 22°C. Other differences between species were seen due to *A. sexfasciatus* exhibiting a relatively higher proportion of no selection across all temperatures compared to the other species (Fig. 5.2, Table 5.1b).

5.4 Discussion

This study demonstrates how ambient water temperate affects habitat preferences of coral reef fishes, and how it can alter the degree of habitat specialisation. These results showed that the effect of water temperature differed among species, with habitat generalists *P. coelestis* and *A. sexfasciatus* modifying their habitat preferences in response to water temperature, whereas the habitat specialist *P. moluccensis*, retained consistent habitat preference for complex coral across all temperature treatments. At elevated water temperature above the current summer average the generalist *P. coelestis* shifted preference to complex coral. This continued preference by *P. moluccensis*, and increased preference by *P. coelestis* for complex coral could be a concern as less complex coral will be available in the future due to ongoing habitat degradation of coral reefs globally (Graham *et al.*, 2014, Pratchett *et al.*, 2014).

The increase in strength of preference shown in this study by the habitat generalists *P. coelestis* and *A. sexfasciatus* for a particular habitat at extreme warm temperature suggests evidence of behavioural plasticity (Wong & Candolin, 2015). *P. coelestis* and *A. sexfasciatus* at ambient summer temperatures (28°C) in the current study exhibited the generalist habitat associations typically observed for these species (Allen, 1991, Pratchett *et al.*, 2012, Coker *et al.*, 2014). However, at both 22°C and 31°C testing temperatures, *P. coelestis* demonstrated stronger habitat preferences, including a preference for complex coral and boulder at 22°C and complex coral at 31°C. Similarly, *A. sexfasciatus* showed a strong preference for boulder habitat at the warmest temperature. For tropical ectotherms adapted to a narrow range of body temperatures, species may make behavioural adjustments when temperatures approach the edges of their thermal performance range, reducing non-essential activities, including swimming, foraging, growth and energy storage (Pörtner, 2002, Pörtner & Peck, 2010). At both 22°C (ambient winter) and 31°C (elevated), *P. coelestis* may experience physiological stress and therefore prioritise selecting the habitat that provides the greatest amount of shelter (Sinervo *et al.*, 2010), i.e. complex coral and boulder respectively. Sheltering may provide protection against the physiological extremes of temperature and predation by increasing the control an individual has over its physiological and biological environment (Hansell, 2005). However, additional time spent sheltering can also come at a cost through reduced time foraging, significantly impacting species persistence (Sinervo *et al.*, 2010).

In contrast, *A. sexfasciatus* only showed a preference for a particular habitat at the warmest testing temperature suggesting this species' habitat preference is robust within the seasonal range of temperatures experienced, and may only experience physiological stress at the elevated temperature of 31°C. The lack of thermal sensitivity at 22°C for *A. sexfasciatus* may not be surprising since the critical thermal minimum for *Abudefduf* spp. is expected to be around 17°C, compared to *P. coelestis* at 19°C (Figueira & Booth, 2010). The strong preference of boulder habitat at the warmest temperature treatment may suggest a trade-off between optimal refuge structure with other areas of the reef that provide sufficient food to live. While the boulder habitat provides a more limited refuge than similarly-sized complex coral, *A. sexfasciatus* is known to aggregate near rocky reefs to feed on its algal and planktonic food sources (Allen, 1991), although food was not provided and feeding during the behavioural trials was not recorded in this study. Similarly, selecting habitats that provide refuge and/or food may explain the preference *P. coelestis* had for boulder in addition to complex coral at the cooler temperature (Randall *et al.*, 1997, Ohman *et al.*, 1998). However, environmental change can cause a mismatch between the quality of a habitat and the cues used by individuals to assess that quality (Schlaepfer *et al.*, 2002) and this might mean *A. sexfasciatus* is making a poor choice for boulder habitat that doesn't provide the most shelter. For both *P. coelestis* and *A. sexfasciatus,* non-complex coral was the least preferred habitat, potentially because it had the lowest habitat complexity of those available and provided the least amount of shelter (Almany, 2004, Johansen *et al.*, 2008, Graham & Nash, 2013). These results generally suggest that as water temperature increases, species previously considered to associate with a range of habitats (i.e. generalists) may become more selective in their habitat associations. Therefore, further research into the physiological responses to these changes in habitat preferences should be investigated to better understand the consequences of switching from using a broad to narrow range of habitats.

