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Geographic variation in ecology of coral feeding butterflyfishes and resilience to large scale disturbances

Thesis submitted by

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Statement on the contribution of others

This thesis includes collaborative work with Dr Morgan Pratchett, Dr Line Bay, Dr Michael Berumen, Dr Vanessa Messmer and Andrew Cole. I led these research collaborations and was responsible for the project design, data collection, data analysis and interpretation. My collaborators provided intellectual guidance, financial support, assistance with field work, technical instruction and editorial assistance.

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Abstract

Ecological specialisation is often correlated with high extinction risk as specialist species are expected to be disproportionately affected by changes in resource availability and disturbance events compared to generalist counterparts. On coral reefs, highly specialised coral-feeding butterflyfish appear to be most vulnerable to the effects of coral loss. Species with large geographic ranges, such as many butterflyfishes, are traditionally thought to have low risk of extinction if disturbances are patchy in time and space. This is because disturbed locations can be recolonised from viable populations elsewhere. However, as the frequency, intensity, magnitude and extent of disturbance events on coral reefs are predicted to increase, many butterflyfishes may be at considerable risk of global extinction in the future. The persistence of these species through future periods of coral loss will be dependent in part upon their ability to use alternative resources if their preferred coral resources are no longer available, the influence of coral resources on local abundance patterns, and the ability of remnant populations to recolonise disturbed habitats. However, all three factors are largely unknown for most butterflyfishes. This thesis examines variation in the ecology of coral-feeding butterflyfishes across five geographic locations and considers the influence of dietary specialisation on the resilience of local versus global populations of butterflyfish to increasing coral loss.

A range of indices can be used to estimate ecological specialisation but their utility to inform vulnerability predictions is largely unknown. To determine the most informative index to use for quantification of dietary specialisation in coral-feeding butterflyfishes, Chapter 2 compared the performance of four different specialisation indices. Feeding observations were conducted for three butterflyfish species at six sites around Lizard Island, Australia. Levels of dietary specialisation were calculated for each species at each site using four specialisation indices.

Differences in the relative levels of dietary specialisation estimated for each of the three butterflyfishes by each of the four indices indicated that the choice of specialisation index can impact considerably on estimates of specialisation. The best estimates of specialisation were provided by indices that incorporated a measure of resource availability because they were able to distinguish between species using a few common resources and those using a few rarer resources disproportionately to availability. Resource selection functions were also found to be highly informative for predicting likely responses of specialist versus generalist consumers to changes in resource availability.

Having determined that specialisation indices incorporating resource availability measures were most appropriate to use, Chapter 3 then examined large-scale geographic variation in dietary specialisation for four coral-feeding butterflyfishes. Detailed estimates of dietary composition and specialisation are available for a few coral-feeding butterflyfishes, however, only a small number of studies have compared resource use to resource availability and these studies have been confined to a few isolated locations. Consequently, the degree that particular butterflyfish species are truly specialised or generalised is unknown. Chapter 3 examined whether patterns of resource use varied among five distinct geographic locations, corresponding with changes in resource availability. Despite varying resource availability, the level of dietary specialisation shown by each of the four species of butterflyfishes varied little among geographically separated locations. *Chaetodon vagabundus, C. citrinellus* and *C. lunulatus* all had low levels of dietary specialisation and used different resources in each location. In contrast, *Chaetodon trifascialis* had high levels of dietary specialisation and used the same few resources in each location. These results indicate that highly specialised species such as *C. trifascialis* will be highly vulnerable to coral loss as they appear to be largely inflexible in their coral diet, and hence, sensitive to changes in the abundance of this resource.

Empirical evidence indicates that both niche breadth and resource availability are key drivers of a species' local abundance and distribution patterns. Numerous studies have found strong links between total hard coral cover and the abundance of coral-feeding butterflyfishes; however, the influence of specific dietary resources on the abundance of individual butterflyfish species has not yet been examined. Chapter 4 investigated the influence of dietary specialisation and resource availability on the local abundance patterns of five butterflyfishes, across five geographic locations. Factors influencing local abundance varied between butterflyfishes with specialised and generalised diets. Resource availability had the strongest influence on the abundance of *C. trifascialis* - the species with the most specialised diet. Local abundance of *C. trifascialis* was best predicted by availability of the *Acropora* corals that it preferentially feeds on. In contrast, abundance of generalist butterflyfishes was best predicted by indices of total resource availability. However, overall, resource availability only explained a small proportion of the variation in local abundance for all five species. These findings suggest that despite their relatively specialised diets, resource availability has limited influence on the local abundance of butterflyfishes and only the most specialised species appear to be consistently limited by prey availability.

Over evolutionary timescales, the resilience of butterflyfishes to coral loss will be determined by their level of population connectivity and the recovery potential of declining populations. Recent studies have indicated that specialised species may have lower genetic diversity and population connectivity than generalist counterparts. Chapter 5 examined whether there were differences in population genetic structure between the dietary specialist *C. trifascialis* and the dietary generalist *C. lunulatus* from five locations across the Pacific. Mitochondrial DNA sequences and microsatellite loci were used to detect evidence of population declines and estimate levels of gene flow to enable predictions of likely recovery potential following coral loss. Genetic analyses revealed contrasting demographic histories and levels of genetic

structure for the two species. Highly significant tests for genetic bottlenecks indicated that *C. trifascialis* populations have experienced significant declines in abundance over both recent and historical timescales; however, low levels of genetic structuring and high levels of gene flow were detected among locations. In contrast, there was little evidence of genetic bottlenecks and population declines for *C. lunulatus*, and higher levels of genetic structuring were detected for this species compared to *C. trifascialis*. The finding of genetic bottlenecks for *C. trifascialis* indicates that this species experiences periodic population decline; however, the high gene flow detected among locations suggests *C. trifascialis* populations will be able to recover from local declines through colonisation from healthy source populations.

Overall, this study has shown that coral-feeding butterflyfishes with specialised diets are inflexible in their dietary requirements and therefore, highly vulnerable to localised coral loss caused by major disturbances. However, the availability of preferred coral resources had limited influence on geographical variation in the abundance of specialist species, which were generally common on surveyed reefs. These findings indicate that macro-ecological theories predicting that specialist species are locally rare are not universally true and specialist species often have other characteristics which confer high ecological resilience. Supporting this, molecular data indicated that specialist butterflyfishes had high levels of large-scale genetic connectivity, providing increased species-level resilience to localised disturbances. These results highlight the need to be wary of assigning species high vulnerability status based solely on their level of ecological specialisation.

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Chapter 1: General Introduction

1.1 Ecological specialisation and vulnerability

The degree to which species are specialised in their use of available resources is thought to be a trade off between their ability to exploit a wide range of resources versus increased performance on a restricted set of resources (Futuyma and Moreno 1988; Kawecki 1994; van Tienderen 1997; Caley and Munday 2003). Specialists are expected to benefit from the use of a narrow range of resources through higher fitness, survival rates, or a competitive advantage over generalist counterparts when using preferred resources (Futuyma and Moreno 1988; Caley and Munday 2003). For example, specialised gobies attained higher growth rates in their preferred coral habitats compared to con-generic habitat generalists (Caley and Munday 2003). Similarly, the dietary specialist woodrat *Neotoma stephensi* more effectively neutralised dietary toxins and therefore greatly increased assimilation efficiency compared to its generalist counterpart *N. albigula* (Dearing et al. 2000; Sorensen et al. 2004). However, there are inherent costs associated with ecological specialisation (Futuyma and Moreno 1988) and several studies have demonstrated that specialists have lower fitness or growth when using non-preferred resources. For example, two subspecies of the black bean aphid (*Aphis fabae*) had lower fitness when maintained on non-preferred host plants (Mackenzie 1996). Likewise, in a growth experiment, the dietary specialist butterflyfish *Chaetodon trifascialis* had fast growth rates when fed an exclusive diet of its preferred coral prey, but failed to grow when fed non-preferred prey (Berumen and Pratchett 2008).

In addition to performance trade-offs, ecological specialisation is often correlated with high extinction risk (McKinney 1997; Colles et al. 2009). Specialists are expected to have a lower ability to cope with environmental stochasticity as the evolution of adaptations to specific resources can make it difficult for species to switch to alternative resources if preferred resources become scarce or unavailable (Futuyma and Moreno 1988). Furthermore, as specialists depend on a narrower range of resources than generalists, they are expected to be disproportionately affected by disturbance events and changes in resource availability (Vazquez and Simberloff 2002). These predictions are supported by empirical data across a range of taxa. For example, specialised coral reef gobies and butterflyfishes suffered proportionally greater declines in abundance compared to generalists following declines in the availability of coral resources (Munday 2004; Pratchett et al. 2006). Similarly, following land use changes in Belgium, Denmark and the Netherlands, populations of specialist carabid beetles have decreased, while generalist species have increased (Kotze and O'Hara 2003). Similar declines in abundance have also been reported for specialised birds (Aitken and Martin 2008), amphibians (Swihart et al. 2003), mammals (Harcourt et al. 2002), and butterflies (Charrette et al. 2006) compared to generalist counterparts following disturbance events and declines in resource availability.

Macro-ecological theory predicts that the susceptibility of specialists to disturbance events will be elevated if population sizes are small and species are locally rare (Brown 1984; Brown et al. 1995). Both demographic models and empirical data show that extinction risk increases with decreasing population size (Arita et al. 1990; Pimm et al. 1995), mostly because demographic stochasticity is much more likely to lead to irreversible declines in small populations (McKinney 1997; Gaston 2003). Supporting this, a number of empirical studies have shown that populations at lower abundances are more susceptible to disturbances than populations at higher abundances (e.g. Bolger et al. 1991; Spiller et al. 1998; Barlow et al. 2002; Henle et al. 2004; Munday 2004). If specialists also have low genetic diversity and/or low population connectivity, then vulnerability is likely to be further increased. Genetic diversity can substantially influence the ability of populations to respond to environmental change (Frankham et al. 2002; Frankham 2005), while gene flow and population connectivity can directly influence population persistence, stability and recovery potential (Hanski 1999). Studies comparing population genetic structure of related species with varying levels of ecological specialisation are relatively rare. However, emerging evidence suggests that specialists have lower genetic diversity and population connectivity compared to generalist counterparts. For example, lower levels of gene flow have been found in specialist snakes (DiLeo et al. 2010), kestrels (Alcaide et al. 2009), beetles (Brouat et al. 2003) geckos (Hoehn et al. 2007) and fishes (Rocha et al. 2005) compared to related generalist species. If these findings represent a general pattern of lower genetic diversity and population connectivity in specialists then vulnerability and extinction risk is likely to be greatly elevated.

1.2 Coral reefs and disturbance events

Coral reefs are among the most threatened natural ecosystems, owing to high levels of anthropogenic exploitation and habitat degradation (Hughes et al. 2003; Carpenter et al. 2008). Globally, coral reefs are showing long term declines in scleractinian coral cover (Gardner et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004; Bruno and Selig 2007; Graham et al. 2008), which are likely to increase as reefs are impacted by on-going climate change (Donner et al. 2005; Hoegh-Guldberg et al. 2007). Coral cover has declined by roughly 80% in the Caribbean over the last 30 years (Gardner et al. 2003), and by 20 to 40% on the Great Barrier Reef over the last two decades (Bellwood et al. 2004). Moreover, it is estimated that on 19% of the world's reefs, coral cover has declined by more than 90% and there is limited chance of recovery (Wilkinson 2008). In addition to widespread coral loss, there has also been a change in the proportional composition of coral taxa on some reefs. For example, in Moorea, French Polynesia, there has been a long-term shift from coral assemblages dominated by *Acropora* and *Montipora sp.* to assemblages dominated by *Pocillopora* and *Porites sp.* following recurrent disturbances (Berumen and Pratchett 2006b; Pratchett et al. 2011).

Scleractinian corals are the primary habitat forming species on coral reefs (Connell et al. 1997) and the presence of live coral is of critical importance to reef-associated species (Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006; Pratchett et al. 2008b; Graham et al. 2009). Roughly 10% of all reef fishes are estimated to have a direct reliance upon live corals for food and/or shelter (Jones et al. 2004; Munday et al. 2007) and up to 65% of reef fishes use live coral for settlement habitat (Jones et al. 2004; Garpe and Ohman 2007). Furthermore, the structural complexity provided by live coral can influence the abundance of reef fishes by moderating biological interactions such as competition and predation (Beukers and Jones 1997; Holbrook and Schmitt 2002; Almany 2004). Given the importance of live coral to reef fishes, it is not surprising that there is now strong evidence that widespread declines in total coral cover and changes in coral species composition are having a significant negative impact on reef-associated fishes (e.g. Wilson et al. 2006; Pratchett et al. 2008b).

Multiple studies have recorded considerable declines in the abundance of reef fishes following coral loss (Halford et al. 2004; Munday 2004; Graham et al. 2006; Pratchett et al. 2006; Wilson et al. 2006; Cheal et al. 2008; Pratchett et al. 2008b). For example, following a 90% decline in live coral cover in Papua New Guinea, more than 75% of all reef fishes declined in abundance, with half of all fish species declining by more than 50% (Jones et al. 2004). Thus far, the impacts of coral loss have been greatest on reef fishes that depend on live coral for food or shelter (Wilson et al. 2006; Pratchett et al. 2008b); however, the response of species within these groups varies considerably (Pratchett et al. 2008b). For example, following a 59% decline in the abundance of *Acropora* corals between 1997 and 2003 in Kimbe Bay, Papua New Guinea, six species of coral-dwelling gobies also declined abundance, however the extent of decline varied between species, ranging from ~ 50 to 100% (Munday 2004). Similarly, following coral depletion on the Great Barrier Reef, percentage declines in abundance of 10 coral-feeding butterflyfish species ranged from <20 to ~80% (Pratchett et al. 2008b). In both studies, species with highly specialised habitat requirements or diets that used only a small subset of available coral resources suffered the greatest declines in abundance (Pratchett et al. 2008b). These findings provide evidence for a strong relationship between the level of ecological specialisation of a species and it's response to coral loss, suggesting that ecological specialisation is a key driver of extinction risk for coral reef fishes.

1.3 Resilience of coral reef butterflyfishes

Butterflyfishes (family Chaetodontidae), and specifically species in the genus *Chaetodon*, are among the most vulnerable of all reef fishes to coral loss, largely because many species within this genus feed directly on live tissue of scleractinian corals (Pratchett 2005; Cole et al. 2008). There is already evidence for local extinctions of some butterflyfish species following extensive coral loss at some locations. For example, localised extinctions of the chevron butterflyfish, *Chaetodon trifascialis*, have occurred following coral loss in Moorea, French Polynesia (Berumen and Pratchett 2006b), the Seychelles (Graham et al. 2006) and the Great Barrier Reef (Pratchett et al. 2006). Empirical data to date suggests that butterflyfishes feeding exclusively on hard corals (obligate corallivores) with highly specialised diets are most vulnerable to coral loss (e.g. Pratchett et al. 2008b). Species with large geographic ranges, such as many butterflyfishes (Allen et al. 1998), are traditionally thought to have low risk of extinction given that disturbances are patchy in time and space and it is assumed that there will always be a viable population that can reseed disturbed locations (Dulvy et al. 2003). However, as the frequency, intensity and magnitude of disturbance events on coral reefs are predicted to increase (Donner et al. 2005; Hoegh-Guldberg et al. 2007), many butterflyfishes may be at considerable risk of global extinction (Pratchett et al. 2008b).

The resilience of coral-feeding butterflyfishes to any future coral loss on reefs will be determined in the short term by their ability to feed on alternative corals or resources when their preferred coral prey becomes scare (Pratchett et al. 2004). However, the capacity of butterflyfishes to switch prey in accordance with changes in prey availability (termed ecological versatility) is largely unknown. Although several studies have provided detailed assessments of the dietary preferences and dietary specialisation of a number of butterflyfishes, these studies have been confined to a few isolated geographic locations (e.g. Johnston Atoll: Irons 1989; Hawaii: Cox 1994; Great Barrier Reef: Pratchett 2005; Seychelles: Graham 2007). However, studies of dietary specialisation conducted on a local scale may not provide a true indication of ecological versatility. Species may utilise a narrower range of resources on a local scale than they are physiologically capable of using because access to resources can be limited by interspecific interactions such as competition or predation (Hutchinson 1957; Colwell and Fuentes 1975) or alterative resources may be locally unavailable (e.g. Varela et al. 2008). Consequently, the level of specialisation estimated for a species may vary with the spatial scale of analysis (Krasnov et al. 2008) such that species may appear to be specialists on a local scale but have generalised ecologies across their entire geographic range (Fox and Morrow 1981; Devictor et al. 2010). As there have been no systematic comparisons of resource availability and dietary specialisation for butterflyfishes across multiple geographic locations using the same methodology, the true level of dietary specialisation of any species, and therefore their vulnerability to ongoing coral loss, remains largely unknown.

Over short time scales (e.g. less than 2 years), the resilience of butterflyfishes to coral loss will be also influenced by the role of coral cover and specific coral resources in determining their local abundance. Local abundance patterns for any species are likely to be influenced by both their level of ecological specialisation and the particular resources that are locally available (Munday 2002). As generalist species can utilise a wide range of resources, their local abundance should be largely determined by total resource availability. In contrast, specialists that depend on a narrow range of resources are likely to be limited by the availability of these specific resources, rather than total resource availability (Munday 2002; Pratchett and Berumen 2008). Strong links between total coral cover and butterflyfish abundance have been demonstrated in a number of studies across a range of spatial scales (e.g. Bell and Galzin 1984; Bouchon-Navaro et al. 1985; Cadoret et al. 1999; Bozec et al. 2005; Pratchett and Berumen 2008; Emslie et al. 2010; but see Bell et al. 1985; Fowler 1990). But, despite the highly specialised diets of some butterflyfishes, the influence of specific coral resources on local abundance patterns has not been examined for any species. If the abundance of specialists is linked to specific coral taxa then their vulnerability to ongoing coral loss will be greatly increased.

Over evolutionary timescales, the resilience of butterflyfishes will be determined by their level of population connectivity and the recovery potential of declining populations. Populations which suffer severe declines in abundance will be unlikely to recover if recruitment is predominantly from local sources and population connectivity is low. But if a significant component of recruitment comes from outside sources and population connectivity is high then recovery may occur via the long distance dispersal of larvae from unaffected populations (Hughes et al. 2005; Jones et al. 2009). There is growing evidence that populations of many coral reef fishes may be connected on much smaller spatial scales than has previously been assumed (Almany et al. 2007; Jones et al. 2009; Planes et al. 2009). Moreover, long distance larval dispersal between populations may be limited by increasing fragmentation of coral reef habitats (Hughes et al. 2005). Population connectivity over large geographic scales is yet to be determined for any species of butterflyfish. However, these findings suggest that, despite their large geographic ranges, many butterflyfishes may still be detrimentally affected by disturbance events occurring on a local scale as repopulation from unaffected areas may not occur at levels high enough to prevent local extinction.

1.4 Aims and thesis outline

The overall goal of this thesis was to assess the resilience of local versus global populations of coral-feeding butterflyfishes to increasing coral loss. To answer this question I first assessed the performance of different specialisation indices and determined which indices best inform predictions of vulnerability to environmental change. I then conducted two observational studies that determined the level of dietary specialisation of butterflyfishes across five geographic locations, and the influence of dietary specialisation and resource availability on the local abundance of butterflyfishes at these five locations. Finally, I examined whether there were differences in population genetic structure between a dietary specialist butterflyfish (*C. trifascialis*) and a dietary generalist (*C. lunulatus*) by comparing demographic history and levels of gene flow for each species among these same five locations.

The different components of this study are addressed in a series of four data chapters which correspond to the publications arising from this thesis (See Appendix 1 for other papers published during my candidature). Chapter 2 quantifies the level of dietary specialisation in three species of coral-feeding butterflyfishes across six sites around Lizard Island, Australia. This chapter investigates how estimates of dietary specialisation vary with the use of different specialisation indices and determines the utility of different specialisation indices to predict the vulnerability of these fishes to the likely impacts of climate-induced coral loss on reefs. Chapter 3 extends the findings of Chapter 2 and explores geographic variation in the feeding ecology of four species of coral-feeding butterflyfishes among five distinct geographic locations. Specifically, this chapter examines whether patterns of resource use and levels of dietary specialisation vary among these geographic locations, corresponding to changes in resource availability. Chapter 4 measures the abundance of butterflyfishes at the same five geographic locations and determines the influence of total resource availability, availability of specific dietary resources and interspecific competition on abundance patterns at these locations. Chapter 5 uses genetic tools to detect evidence of population declines and estimate levels of population connectivity for two butterflyfishes to enable predictions of likely recovery potential following coral loss. Finally, Chapter 6 is a general discussion that assesses the likely resilience of coral-feeding butterflyfishes to coral loss, based on the findings of this thesis, and highlights directions for future research. The chapters in this thesis have deliberately been created as stand-alone papers suitable for publication, however, they are complementary with a clear narrative that has a common underlying theme: investigating the vulnerability of coral-feeding butterflyfishes to coral loss on reefs.