Our results confirm the expectation that a habitat specialist maintains the level of specialisation across changes in environmental parameters and are therefore likely to be particularly vulnerable to degradation or decline of specific habitat types (Pratchett *et al.*, 2012, Coker *et al.*, 2014). The habitat specialist tested in this study (*P. moluccensis*) maintained its habitat preference for complex coral across all temperatures, making them particularly vulnerable to continued degradation and loss of coral cover as a result of ocean warming events (Gardner *et al.*, 2003, Bellwood *et al.*, 2004, Alvarez-Filip *et al.*, 2009). For species that rely on live coral, especially across life stages, declining complexity and availability of coral habitat will mean substantial negative impacts to populations (Jones *et al.*, 2004, Munday, 2004). For instance, declines in populations of *P. moluccensis* have been documented in response to localised loss of complex branching coral (Pratchett *et al.*, 2012). Species that rely on specific habitats for survival may be at an increased risk of their niche disappearing completely (McKinney, 1997). Conversely, other species may be able to escape the effects of environmental change if the habitat they rely on, unlike most coral habitat, is resilient to disturbance (Pratchett *et al.*, 2012).

If more habitat generalists shift their preferences with ocean warming towards habitats already preferred by other species, it could lead to increased competition for resources as niches start to show greater overlap. The results of this study suggest that while the habitat generalist *P. coelestis* does not currently occupy the same habitat as the coral habitat specialist *P. moluccensis*, under expected ocean warming they could be competing for similar complex coral resources. Alternatively, species may undergo a competitive release if niche breadth declines when they become more selective (Bolnick *et al.*, 2010), as was the case for *A. sexfasciatus* in the current study, where association with complex coral habitat was significantly reduced at the elevated testing temperature and boulder became the preferred habitat. This suggests that *A. sexfasciatus* may represent a resilient generalist species in the future in terms of habitat preferences. Of course, outcomes of habitat preferences and potential competitive interactions in the future are likely to be complex and require direct testing (Warren *et al.*, 2016).

In common with all laboratory-based experiments, the results of this study cannot fully replicate all factors involved in habitat selection in the wild. In order to isolate the effect of temperature on habitat preference within a controlled experimental setting, other factors likely to influence behaviour (such as competition, predation, resource availability and priori effects) were necessarily excluded. In addition, the temporal scale of our observations does not reveal any plastic responses to temperature with developmental and cross-generational exposure (Donelson *et al.*, 2011, Donelson *et al.*, 2012, Sorensen *et al.*, 2014). Longer exposure to elevated temperature could therefore potentially lead to different effects on habitat preferences since developmental exposure length has been found to influence both intra- and interspecific competitive interactions for habitat (Warren *et al.*, 2016). Although beyond the scope of the current study, these longer-term temporal dimensions would represent interesting extensions of our results and increase our understanding of how thermal environment can influence habitat preference of specialist and generalist reef fishes.

In the future, there will likely be a reduction in the quality of habitat resources and, as global temperatures rise, we can expect to see increasing pressure on species that rely on a particular habitat (such as complex coral) for survival (Gardner *et al.*, 2003, Bellwood *et al.*, 2004, Alvarez-Filip *et al.*, 2009). The shifts in habitat preferences observed in this study suggest that we may also see increased pressure on species that currently occupy a variety of habitat niches (habitat generalists), indicating that climatic warming could affect ecological relationships in subtle and unexpected ways. Furthermore, the impacts of rising temperatures on organisms' realised niches should be considered further to better understand and predict ecosystem functioning as environments continue to change.