Chapter 2: The use of specialisation indices to predict vulnerability of coral-feeding butterflyfishes to environmental change[†]

2.1 ABSTRACT

In the absence of detailed assessments of extinction risk, ecological specialisation is often used as a proxy of vulnerability to environmental disturbances and extinction risk. Numerous indices can be used to estimate specialisation; however, the utility of these different indices to predict vulnerability to future environmental change is unknown. This study compares the performance of specialisation indices using coral-feeding butterflyfishes as a model group. The specific aims were to (i) quantify the dietary preferences of three butterflyfish species across habitats with differing levels of resource availability; (ii) investigate how estimates of dietary specialisation vary with the use of different specialisation indices; (iii) determine which specialisation indices best inform predictions of vulnerability to environmental change; and (iv) assess the utility of resource selection functions to inform predictions of vulnerability to environmental change. The relative level of dietary specialisation estimated for all three species varied when different specialisation indices were used, indicating that the choice of index can have a considerable impact upon estimates of specialisation. Specialisation indices that do not consider resource abundance may fail to distinguish species that primarily use common resources from species that actively target resources disproportionately more than they are available. Resource selection functions provided the greatest insights into the potential response of species to changes in resource availability. Examination of resource selection functions, in addition to specialisation indices, indicated that *Chaetodon trifascialis*

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was the most specialised feeder, with highly conserved dietary preferences across all sites, suggesting that this species is highly vulnerable to the impacts of climate-induced coral loss on reefs. The results of this study indicate that vulnerability assessments based on some specialisation indices may be misleading and the best estimates of dietary specialisation will be provided by indices which incorporate resource availability measures, as well as assessing responses of species to changes in resource availability.

2.2 INTRODUCTION

With limited funding and constrained resources, there is limited capacity to effectively protect the increasing number of species at risk of extinction due to environmental change, habitat loss and other anthropogenic disturbances (James et al. 1999; Bottrill et al. 2008). Identification of species or populations that face the greatest risk of extinction is therefore necessary to prioritise conservation efforts. For many species, assessment of extinction risk or vulnerability to predicted environmental change is costly, time-consuming and often impractical. This has lead to widespread efforts to identify factors correlated with high extinction risk or vulnerability across a wide range of taxa (e.g. McKinney 1997; Purvis et al. 2000b) that can be used in the absence of detailed assessments to predict which species are likely to be most vulnerable to future environmental change (Purvis et al. 2000a; Dulvy et al. 2003).

One factor often correlated with high extinction risk and vulnerability is ecological specialisation (McKinney 1997; Fisher and Owens 2004; Colles et al. 2009). Ecological specialists are thought to be more vulnerable to environmental changes and disproportionately affected by changes in resource availability compared to generalist counterparts. Studies across both terrestrial and aquatic organisms and a range of specialisation types support this prediction (e.g. dietary and habitat specialisation: Harcourt et al. 2002; habitat specialisation: Fisher et al. 2003; Kotze and O'Hara 2003; Munday 2004; dietary specialisation: Charrette et al. 2006; Graham 2007; nesting cavity specialisation: Aitken and Martin 2008) suggesting that in many cases ecological specialisation is a key driver of extinction risk. Thus, identifying species that are ecological specialists can provide a useful starting point to predict likely vulnerability and prioritise conservation actions. However, binary classifications of species as either specialists or generalists can mask interspecific variation in ecological versatility. This is of critical importance if specialisation is used as a vulnerability proxy as grouping specialists into a single category assumes equal vulnerability among all specialists, whereas recent research suggests that vulnerability increases with increasing specialisation (Pratchett et al. 2008b). Furthermore, the use of different specialisation indices can result in different estimates of specialisation, even when the same data are considered (Devictor et al. 2010). As biodiversity becomes increasingly threatened by the combined effects of climate change and anthropogenic disturbances (Chapin et al. 2000; Thomas et al. 2004), there is a need for greater focus on the way that specialisation is assessed and interpreted to estimate vulnerability.

A variety of approaches are used to quantify ecological specialisation. The most basic measures report the number of different resource categories which are used by a particular species or population and conclude that a species is specialised if they are only using resources from a few categories (e.g. Eeley and Foley 1999; Owens and Bennett 2000). More commonly, specialisation is quantified using niche breadth indices such as the Simpsons index or the Shannon-Wiener diversity index, which provide estimates of specialisation based on richness and evenness of resource use (e.g. Munday 2004; Christensen and Kleindorfer 2009). While these types of analyses provide very general information about the degree of specialisation, if resources are not equally available they can result in misleading estimates of specialisation as species using resources in proportion to their availability may appear to have narrower niches than more specialised species (Petraitis 1979). A number of studies have addressed this issue through the use of specialisation indices such as Smiths niche breadth measure or chi square log likelihood statistics that incorporate estimates of resource availability (e.g. Gardiner and Jones 2005; Pratchett 2007a). An alternative approach to quantifying specialisation is to use measures of among-individual specialisation. In contrast to specialisation indices which determine the niche of the population as a whole, among-individual specialisation indices provide information about how variation in resource use is spread between individuals within a population (e.g. Araujo and Gonzaga 2007; Araujo et al. 2008). These metrics compare the niche size of individuals within a population to the overall population niche to estimate the degree that resource use differs between individuals (Bolnick et al. 2003). Further information on ecological specialisation can also be provided by resource selection functions. In contrast to specialisation indices, which provide a single measure of specialisation integrated across all resources categories, resource selection functions calculate selectivity for individual resource categories (Dirnwoeber and Herler 2007; Graham 2007). These functions determine whether an individual resource is used significantly more or less than expected based on its availability (Manly et al. 2002), potentially enabling predictions of how species may respond to changes in resource availability and allowing the detection of key resources that may be critical to species persistence.

This study compares the performance of specialisation indices using coral-feeding butterflyfishes as a model group. Using a single dataset, levels of dietary specialisation in three species of coral-feeding butterflyfishes (Chaetodontidae) around Lizard Island in the Northern Great Barrier Reef, Australia, are calculated using four different indices of specialisation - a count of the total number of prey types consumed, the Shannon-Wiener diversity index, a chi-square log likelihood index that incorporates a measure of resource availability, and an among-individual specialisation index. We then calculate resource selection functions to investigate how individual resources are used in relation to their availability. To investigate how spatial variation in resource availability may affect estimates of specialisation, levels of dietary specialisation and resource selection functions for each species were compared across three sites in exposed front reef habitats and three sites in sheltered back reef habitats that differ in the composition and abundance of scleractinian corals which these fish feed on. Unlike many other organisms for which dietary composition has to be inferred through stomach content analysis or scat analysis, the dietary composition of butterflyfishes can be directly quantified via in-situ observations of feeding behaviour, allowing highly accurate and detailed estimation of dietary specialisation. Furthermore, the availability of dietary resources can be directly measured with ease at the same locations where feeding is observed (Pratchett 2005). Previous research has shown that coral-feeding butterflyfishes vary in their level of dietary specialisation (e.g. Pratchett 2005, 2007a) and in their response to changes in resource availability, with specialised butterflyfishes showing the greatest declines in abundance following coral loss on reefs (e.g. Pratchett et al. 2004; Pratchett et al. 2006; Graham 2007; Wilson et al. 2006). These characteristics make coral-feeding butterflyfishes appropriate models for general principles of ecological specialisation.

The specific aims of this study were to (i) quantify the dietary preferences of three butterflyfish species across habitats with differing levels of resource availability; (ii) investigate how estimates of dietary specialisation vary with the use of different specialisation indices; (iii) determine which specialisation indices best inform predictions of vulnerability to environmental change; and (iv) assess the utility of resource selection functions to inform predictions of vulnerability to environmental change. The level of dietary specialisation calculated for each species was expected to vary between exposed and sheltered sites that differed in the availability of coral prey resources. Estimates of specialisation were also expected to vary between the four different specialisation indices for each species.

2.3 METHODS

2.3.1 Study sites

This study was carried out in November 2008 at Lizard Island (14°40'S, 145°27'E), in the northern section of the Great Barrier Reef, Australia. Sampling was conducted across six sites around the island, representative of exposed front reef and sheltered back reef habitats. Lizard Head, Bird Islet and South Island are directly exposed to the prevailing winds and represent front reef habitats. Corner Beach, Osprey Islet and Vickies are relatively sheltered, large patch reefs, representative of back reef habitats. Sampling was conducted in 2 – 5m depth along the reef crest at front reef sites, and along the tops of reefs in 3 – 6m depth at back reef sites.

2.3.2 Resource availability

Variation in the availability of coral prey was assessed using 50m point intercept transects. At each site, five replicate transects were randomly placed along the reef crest or reef top in the same area where feeding observations took place. For each transect, the substrate directly beneath 50 sampling points was recorded to species level for corals, and to broad categories for all other substrate types (e.g., reef substrate, macroalgae). Variation in coral cover and community composition among sites was assessed using a nested MANOVA, which compared the mean abundance of the most common corals (grouped into 9 taxa) between sites nested within habitat types. Data were arc-sin transformed to satisfy assumptions of multivariate homogeneity and normality. Pillai's trace statistic was used to determine the significance of MANOVA results. Patterns in the coral composition at each site were explored using a canonical discriminant analysis (CDA). To assist with interpretation of the CDA, structural co-efficients of the 9 coral taxa were plotted as vectors to indicate the predominant taxa at each site.

2.3.3 Feeding observations

Feeding observations were conducted for three common and widespread species of butterflyfishes; *Chaetodon citrinellus*, *C. lunulatus*, and *C. trifascialis*. *Chaetodon citrinellus* is a facultative corallivore, consuming hard corals in addition to soft corals, other macro-invertebrates and non-coral prey items, while *C. trifascialis* and *C. lunulatus* are obligate corallivores, both feeding almost exclusively on hard (scleractinian) corals (Pratchett 2005). The dietary preferences and proportional use of different prey types for each species were determined from field observations of feeding behaviour across the six sites. Individual butterflyfishes were randomly selected and followed at a distance of 2 - 5 metres for a 3-minute period. The total number of bites taken from each species of coral, other non-coral macro-invertebrates, and non-coral substrata during each observation was recorded, following Pratchett (2005). Twenty observations for each species were conducted on adult fish throughout the day at each site. Every effort was made to ensure that individual fish were not observed more than once. Variation in dietary composition of the three species was analysed using a nested multivariate analysis of variance (MANOVA), which simultaneously compared the mean number of bites taken from each of 15 major prey types at each site, nested within habitat type. Pillai's trace statistic was used to determine the significance of MANOVA results.

2.3.4 Dietary specialisation and selectivity

To investigate how different specialisation indices may vary in their estimates of specialisation, dietary specialisation for each species at each site was assessed using four different indices – a simple count of the total number of different prey types consumed, the Shannon-Wiener diversity index (Zar 1999), the Chi square log likelihood statistic X_{L2}^2 (Manly et al. 2002) and an index of among-individual dietary specialisation (Araujo et al. 2008). For calculation of the Shannon-Wiener diversity index, the log likelihood statistic and among-individual dietary overlap, all dietary items were grouped into 15 major prey categories (listed in Table 2.3) and indices were calculated based on these categories. Dietary selectivity for each species at each site was assessed using resource selection functions (Manly et al. 2002), which were also calculated based on 15 major prey categories.

The Shannon-Wiener diversity index assesses specialisation based on the number and evenness of different prey categories consumed and was calculated using the formula:

$$H' = -\sum_{i=1}^{k} p_i \log p_i \qquad \text{eqn 1.}$$

where k is the number of prey categories and p_i is the proportional use of each prey category (Zar 1999). Values of H' can range from zero to one, with lower values indicating increasing specialisation.

The Chi square log-likelihood statistic X_{L2}^2, was calculated following Manly et al. (2002). As data were collected on selection of resource units by individual animals, but resource availability was assessed at the population level, Model Design II with Sampling Protocol A was used (Manly et al. 2002, eqn 4.27). X_{L2}^2 was calculated using the formula:

$$X_{L2}^2 = 2 \sum_{j=1}^{n} \sum_{i=1}^{I} u_{ij} \log_e\{u_{ij} / E(u_{ij})\} \qquad \text{eqn 2.}$$

where u_{ij} is the proportional use of each prey type (i) by each individual (j) and $E(u_{ij})$ is the expected number of bites taken from prey type i by the jth individual if use is proportional to availability (Manly et al. 2002). The resulting value of X_{L2}^2 was compared to the chi-squared distribution with $n(I\text{-}1)$ degrees of freedom (where I is the total number of prey categories) to determine the significance of selectivity exhibited by each butterflyfish species at each site. Higher values of X_{L2}^2 indicate increasing specialisation.

Variation in dietary composition between individual butterflyfishes (among-individual specialisation) was assessed using an individual niche overlap network following Araujo et al. (2008). For each species at each site a niche overlap network was defined using the programme DIETA1.0 (Araujo et al. 2008) in which the nodes of the network represented individual fishes and the connections between nodes measured the degree of dietary overlap among pairs of individuals. Each connection was assigned a weight (w_{ij}) ranging from 0 for no overlap to 1 for total overlap ($0 < w_{ij} > 1$) as a measure of the pairwise dietary overlap between individuals i and j. Among-individual dietary variation (E) was then measured as the average density of all connections in the network, quantified as $E = 1 - \bar{w}_{ij}$. Low values of E indicate that there is little individual dietary specialisation, with E equal to 0 when all individuals have identical diets; high values of E indicate that individual dietary specialisation is high, with E equal to 1 when each individual uses a unique resource. If individual-level specialisation is high, then species-level specialisation is generally low. Monte Carlo bootstrap simulations were run using DIETA1.0 for each species at each site to test the null hypothesis that any observed dietary variation arose from individuals sampling stochastically from a shared distribution (Araujo et al. 2008). In these simulations each individual was reassigned the same number bites that it was observed taking, drawn randomly from the observed distribution of the population diet via multinomial sampling. 10,000 such populations were simulated and among individual dietary variation, E, was recalculated for each simulated population. The null hypothesis was rejected if the empirical (observed value) E was higher than 95% of the E values of the simulated populations.

To investigate dietary selectivity and determine which prey corals were used significantly more or less frequently than expected, resource selection functions were calculated for major prey corals for each species at each site following Manly et al.'s (2002) Model Design II, Sampling Protocol A, using the formula:

$$w_i = \{ \sum_{j=1}^{n} u_{ij} / p_i \}/n \qquad \text{eqn 3.}$$

where u_i is the proportional use of prey category *i* by the *j*th individual, *n* is the number of individuals sampled and p_i is the proportional availability of each prey category within each site. These functions allow for sampling of resource use at the individual level and resource availability at the population level (Manly et al. 2002, eqn 4.29). Bonferroni corrected 95% confidence intervals were calculated around each selection function such that the use of a particular prey was deemed to be significantly disproportionate to its availability if the 95% confidence interval did not encompass one (Manly et al. 2002). Selection functions significantly greater than one indicated selection (i.e. coral prey was consumed significantly more than expected based on availability); selection functions significantly less than one indicated avoidance (i.e. coral prey was consumed significantly less than expected based on availability).

2.4 RESULTS

2.4.1 Coral cover and composition

Cover and community composition of scleractinian corals varied among habitat types and sites. Cover of scleractinian corals was highest at exposed sites, covering 51% (±3.7 S.E.) of hard substrate at South Island, and 41% (±3.0 S.E.) and 40% (±0.9 S.E.) of hard substrate at

Lizard Head and Bird Islet respectively. At sheltered sites, cover of scleractinian corals was highest at Osprey Islet (32% ±3.5 S.E. of hard substrate) and Vickies (32% ±4.5 S.E. of hard substrate), and lowest at Corner Beach (29% ±5.6 S.E. of hard substrate). Variation in coral community composition was highly significant among habitats (MANOVA, Pillai's trace=14.1, df = 9,16, *P*<0.001) and sites (MANOVA, Pillai's trace=2.6, df = 36,76, *P*<0.001). Exposed sites were characterised by a high abundance of tabular and digitate *Acropora* corals, while sheltered sites were dominated by soft corals (family Alcyonacea) (Fig. 2.1).

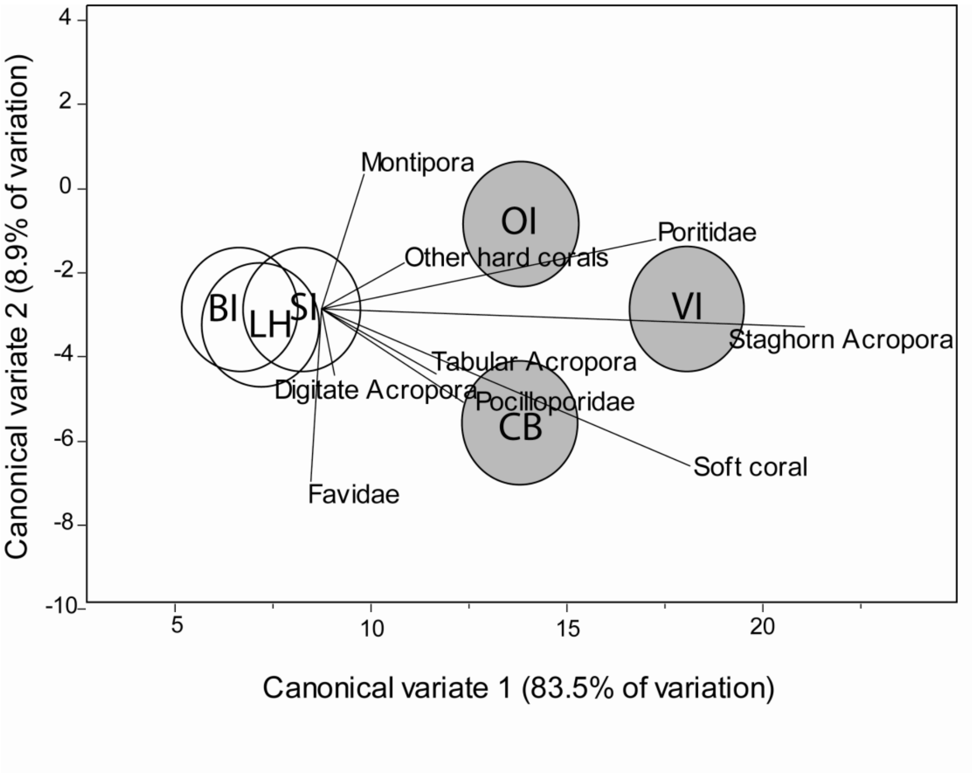

Figure 2.1 Canonical discriminant analysis showing coral assemblages at three exposed front reef sites (BI: Bird Islet; LH: Lizard Head; SI: South Island) and three sheltered back reef sites (OI: Osprey Islet; CB: Corner Beach; VI: Vickies) around Lizard Island, Great Barrier Reef. Circles plotted represent 95% confidence intervals around the group centriod for each site (unfilled circles: exposed sites; filled circles: sheltered sites). Vectors are structural co-efficients indicating the relative abundance of the major coral taxa among the six sites.

2.4.2 Dietary composition

Chaetodon citrinellus fed predominantly on hard corals at each site (taking between 39 to 75% of all bites from hard corals), but also supplemented its diet with small amounts of soft corals, other non-coral macro invertebrates and bites on reef substrates (Table 2.1). Consumption of hard corals was highest at exposed sites where hard corals were more abundant. Both *C. lunulatus* and *C. trifascialis* fed almost exclusively on hard corals at all sites. *Chaetodon lunulatus* took between 96 to 99% of all bites from hard corals, while *C. trifascialis* took 100% of all bites from hard corals at all sites except Lizard Head (Table 2.1). Dietary composition varied significantly (MANOVA, *P*<0.05) for all three species between habitats and sites (Table 2.2).