Chapter 6: General Discussion

Coral reef fishes are under increasing pressure from elevated water temperatures and habitat degradation associated with climatic warming (Graham *et al.*, 2014, Pratchett *et al.*, 2014). Their ability to cope with the rapid rise in ocean temperature is critical to understanding the probability of species persistence and population sustainability (Donner *et al.*, 2005, Brierley & Kingsford, 2009, Hofmann & Todgham, 2010). The poleward shift in the distribution of tropical fishes has been documented in response to increasing ocean temperatures (Figueira & Booth, 2010, Wernberg *et al.*, 2013, Feary *et al.*, 2014, Verges *et al.*, 2014). However, high latitude reefs present novel conditions which influence the ability of species to successfully colonise these areas (Feary *et al.*, 2014). This thesis examines the habitat associations of tropical fishes from tropical to temperate reefs to inform predictions of their ability to cope with future climate change, including which species are likely to successfully redistribute to higher latitudes (Chapter 2, 3) and which species may be most affected by ocean warming in natal tropical reefs (Chapter 5). Specifically, this thesis illustrates that local benthic composition is likely to play a role in determining which tropical fishes could successfully colonise temperate reefs in the future (Chapter 2). In addition, it describes how behavioural time budgets and social group structure of juvenile tropical fishes vary among latitudes and species (Chapter 3). Finally, this thesis shows that habitat preferences of juvenile tropical fishes are influenced by temperature (Chapter 5), with shifts in the habitat preferences of some species suggesting we may currently be underestimating the impact of climatic warming on species that are known to associate with a range of habitats.

Potential for habitat availability to structure species range expansion

Despite an increase in the abundance of tropical fishes in temperate ecosystems globally, many of the factors that may facilitate or constrain such range expansions are not well understood (Feary *et al.*, 2014). In particular, the role of the receiving environment in organising the redistribution of tropical fishes remains largely unresolved (Bates *et al.*, 2014a). Although larval supply and increasing water temperatures are expected to support future range expansion of tropical fishes (Booth *et* *al.*, 2007, Figueira & Booth, 2010), this thesis provides evidence to suggest population establishment in temperate regions may be restricted by species habitat requirements (Chapter 2). Previous studies have indicated that the level of wave exposure and macroalgal cover of temperate reefs may determine where tropical species can successfully recruit (Beck, 2015, Beck *et al.*, 2016b). Expanding on these findings, this thesis suggests that variation in tropical fish assemblages is closely linked to variation in benthic assemblages across a tropical-to-temperate gradient (Chapter 2). Thus, benthic composition is likely to play a role in structuring the availability of suitable habitat and trophic resources within high latitude reef environments, and may constrain the establishment of some tropical fish species, while promoting others.

This is one of few studies to compare densities of adults and juveniles among fish assemblages at this latitudinal scale (Chapter 2). Results revealed there were no differences in the density of tropical juveniles among locations; however, there were fewer tropical adults at the temperate location compared to the tropical locations (Chapter 2). The low density of tropical adults at the temperate location could indicate that although temperate reefs may provide appropriate conditions for some tropical species to settle, they may lack the resources needed for growth and survival into adulthood. Furthermore, the few tropical adults present at the temperate location were species that do not rely principally on corals for habitat or food (e.g. the damselfishes *Abudefduf sexfasciatus, Abudefduf vaigiensis,* and the butterflyfish *Chaetodon flavirostris*). These results support previous predictions that habitat generalists are more likely to colonise high latitude reefs due to a limited reliance on coral habitat (Nakamura *et al.*, 2013, Feary *et al.*, 2014).

Understanding the trophic resources that support fish assemblages in different habitats is critical for their sustainable management, especially for species that participate in food webs that span across several reef ecosystems (Abrantes *et al.*, 2015). This thesis showed that at tropical locations fish clustered into four trophic groups, including obligate corallivores, omnivores, apex predators and detritivores (Chapter 2). In contrast, trophic separation of assemblages at the subtropical and temperate locations corresponded with benthic herbivores, planktivores and mesopredators. Moreover, the focal behavioural studies in this thesis showed latitudinal differences in the feeding behaviour of *C. auriga,* with greater bite rates as well as quicker rate of intake (i.e. more bites taken in a shorter amount of foraging time) at the tropical location compared to the higher latitude reefs (Chapter 3). A recent study suggests the feeding behaviour of the tropical damselfish, *A. vaigiensis*, was affected by temperate predators and seasonal water temperatures in temperate reefs (Beck *et al.*, 2016a). A reduction in the feeding rate and subsequent mortality of *A. vaigiensis* was also documented in experimental conditions where they were held at cooler water temperatures, despite abundant food supply (Figueira *et al.*, 2009). Therefore, the possible mechanisms (e.g. temperature, predators, competitors, resource availability) driving the differences in feeding behaviour observed in this study (Chapter 3) require further investigation.