Table 2.1 Dietary composition of *Chaetodon citrinellus, C. lunulatus* and *C. trifascialis* at 3 exposed front reef sites (Bird Islet, Lizard Head, South Island) and 3 sheltered back reef sites (Corner Beach, Osprey Islet, Vickies) at Lizard Island, Great Barrier Reef.

Species	Site	Hard corals (%)	Soft corals (%)	Other macro invertebrates (%)	Imperceptible items[1] (%)	Total number hard coral species consumed
C. citrinellus	Bird Islet	75.3	1.1	2.4	21.1	23
	Lizard Head	55.9	6.8	3.1	34.2	21
	South Island	74.9	1.3	2.5	21.3	29
	Corner Beach	39.1	3.0	2.5	55.5	18
	Osprey Islet	49.6	0.0	0.0	50.4	12
	Vickies	59.5	11.8	1.6	27.1	28
C. lunulatus	Bird Islet	98.6	0.4	0.5	0.5	34
	Lizard Head	99.6	0.0	0.0	0.4	25
	South Island	99.0	0.2	0.0	0.8	27
	Corner Beach	99.2	0.0	0.0	0.8	26
	Osprey Islet	100.0	0.0	0.0	0.0	26
	Vickies	96.2	0.0	3.4	0.4	26
C. trifascialis	Bird Islet	100.0	0.0	0.0	0.0	15
	Lizard Head	99.4	0.0	0.0	0.6	14
	South Island	100.0	0.0	0.0	0.0	17
	Corner Beach	100.0	0.0	0.0	0.0	15
	Osprey Islet	100.0	0.0	0.0	0.0	14
	Vickies	100.0	0.0	0.0	0.0	15

[1] Refers to bites taken on reef pavement, sand and rubble. It was assumed that these bites were targeting small motile invertebrates such as polychaetes and crustaceans.

Table 2.2 MANOVA results for dietary composition of *Chaetodon citrinellus, C. lunulatus* and *C. trifascialis* among habitats (exposed front reef and sheltered back reef) and sites (Bird Islet, Lizard Head, South Island, Corner Beach, Osprey Islet, Vickies) nested within habitats at Lizard Island, Great Barrier Reef.

Species	Source	Pillai's trace	d.f.	*P*
C. citrinellus	Habitat	4.29	15, 100	<0.001
	Site (Habitat)	1.52	60, 412	<0.05
C. lunulatus	Habitat	5.52	15, 100	<0.001
	Site (Habitat)	2.82	60, 412	<0.001
C. trifascialis	Habitat	5.77	9, 106	<0.001
	Site (Habitat)	1.60	36, 436	<0.02

Based on significant differences in the proportional consumption versus availability of different coral prey, all three species showed highly significant dietary selectivity at each site (P<0.001 for all species, Table 2.3). Patterns of dietary selectivity indicated by the Chi square log-likelihood statistic (X_{L2}^2) were different to patterns of dietary evenness indicated by the Shannon Wiener index and levels of specialisation estimated using a count of total number of prey categories consumed. *Chaetodon trifascialis* was the most selective, closely followed by *C. lunulatus,* while *C. citrinellus* was the least selective. Selectivity was higher at sheltered sites compared to exposed sites for all three species (Fig. 2.2).

Chaetodon citrinellus showed a high degree of dietary versatility, consuming a number of different hard coral taxa at each site (Table 2.1) and resource selection functions indicated that *C. citrinellus* was a fairly generalised feeder (Table 2.3). Significant selectivity or avoidance was only shown for a few prey categories and most categories were consumed in proportion to their availability (Table 2.3).

Although overall dietary selectivity (X_{L2}^2) was high for *C. lunulatus* at each site and comparable to that of *C. trifascialis* (Fig. 2.2), resource selection functions for individual coral taxa indicated that *C. lunulatus* was a much more generalised feeder (Table 2.3). *Chaetodon lunulatus* consumed a large number (between 25 and 34) of different hard coral taxa at each site (Table 2.1) and only showed avoidance of non hard coral prey categories (Table 2.3). At exposed sites *C. lunulatus* exhibited significant feeding selectivity for *Acropora* corals and *Pocillopora* corals, but fed on most hard coral prey categories in proportion to their availability across both exposed and sheltered sites.

In contrast, *C. trifascialis* had much more specialised feeding preferences, consuming 17 or fewer different hard coral taxa at each site (Table 2.1) and never using a large number of hard coral taxa across all sites, regardless of their availability (Table 2.3). *Chaetodon trifascialis* only fed on corals from three genera – *Acropora, Pocillopora* and *Montipora* – and only showed selectivity for *Acropora* corals (Table 2.3), taking more than 90% of all bites from *Acropora* corals at each site. Particularly strong selectivity was exhibited for *Acropora hyacinthus,* with *C. trifascialis* taking between 45 and 78% of all bites from this species at each site.

All three species showed significant among-individual dietary variation at each site (*P*<0.001, Monte Carlo simulations). Both *C. citrinellus* and *C. lunulatus* showed high levels of among individual dietary variation across all sites (*E* >0.5, Individual niche overlap network), while *C. trifascialis* showed some among individual dietary variation at sheltered sites and low levels of among individual dietary variation at exposed sites (Fig. 2.2).

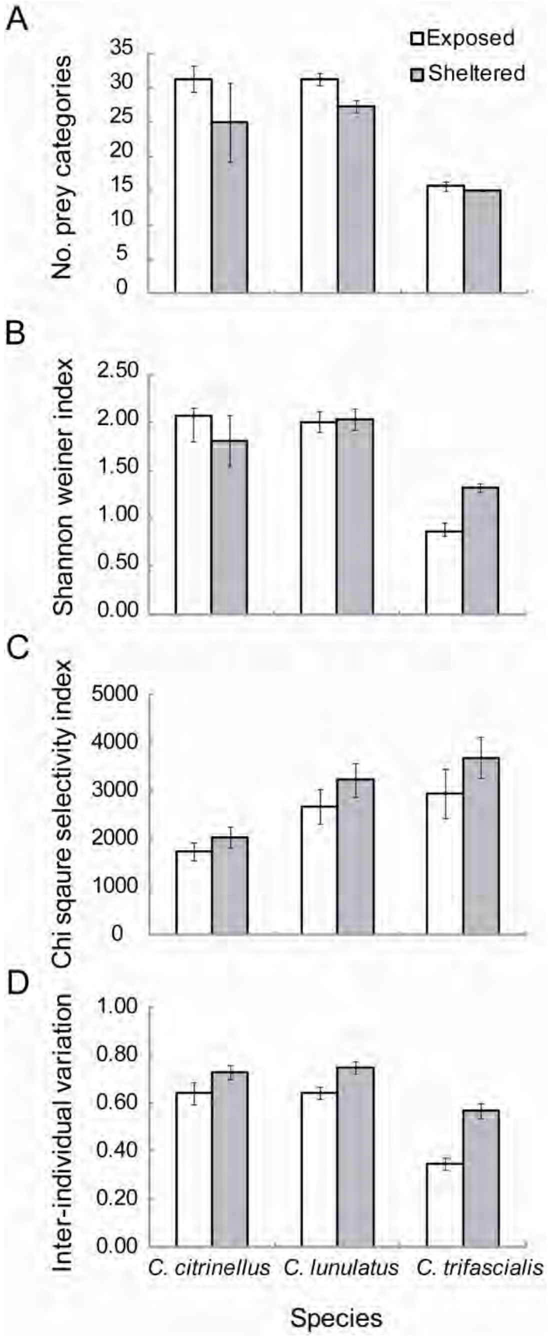

Figure 2.2 Dietary specialisation shown by *Chaetodon citrinellus, C. lunulatus* and *C. trifascialis* across 3 exposed front reef sites (Bird Islet, Lizard Head, South Island) and three sheltered back reef sites (Corner Beach, Osprey Islet, Vickies) at Lizard Island, Great Barrier Reef. Dietary specialisation is calculated using (A) total number of prey categories consumed; (B) Shannon Wiener index; (C) Chi square log likelihood statistic, X_{L2}^{2}; and (D) among-individual dietary variation, *E*. Data are means for each habitat type ± 1SE.

Table 2.3 Dietary selectivity of *Chaetodon citrinellus, C. lunulatus* and *C. trifascialis* at three exposed front reef sites (Bird Islet, Lizard Head, South Island) and 3 sheltered back reef sites (Corner Beach, Osprey Islet and Vickies) at Lizard Island, Great Barrier Reef for 15 major prey categories. +: category used significantly more than expected (selected); =: category used in proportion to availability; -: category used significantly less than expected (avoided); 0: category unused (strongly avoided); NA: category not available.

	X_{L2}^2	d.f.	*P*	*Acropora hyacinthus*	*A. muricata*	*A. nasuta*	Staghorn *Acropora*	Other *Acropora*	*Pocillopora damicornis*	Other *Pocilloporidae*	*Montipora sp.*	*Porites sp.*	*Favidae*	*Isopora sp.*	Other hard corals	Soft coral	Reef substrate[a]	Other
C. citrinellus																		
Exposed																		
Bird Islet	2103	220	<0.001	=	0	0	=	+	=	+	=	=	=	=	=	-	-	=
Lizard Head	1520	220	<0.001	=	NA	=	NA	+	=	+	=	=	-	=	=	=	=	=
South Island	1557	240	<0.001	=	0	=	=	=	=	=	=	-	=	=	=	-	-	=
Sheltered																		
Corner Beach	1602	180	<0.001	=	=	-	=	+	=	NA	=	=	0	NA	0	-	+	=
Osprey Islet	2227	180	<0.001	=	=	=	0	=	+	NA	=	-	=	NA	0	0	+	0
Vickies	2261	280	<0.001	=	=	=	=	=	=	=	=	=	=	=	=	-	=	=
C. lunulatus																		
Exposed																		
Bird Islet	2731	220	<0.001	+	0	=	=	+	+	=	=	=	+	=	=	-	-	-
Lizard Head	3390	180	<0.001	=	NA	=	NA	+	=	+	=	=	=	=	=	0	-	0
South Island	1869	200	<0.001	+	0	=	=	+	=	+	=	=	=	=	=	-	-	0
Sheltered																		
Corner Beach	3928	180	<0.001	=	+	=	=	+	=	NA	=	=	=	NA	=	0	-	0
Osprey Islet	2950	180	<0.001	=	=	=	=	=	=	NA	=	=	=	NA	=	0	0	0
Vickies	2782	240	<0.001	=	=	=	=	=	=	=	=	+	=	=	=	0	-	=
C. trifascialis																		
Exposed																		
Bird Islet	3693	80	<0.001	+	0	0	=	=	=	=	0	0	0	0	0	0	0	0
Lizard Head	3146	100	<0.001	+	NA	=	NA	=	-	=	0	0	0	0	0	0	-	0
South Island	1969	100	<0.001	+	0	=	=	+	=	=	0	0	0	0	0	0	0	0
Sheltered																		
Corner Beach	3810	80	<0.001	+	=	-	=	=	-	NA	NA	0	0	NA	0	0	0	0
Osprey Islet	4357	120	<0.001	+	=	=	=	+	=	NA	=	0	0	NA	0	0	0	0
Vickies	2879	100	<0.001	+	=	=	=	=	=	0	0	0	0	0	0	0	0	0

[a] Includes reef pavement, sand and rubble. It was assumed that bites on reef substrates were targeting small motile invertebrates such as polychaetes and crustaceans.

2.5 DISCUSSION

The strengths and weaknesses of different specialisation indices have been reviewed several times, and most recently by DeVictor et al. (2010), but this is the first study to directly compare the performance of such indices using the same dataset. Similarly, the link between specialisation and vulnerability has been explored in depth (Colles et al. 2009), but there has been little consideration of how the measurement of specialisation may affect estimates of vulnerability. This is the first study to investigate the utility of different specialisation indices within the context of predicting vulnerability to environmental change. The level of dietary specialisation estimated for all three butterflyfish species varied when different specialisation indices were used, indicating that the choice of index can have a considerable impact upon estimates of the degree of specialisation. These impacts are likely to be less important for generalist species. For example patterns of dietary specialisation for *C. citrinellus*, the most generalist of the three study species, were similar between all four specialisation indices. But for species that are neither true generalists nor extreme specialists, indices based solely on patterns on resource use (e.g. Shannon-Wiener index) may give somewhat different estimates of specialisation to indices which incorporate resource availability (e.g. Chi square selectivity index). *Chaetodon lunulatus* feeds almost exclusively on hard corals and therefore could be considered to have a specialised diet, yet it feeds across a broad range of hard coral species and is considered more of a generalist feeder within the butterflyfishes that are obligate corallivores (Pratchett 2005, 2007a). Specialisation levels estimated by the Shannon Wiener index for *C. lunulatus* were similar to those of the generalist *C. citrinellus*, while specialisation levels estimated by the Chi square index (which considers resource availability) were more similar to those of the specialist *C. trifascialis*.

The importance of incorporating resource availability into specialisation estimates has long been recognised by ecologists (Hurlbert 1978; Petraitis 1979). Although the use of indices which only evaluate patterns of resource use is no longer as widespread as it once was (see MacNally 1995), many current studies continue to use these types of indices to measure specialisation (e.g. Kotze and O'Hara 2003; Julliard et al. 2004; Munday 2004; Charrette et al. 2006; Christensen and Kleindorfer 2009). Specialisation indices which ignore resource availability may be highly misleading as a species that uses only a few resources will be classified as a specialist, even if those resources are highly abundant (Hurlbert 1978). In contrast, when specialisation indices incorporating measures of resource availability are used, a species will only be classified as a specialist if resources are used disproportionately to their availability. Some may believe this distinction is a somewhat semantic issue and may argue that regardless of whether or not resource availability is considered, any type of specialisation index will always classify extreme specialists as such. However, resource use may actually reflect patterns of resource availability rather than specialisation per se. Specialisation indices that do not consider resource availability will be unable to distinguish between a species using a few commonly available resources and one that uses a narrow subset of available resources. Both types of species will be classified as extreme specialists, even though the first species may actually have a generalised ecology and utilise a large number of resources in cases where it is not limited by resource availability (e.g. Pampas fox, Varela et al. 2008). While any species using resources which are threatened will be at risk of extinction, in the context of predicting vulnerability, a species that uses resources disproportionately to their availability is much more likely to be vulnerable to changes in the abundance of those resources than a species that uses a few commonly available resources. Therefore, the use of specialisation indices that incorporate measures of resource availability is preferable if specialisation is used as a proxy for vulnerability.

Consideration of several locations or time periods is also essential when quantifying ecological specialisation in order to understand responses to changes in resource availability (Devictor et al. 2010). The degree of specialisation estimated for all three species in this study varied between individual sites and habitats. Consideration of specialisation patterns at only a single site (e.g. Pratchett 2007a) may have resulted in specialisation estimates that were not reflective of the true versatility of each species. It is possible that species classified as specialists based on studies in a single location may only be functioning as specialists on a local scale, and across their entire geographic range these species may in fact have generalised ecologies (Fox and Morrow 1981). For example, on the south coast of Japan two species of decorator crab (*Micippa platipes* and *Tiarinia cornigera*) were highly selective in their preferences for algae, but on the north coast both species showed no selectivity (Hultgren et al. 2006). Consideration of temporal and spatial variation in specialisation is crucial in systems where resources can become depleted (e.g. Pratchett et al. 2006) or where the availability of resources may vary seasonally (e.g. Varela et al. 2008) in order to accurately determine specialisation and predict vulnerability.

Understanding how ecological specialisation varies between individuals within a population may also be important in predicting how a species will respond to changes in resource availability. A population of individuals each specialising on a different resource may still look like a “generalist” species by some measures, but such a population may respond differently to resource depletion than another population composed of individual generalists. Theory suggests that populations of individual specialists may be more stable and open to future evolutionary diversification (Kendall and Fox 2002; Bolnick et al. 2003; Kendall and Fox 2003). Furthermore, niche variation within a population may help to buffer against loss of particular habitats or resources and provide genetic variation needed to adapt to changing environments (Durell 2000; Bolnick et al. 2003). In cases where estimation of resource availability is not possible, measurement of among-individual variation in resource use may provide additional information about ecological specialisation and vulnerability to that gained from the use of traditional niche breadth measures. As highly specialised species are likely to have low levels of among-individual variation due to their narrow niche breadth, use of among-individual specialisation indices may be most informative when comparing vulnerability of species with more generalised ecologies.

Resource selection functions provide fine scale information on ecological specialisation, enabling greater insights into the potential response of species to changes in resource availability, and therefore vulnerability to future environmental changes, than can be gained from overall estimates of specialisation. Although overall levels of dietary specialisation estimated by the Chi square selectivity index were similar for *C. lunulatus* and *C. trifascialis*, resource selection functions indicated that the diet of *C. trifascialis* was much more specialised and its feeding preferences were more conserved, both in the terms of the number of resources it showed selectivity for and in the spatial variation of its selectivity. Consequently, *C. trifascialis* is likely to be highly vulnerable to changes in resource availability, particularly to changes in the abundance of the *Acropora* corals that it preferentially feeds on (Pratchett 2005, 2007a). In contrast, *C. lunulatus* utilised a large number of resources at each site and selectivity of specific dietary items varied between sites which also varied in their resource availability. These findings suggest that even though *C. lunulatus* has a reasonably specialised diet, it is likely to be fairly resilient to changes in resource availability. Such responses to changes in resource availability have already been reported for both species. In French Polynesia, the abundance of *C. trifascialis* declined by almost 100% following declines in the abundance of its preferred *Acropora* corals (Berumen and Pratchett 2006b), while on the Great Barrier Reef, *C. lunulatus* has been shown to alter its diet in response to a loss of some coral taxa (Pratchett et al. 2004). These responses highlight the predictive value of resource selection functions and provide justification for their use in the identification of key resources which may be critical to a species' persistence.

In addition to current threats, effective conservation strategies need to consider future threats to habitats and the potential resultant habitat composition. For coral reefs, the frequency of mass bleaching events, disease and mortality are predicted to increase as a result of anthropogenic climate change (Hoegh-Guldberg et al. 2007). As the dietary preferences of *C. trifascialis* are highly conserved - the same coral prey was selected at each site regardless of availability – this species is likely to have a very low capacity to respond to changes in the availability of coral prey. Acroporid corals, including *Acropora hyacinthus,* the preferred prey of *C. trifascialis*, are highly susceptible to bleaching (Marshall and Baird 2000), and the abundance of these corals is likely to decline in the future with increased frequency of bleaching events. Consequently, the vulnerability of *C. trifascialis* to the impacts of climate change on coral reefs is only likely to increase and this species should be assigned a high extinction risk based on its level of dietary specialisation.

While the example presented here comes from a single family of coral reef fishes, butterflyfishes are useful models for understanding more general trends and these findings reflect ecological principles that transcend the system. Calculating the four specialisation indices from the same dataset removes any variation that might have resulted from simply comparing the findings of several independent studies. Consequently, the differences in the levels of specialisation estimated by each of the four indices most likely reflect actual differences and not sampling effects. The three species included in this analysis displayed a range of specialisation levels, from generalist to extreme specialist, and provide an indication of how these indices are likely to perform across species with varying levels of specialisation.

Moreover, the comparison of two differing habitats illustrates how estimates of specialisation may be affected by temporal or spatial differences in resource availability.

2.5.1 Conclusions

This is the first study to compare the effects of using different indices on estimates of ecological specialisation and predictions of vulnerability. Although decision makers are often limited in their ability to conduct extensive assessments, these results demonstrate that vulnerability assessments based on a single specialisation index may be misleading and the best estimates of specialisation will be provided by indices which incorporate resource availability measures. Furthermore, the use of resource selection functions in addition to overall specialisation indices will provide a more accurate picture of ecological versatility and therefore vulnerability to future environmental changes. For example, the highly conserved dietary preferences and high specialisation values estimated for *C. trifascialis* in this study suggest that this species is likely to be highly vulnerable to the impacts of climate-induced coral loss on reefs.