Novel interactions with resident temperate species

In addition to habitat use (Chapter 2), behavioural ecology is one of several key areas of research requiring greater focus to better understand range shifts among tropical species (Feary *et al.*, 2014). Findings of this thesis contribute to resolving this knowledge gap (Chapter 3) by showing that the behavioural time budgets and social group structure of tropical fishes vary both among reef environments (tropical, subtropical, temperate) and species (*C. auriga, A. sexfasciatus, Pomacentrus coelestis*). These differences in species behaviour among locations may highlight the constraints of novel high latitude reef environments (e.g. temperature, resource availability, predation and competition) (Feary *et al.*, 2014). Being ectotherms, tropical fishes are particularly sensitive to cooler temperatures. Previous work has documented significant declines in the abundance of tropical species in temperate reefs when ocean temperatures dropped over winter (Figueira & Booth, 2010). Experimental work has also shown declines in feeding and swimming performance at cooler temperatures (Figueira *et al.*, 2009). Hence, thermal tolerance may drive these behavioural differences among locations (Chapter 3). *C. auriga* tended to spend less time swimming and feeding, and more time sheltering and hovering at the temperate location (Chapter 3). Sheltering provides protection against the extremes of temperature and the threat of predation by increasing the control an individual has over its physiological and biological environment (Hansell, 2005).

Native predators and/or competitors can significantly alter fish behaviour by restricting access to resources, including food and habitat (Hixon & Jones, 2005, Holt & Barfield, 2009, Beck *et al.*, 2016a). As evidenced by *P. coelestis,* antagonistic interactions differ between temperate and tropical locations (Chapter 3). Resource availability (e.g. food, habitat, conspecifics) is also likely to cause variation in the behavioural patterns observed at the higher latitudes for all species. Although the physiological constraints of temperature at the temperate locations are likely to be reduced with continued warming (Figueira & Booth, 2010, Feary *et al.*, 2014), predation risk and species resource requirements may still impact the establishment of some species. For example, the reduction in foraging activity of *A. sexfasciatus* at the subtropical location (Chapter 3) will likely reduce growth rates and extend the period of vulnerability to gape-limited predators (Sogard, 1997). Further studies should therefore be directed at interactions with predators/competitors to better understand the mechanisms driving the differences in the composition of tropical fish assemblages and individual behaviour across latitudes (Chapter 2, Chapter 3).

Variation in the rate and extent that species respond to environmental warming can disrupt interactions among species and promote the development of novel interactions (Gilman *et al.*, 2010, Verges *et al.*, 2014). A key outcome of this thesis was the finding of novel social groups at the higher latitudes, not observed at the tropical location (Chapter 3). Surprisingly, at the higher latitudes juvenile *C. auriga, A. sexfasciatus* and *P. coelestis* generally formed heterospecific groups with other tropical, subtropical or temperate fishes. Group behaviour among animals has been shown to benefit their energy use, predator avoidance and foraging opportunities (Shaw, 1978, Krause & Ruxton, 2002, Nadler *et al.*, 2016). For instance, tropical fishes may benefit from native heterospecifics as they could be better at recognising temperate predators (Roberts, 1996, Ward *et al.*, 2011). Heterospecifics or older conspecifics could also serve as experienced guides to beneficial resources in novel environments (Childress & Herrnkind, 2001, Leis & Carson-Ewart, 2002, Lecchini *et al.*, 2007). However, it is also possible that these patterns were driven by density dependence, with fewer conspecifics with whom to form groups at the higher latitudes. Furthermore, it is important to consider the potential effects that these social group interactions may have on local species and the potential costs and benefits of living in mixed groups to both invader and native species.