Chapter 3: Geographic variation in resource use by specialist versus generalist butterflyfishes[‡]*.*

3.1 ABSTRACT

Localised patterns of resource use can be constrained by multiple factors. Comparison of resource use at multiple locations with differing resource availability can allow fundamental specialists to be distinguished from species that simply feed predominantly on prey types that are locally abundant. This study investigates geographic variation in the feeding ecology of coral-feeding butterflyfishes to examine whether patterns of resource use and levels of dietary specialisation vary among distinct locations, corresponding with changes in resource availability. The specific aims were to investigate whether the dietary niche breadth of four butterflyfishes varied among five geographically separated locations and assess whether each species utilised similar resources in each location. Resource availability and dietary composition of four butterflyfishes were quantified at three sites across each of five geographic locations throughout the Pacific. Niche breadth, niche overlap, and resource selection functions were calculated for each species at each site and compared among locations. Availability of dietary resources varied significantly among locations and sites. *Chaetodon vagabundus, C. citrinellus* and *C. lunulatus* had low levels of dietary specialisation and used different resources in each location. *Chaetodon trifascialis* had high levels of dietary specialisation and used the same few resources in each location. These results indicate that relative levels of dietary specialisation among different butterflyfishes do hold at larger spatial scales, however, geographical variation in the dietary composition of all butterflyfishes indicates that prey availability has a fundamental influence on dietary composition. Highly

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specialised species such as *C. trifascialis* will be highly vulnerable to coral loss as they appear to be largely inflexible in their dietary composition. However, the increased feeding plasticity observed here for *C. trifascialis* suggests this species may have a greater capacity to respond to coral loss than previously assumed.

3.2 INTRODUCTION

Many studies have shown that the range of resources used by an organism can be considerably smaller than the range of resources they are physiologically capable of using (Colwell and Fuentes 1975; Fox and Morrow 1981). Localised patterns of resource use can be constrained by a number of factors. Access to resources may be restricted by interactions with other organisms such as competition and predation (Colwell and Fuentes 1975). Local patterns of resource use can be also limited by resource availability at these local scales. A species may use a narrow range of resources because they are highly abundant and widely available, or because there are no alternative resources available (Lawton et al. In press-a). Thus, on a local scale, some species may appear to be functioning as specialists, but across their entire geographic range they have generalised ecologies (Fox and Morrow 1981). Despite recognition that niche breadth may vary with spatial scale (Brown 1984; Gaston et al. 1997), species are often considered to be equally specialised across all spatial scales (Devictor et al. 2010). Very few studies have compared local and regional patterns of specialisation (e.g. Hughes 2000; Krasnov et al. 2008) and only a small number have specifically compared spatial variation in resource use to variation in resource availability (e.g. Kuussaari et al. 2000; Stachowicz and Hay 2000; Flesch and Steidl 2010). This incomplete understanding of species' global ecology may result in inaccurate characterisations of vulnerability and extinction risk and hinder conservation efforts.

Ideally, a species' niche breadth should be determined experimentally by measuring their performance separately across several resources, or along a controlled resource gradient (Devictor et al. 2010). Unfortunately, these types of experiments are difficult to conduct for many species, so an alternative approach is to record patterns of resource use across multiple locations with differing resource availability and compare local and regional patterns of specialisation. This can allow species that are fundamental specialists to be distinguished from those that are local specialists as a result of constraining factors (Hughes 2000). A fundamental specialist will use the same narrow range of resources across multiple locations, regardless of their availability. For example, the parasitic flea *Tarsopsylla octodicemdentata* almost exclusively exploits the red squirrel *Sciurus vulgaris* across its entire geographic range (Krasnov et al. 2008). In contrast, a local specialist will use a narrow range of resources on a local scale, but the particular resources that are used will vary regionally and/or with resource availability. For example, the checkerspot butterfly (*Euphydryas editha*) uses a single host plant genus locally, but the particular host plant species that is used varies regionally (Hughes 2000).

This study compares the dietary niche breadth of coral-feeding butterflyfishes (Family Chaetodontidae) across multiple geographic locations with differing resource availability. Butterflyfishes provide an ideal model in which to investigate local and regional patterns of dietary specialisation. Species within this diverse family vary significantly in their dietary preferences and level of dietary specialisation (Reese 1981; Harmelin-Vivien and Bouchon-Navaro 1983; Pratchett 2005, 2007a). Some species, such as *Chaetodon trifascialis,* only feed on a small number of hard coral species; while other species, such as *C. citrinellus*, feed across a broad range of dietary items including hard corals, soft corals and other reef macro-invertebrates (Pratchett 2005). There is also anecdotal evidence that dietary composition varies geographically for some species. For example, based on stomach content analysis hard corals account for over 82% of the diet of *C. vagabundus* at locations in the Indian Ocean

(Harmelin-Vivien 1989), but in the Pacific Ocean they comprise less than 20% of its diet (Harmelin-Vivien 1989; Pratchett 2005). Importantly, the feeding behaviour of butterflyfishes is readily observable in the field and the availability of dietary resources can be directly measured at the same time and place (Berumen et al. 2005; Lawton et al. In press-a). These characters allow patterns of dietary preference and specialisation to be established in a group of closely related species and determine whether species are fundamentally specialised or simply feeding predominantly on prey types that are locally abundant.

Coral-feeding butterflyfishes have been identified as one of the most vulnerable groups of reef fishes to the combined effects of ongoing global coral loss and habitat degradation on reefs (Wilson et al. 2006; Pratchett et al. 2008b). Characterising their local and regional patterns of dietary specialisation has important implications for understanding how butterflyfishes are being impacted by climate change (Wilson et al. 2010). Specialist coral feeders, such as *C. trifascialis*, are thought to be most vulnerable as the *Acropora* corals they preferentially feed on are highly sensitive to climate induced coral bleaching (Pratchett et al. 2008b). The resilience of coral-feeding butterflyfishes to any future coral loss will be determined by their ability to use alternative resources if the abundance of preferred corals declines (Pratchett et al. 2004); however, this is currently unknown for most specialist coral-feeders. Although in-situ feeding observations have provided detailed estimates of dietary composition and specialisation (at high taxonomic resolution) only a small number have compared resource use to resource availability and these studies have been confined to a few isolated locations (e.g. Johnston Atoll: Irons 1989; Hawaiian Islands: Cox 1994; Great Barrier Reef: Berumen et al. 2005; Pratchett 2007a; Seychelles: Graham 2007;). As yet, there have been no systematic comparisons of resource availability and butterflyfish dietary specialisation across multiple geographic locations using the same methodology. Consequently, the degree that particular butterflyfish species are truly specialised or generalised is unknown, and therefore their vulnerability to global climate change is not fully appreciated.

The objective of this study is to investigate geographic variation in the feeding ecology of coral-feeding butterflyfishes and examine whether patterns of resource use and levels of dietary specialisation vary among distinct locations, corresponding with changes in resource availability. The specific aims were to (i) investigate whether the dietary niche breadth of four butterflyfishes varies among five geographically separated locations; and (ii) assess whether each species utilises similar resources in each location. If dietary specialisation is high but resource use varies among locations, then local resource use is likely to be constrained. In contrast, if dietary specialisation is high and the same resources are used in each location, then patterns of resource use most likely reflect fundamental specialisation rather than local constraints.

3.3 METHODS

3.3.1 Study sites

Feeding observations were conducted at five geographically separated locations throughout the Pacific - Lizard Island, Northern Great Barrier Reef; Heron Island, Southern Great Barrier Reef; Kimbe Bay, Papua New Guinea; Noumea, New Caledonia and Moorea, French Polynesia (Fig 3.1). These five locations are situated along known diversity gradients, with pairwise distances between 1100km and 6600km apart. Species diversity of both corals and reef fish is highest in a region which includes Papua New Guinea, known as the Indo-Australian Archipelago (IAA) and declines with increasing distance from this region, being lowest in the eastern Pacific (Bellwood and Hughes 2001). Among scleractinian corals, species richness in Papua New Guinea is approximately double that of French Polynesia (Karlson et al. 2004). At each location, three distinct sites were chosen for feeding observations. Sites were standardised for habitat type and depth. At each site sampling was conducted along the exposed to semi-exposed reef crest to eliminate potential effects of variable exposure (e.g. Berumen et al. 2005).

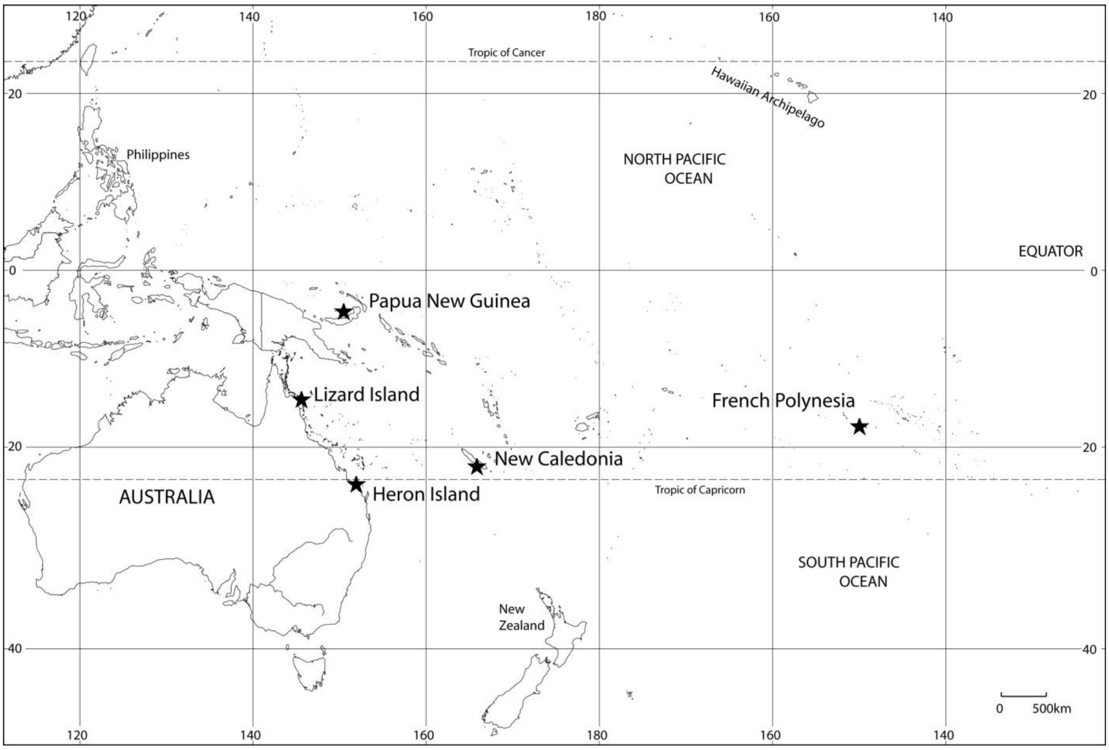

Figure 3.1 Map of the five locations sampled in this study. Abbreviations used throughout this chapter are indicated for each location. Heron Island, Great Barrier Reef (HI); Lizard Island, Great Barrier Reef (LI); Kimbe Bay, Papua New Guinea (PNG); Noumea, New Caledonia (NC); and Moorea, French Polynesia (FP).