Influence of elevated temperature on habitat preferences

Previous studies have documented the negative impacts of habitat degradation, including coral loss and habitat fragmentation on coral reef fishes (Munday, 2004, Bonin, 2011, Pratchett *et al.*, 2011, Pratchett *et al.*, 2012). However, few studies have explored the effects of increasing temperature on habitat preference. This thesis addresses this knowledge gap by showing how temperature may influence the habitat preferences of juvenile coral reef fishes, with the magnitude and direction of the effect varying significantly across the three species tested (Chapter 5). As predicted, *P. moluccensis* remained consistent in their preference for complex coral habitat across all temperature treatments. Unexpectedly, however, there were shifts in the habitat preferences of *P. coelestis* and *A. sexfasciatus* in response to warming temperature, becoming more selective in habitat association. This may suggest behavioural plasticity in response to changes in ocean temperature (Wong & Candolin, 2015). However, behaviourally plastic responses can be adaptive or maladaptive (Sinervo *et al.*, 2010, Merila & Hendry, 2014). Moreover, habitats that provide one benefit may lack others, such as food, predator protection or mates (Brown, 1999, Merilaita *et al.*, 1999, Pitt, 1999, Shine *et al.*, 2002, Ahnesjo & Forsman, 2006). Hence, further studies are required to explore how shifting from using a broad to narrow range of habitats may impact fitness related activities and determine whether such potentially behaviourally plastic responses are beneficial.

Novel procedures were developed in the course of habitat preference work (Chapter 4). First, I determined that observation length was critical in accurately describing behaviors and that the normal 10 min was too short. Secondly, I demonstrated the usefulness of discrete choice modelling in providing a flexible way to model organism preferences based on a set of factors of interest (Chapter 4, 5), which could be applied to data collected from the field. This type of modelling approach would also allow for testing whether a categorical variable was related to habitat choice and be applied to future research questions aimed at predicting the effects of habitat degradation (e.g.

coral bleaching) or other aspects of climate change (e.g. elevated CO_2) on the habitat selection of coral reef fishes as well as other species within a particular ecosystem (Johnson & Wichern, 2007).

Potential for niche overlap with shifts in species habitat preferences

If more species show changes and less flexibility in their habitat preferences during stressful ocean warming events this may lead to increased competition for resources as niches overlap. For instance, while *P. coelestis* does not directly compete with *P. moluccensis*, results of this thesis suggest they may compete for similar complex coral resources under ocean warming (Chapter 5). Therefore, even if species can escape the effects of habitat degradation (e.g. if the habitat they rely on is resilient to disturbance) this may be outweighed by an increase in competition for resources as niches overlap in future ocean conditions. In contrast, species may undergo a competitive release if niche breadth declines as species become more selective, reducing niche overlap with other species (Bolnick *et al.*, 2010). This may be the case for *A. sexfasciatus* as their preference for complex coral habitat was significantly reduced at the elevated temperature treatment and boulder became the preferred habitat (Chapter 5). It is therefore unlikely that *A. sexfasciatus* will have to compete for the same habitat resources as *P. moluccensis* as oceans warm. Likewise, the range expansion of tropical species into temperate environments may cause an overlap of resource use with local species (Chapter 2, Chapter 3). This research therefore highlights the potential for novel competitive interactions among species as niches overlap with ongoing warming and should be a priority of future research to better understand the consequences of such overlap.

Concluding remarks

This thesis addresses knowledge gaps on how the habitat associations of tropical fishes may influence their ability to cope with climate change, including which species are likely to successfully redistribute to higher latitudes (Chapter 2, Chapter 3) and which species may be most affected by ocean warming in natal tropical reefs (Chapter 5). This work also illustrates how the receiving environment may affect the distribution of fishes, not just at the species level but also at the assemblage/community level (Chapter 2, Chapter 3). Finally, this thesis highlights the range of questions still unanswered about the factors that may facilitate or constrain range expansions (Chapter 2, Chapter 3) as well as the influence of climatic warming on the ecology and behaviour of species, particularly on coral reefs (Chapter 5). Future work will be able to build on these findings to create more accurate predictions about which species will geographically respond to warming oceans and when this is likely to occur.

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Appendix A: Supplemental information for Chapter 5

Table A1. Model estimates for the mixed logit model for the selection of habitat (rubble, boulder, complex coral, non-complex coral, no selection) by juvenile *Pomacentrus moluccensis, Pomacentrus coelestis* and *Abudefduf sexfasciatus*. This model includes main effects and the two-way interaction for species and temperature (22°C, 28°C and 31°C). The two-way interaction is significant (p-value < 0.001).

Parameter	Estimate	Std. Error	t-value	P-value	Effect P-value
Boulder:(intercept)	2.651	0.192	13.801	< 0.001	
Non-complex coral:(intercept)	3.190	0.194	16.400	< 0.001	
Rubble:(intercept)	-1.959	0.227	-8.637	< 0.001	
Complex coral:(intercept)	-1.003	0.248	-4.044	< 0.001	
Boulder: *A. sexfasciatus*	-2.555	0.233	-10.976	< 0.001	< 0.001
Non-complex coral: *A. sexfasciatus*	-2.289	0.228	-10.039	< 0.001	
Rubble: *A. sexfasciatus*	-1.368	0.254	-5.380	< 0.001	
Complex coral: *A. sexfasciatus*	0.200	0.269	0.745	0.456	
Boulder: *P. coelestis*	-1.184	0.253	-4.689	< 0.001	
Non-complex coral: *P. coelestis*	-1.525	0.254	-6.015	< 0.001	
Rubble: *P. coelestis*	-1.490	0.245	-6.086	< 0.001	
Complex coral: *P. coelestis*	-0.508	0.267	-1.903	0.057	
Boulder: 22°C	-0.632	0.241	-2.617	0.009	< 0.001
Non-complex coral: 22°C	-0.422	0.248	-1.703	0.089	

Rubble: 22°C	-0.680	0.245	-2.772	0.006	
Complex coral: 22°C	-0.555	0.275	-2.020	0.043	
Boulder: 31°C	-0.943	0.246	-3.836	< 0.001	
Non-complex coral: 31°C	-0.340	0.251	-1.353	0.176	
Rubble: 31°C	1.963	0.300	6.537	< 0.001	
Complex coral: 31°C	0.981	0.323	3.039	0.002	
Boulder: *A. sexfasciatus*: 22°C	0.460	0.313	1.468	0.142	< 0.001
Non-complex coral: *A. sexfasciatus*: 22°C	0.683	0.302	2.260	0.024	
Rubble: *A. sexfasciatus*: 22°C	1.972	0.332	5.942	< 0.001	
Complex coral: *A. sexfasciatus*: 22°C	-0.061	0.351	-0.173	0.863	
Boulder: *P. coelestis*: 22°C	0.004	0.332	0.013	0.990	
Non-complex coral: *P. coelestis*: 22°C	0.645	0.332	1.943	0.052	
Rubble: *P. coelestis*: 22°C	1.459	0.299	4.878	< 0.001	
Complex coral: *P. coelestis*: 22°C	-0.324	0.342	-0.948	0.343	
Boulder: *A. sexfasciatus*: 31°C	1.332	0.304	4.384	< 0.001	
Non-complex coral: *A. sexfasciatus*: 31°C	-0.488	0.307	-1.591	0.112	
Rubble: *A. sexfasciatus*: 31°C	3.329	0.491	6.781	< 0.001	
Complex coral: *A. sexfasciatus*: 31°C	1.004	0.529	1.898	0.058	

Boulder: *P. coelestis*: 31°C	3.240	0.490	6.613	< 0.001
Non-complex coral: *P. coelestis*: 31°C	3.167	0.495	6.392	< 0.001
Rubble: *P. coelestis*: 31°C	2.651	0.192	13.801	< 0.001
Complex coral: *P. coelestis*: 31°C	3.190	0.194	16.400	< 0.001