3.3.2 Resource availability

Variation in the availability of coral prey was assessed using 50m point intercept transects. At each site, five replicate transects were laid consecutively, following the contour of the reef crest, in the same area where feeding observations took place. For each transect, the substrate directly beneath 200 uniform sampling points (spaced every 25cm) was recorded to species level for corals, and to broad categories for all other substrate types (e.g. non-coral substrate, macroalgae). Variation in total coral cover among locations and sites (nested within locations) was assessed using a nested ANOVA. Variation in proportional cover of dietary resources (grouped into 12 resource categories, listed in Table 3.1) among locations and sites (nested within locations) was compared using a nested multivariate analysis of variance (MANOVA). Availability of individual resource categories was compared among locations and sites (nested within locations) using univariate analyses of variance. Alpha values were adjusted for multiple tests using a Bonferroni correction (Miller 1981). Data were arc-sin transformed to satisfy assumptions of homogeneity and normality. Residual plots, homogeneity tests and sphericity tests were used to ensure assumptions were met. Pillai's trace statistic was used to determine the significance of MANOVA results. All statistical analyses were conducted using SPSS Statistics 18.0.

3.3.3 Feeding observations

Feeding observations were conducted for four common and widespread species of butterflyfishes - *Chaetodon vagabundus, C. citrinellus, C. lunulatus* and *C. trifascialis*. All four species have been documented to consume hard (scleractinian) corals as part of their diet in at least some locations throughout their geographic range (Cole et al. 2008). Both *C. vagabundus* and *C. citrinellus* have been previously reported as facultative corallivores – consuming hard corals as well as other macro-invertebrates and soft corals; while *C. lunulatus* and *C. trifascialis* are both reported as obligate corallivores, feeding almost exclusively on hard corals (Pratchett 2005; Cole et al. 2008). Dietary composition was determined for each species from field observations of feeding behaviour at each site. Individual adult butterflyfishes were randomly selected and followed at a distance of 2 - 5 metres for a 3-minute period. Every effort was made to ensure individual fish were not observed more than once. The total number of bites taken from each species of coral, other non-coral macro-invertebrates, and non-coral substrates during each observation was recorded, following Pratchett (2005). At least twenty observations for each species were conducted throughout the day at each site, giving a total of at least 60 observations at each location for each species.

3.3.4 Dietary specialisation and selectivity

Due to the large geographic scale of this study, the specific coral species present in each location varied. Therefore, all dietary resources were grouped into 12 categories (listed in Table 3.1) to enable comparisons of dietary specialisation and selectivity to be made between locations. Variation in overall dietary composition among locations and sites (nested within locations) for each species was analysed using MANOVAs, which simultaneously compared the proportion of bites taken by each species on each of the 12 resource categories. Variation in proportional composition of individual resource categories was compared among locations and sites (nested within locations) for each species using univariate analyses of variance. Alpha values were adjusted for multiple tests using a Bonferroni correction (Miller 1981). Residual plots, homogeneity tests and sphericity tests were used to ensure assumptions were met. Pillai's trace statistic was used to determine the significance of results.

Smith's measure of niche breadth (*FT)* was used to determine the relative degree of dietary specialisation for each species across the 12 resource categories at each site (Smith 1982). This measure takes into account resource availability and is less sensitive to the use of rare resources compared to other niche breadth measures (Krebs 1999). *FT* is a standardised measure, ranging from 0 (most specialised) to 1 (least specialised), therefore allowing comparison of the level of specialisation between sites and locations for each species. Niche breadth was compared among locations using separate one way ANOVAs for each species. Data were arcsin transformed and residual plots and homogeneity tests were used to ensure ANOVA assumptions were met.

Niche overlap between locations was measured for each species using Morista's similarity index. This index reduces bias due to small sample sizes and is least affected by the number of resource categories compared to other niche overlap measures (Krebs 1999). Morista's similarity index (C_λ) ranges from 0 (no similarity) to 1 (complete similarity) and was calculated following Krebs (1999). The total number of bites taken by each species on each of the 12 resource categories was pooled across the three sites for each location and these pooled values were used in calculations.

Resource selection functions were used to investigate variation in dietary selectivity between locations and determine which resources were used significantly more or less frequently than expected based on their availability. Resource selection functions were calculated for the 12 resource categories for each species at each site following Manly et al.'s (2002) Model Design II, Sampling Protocol A. These functions allow for sampling of resource use at the individual level and resource availability at the population level (Manly et al. 2002). Bonferroni corrected 95% confidence intervals were calculated around each selection function such that the use of a particular prey was deemed to be significantly disproportionate to its availability if the 95% confidence interval did not encompass one (Manly et al. 2002). Selection functions significantly greater than one indicated selection (i.e. resource was consumed significantly more than expected based on availability); selection functions significantly less than one indicated avoidance (i.e. resource was consumed significantly less than expected based on availability).

3.4 RESULTS

3.4.1 Resource availability

Total coral cover was highest at sites in New Caledonia (41% ±4.2 S.E. to 80% ±8.4 S.E.) and Papua New Guinea (48% ±5.2 S.E. to 63% ±3.2 S.E.) and lowest at sites in French Polynesia

(26% ±2.9 S.E. to 37% ±6.1 S.E.). Differences in total coral cover among locations were not significant (nested ANOVA, $F_{4,10}$=3.009, *P*=0.072), however there were significant differences among sites nested within locations (nested ANOVA, $F_{10,60}$=6.888, *P*<0.001). Availability of dietary resources varied significantly among locations (nested MANOVA, Pillai's trace=3.401, df = 48,208, *P*<0.001) and sites nested within locations (nested MANOVA, Pillai's trace=3.775, df = 120,580, *P*<0.001). The Heron Island coral assemblage was dominated by *Acropora* corals, with *Acropora hyacinthus,* 'Staghorn *Acropora*' and 'Other *Acropora*' resource categories comprising more than 55% of the total coral cover at this location (Fig 3.2). Lizard Island was the only location where soft corals were available in any meaningful quantity (10.5% ±0.6 S.E. cover compared to <1% cover in all other locations (Fig 3.2). Cover of *A. hyacinthus* was highest in Papua New Guinea (14.3% ±1.0 S.E., all other locations <10%), while New Caledonia sites had a much higher cover of Staghorn *Acropora* (25.9% ±0.8 S.E.) compared to all other locations (<5%) (Fig 3.2). French Polynesia sites were dominated by *Porites sp.* and *Montipora sp.* – these two resource categories accounting for >80% of the total coral cover in this location (Fig 3.2). The availability of all individual resource categories except 'Other hard corals' varied significantly among locations (Table 3.1). Post hoc tests indicated that percentage cover of *A. hyacinthus* was significantly higher in Papua New Guinea compared to Lizard Island, Heron Island and French Polynesia, cover of *A. hyacinthus* was also significantly higher in New Caledonia compared to French Polynesia (Tukey's HSD *P*<0.01). Percentage cover of 'Staghorn *Acropora'* was significantly higher in New Caledonia compared to all other locations (Tukey's HSD *P*<0.001), while percentage cover of 'Other *Acropora*' was significantly lower in French Polynesia and higher at Lizard Island, Heron Island and New Caledonia relative to all other locations (Tukey's HSD *P*<0.01). Lizard Island and Papua New Guinea had significantly higher cover of *Pocillopora sp.* compared to all other locations (Tukey's HSD *P*<0.001). Percentage cover of *Porites sp.* was significantly lower in Lizard Island, Heron Island and New Caledonia compared to Papua New Guinea and French Polynesia (Tukey's HSD *P*<0.001). Percentage cover of *Montipora sp.* was significantly higher in French Polynesia compared to Lizard Island and Heron Island (Tukey's HSD *P* <0.01), while percentage cover of soft corals was significantly higher at Lizard Island compared to all other locations (Tukey's HSD *P* <0.001). The availability of all individual resource categories except *A. hyacinthus, Montipora sp., Porites sp*, Soft Corals and 'Other' also varied significantly among sites nested within locations (Table 3.1).

Table 3.1 ANOVA results for variation in availability of dietary resource categories between 15 sites nested within five locations. Significant values at Bonferroni corrected α=0.004 are shown in bold.

Source	Variable	SS	d.f.	MS	F	*P*
Location	Non-coral substrate	1.199	4	0.300	31.756	**<0.001**
	Soft coral	0.128	4	0.032	98.718	**<0.001**
	Acropora hyacinthus	0.169	4	0.042	9.808	**<0.001**
	Staghorn *Acropora*	0.786	4	0.196	22.441	**<0.001**
	Other *Acropora*	0.311	4	0.078	33.983	**<0.001**
	Pocillopora sp.	0.051	4	0.013	51.402	**<0.001**
	Montipora sp.	0.026	4	0.006	5.680	**0.001**
	Porites sp.	0.383	4	0.096	49.658	**<0.001**
	Favidae	0.022	4	0.005	10.138	**<0.001**
	Isopora sp.	0.103	4	0.026	35.378	**<0.001**
	Other hard corals	0.001	4	0.000	2.213	0.078
	Other	0.012	4	0.003	4.084	0.005
Site(Location)	Non-coral substrate	0.642	10	0.064	6.808	**<0.001**
	Soft coral	0.008	10	0.001	2.320	0.022
	Acropora hyacinthus	0.076	10	0.008	1.762	0.088
	Staghorn *Acropora*	1.060	10	0.106	12.105	**<0.001**
	Other *Acropora*	0.269	10	0.027	11.771	**<0.001**
	Pocillopora sp.	0.031	10	0.003	12.554	**<0.001**
	Montipora sp.	0.095	10	0.010	8.400	**<0.001**
	Porites sp.	0.028	10	0.003	1.443	0.184
	Favidae	0.009	10	0.001	1.715	0.098
	Isopora sp.	0.038	10	0.004	5.206	**<0.001**
	Other hard corals	0.004	10	0.000	3.371	**0.002**
	Other	0.007	10	0.001	.926	0.516

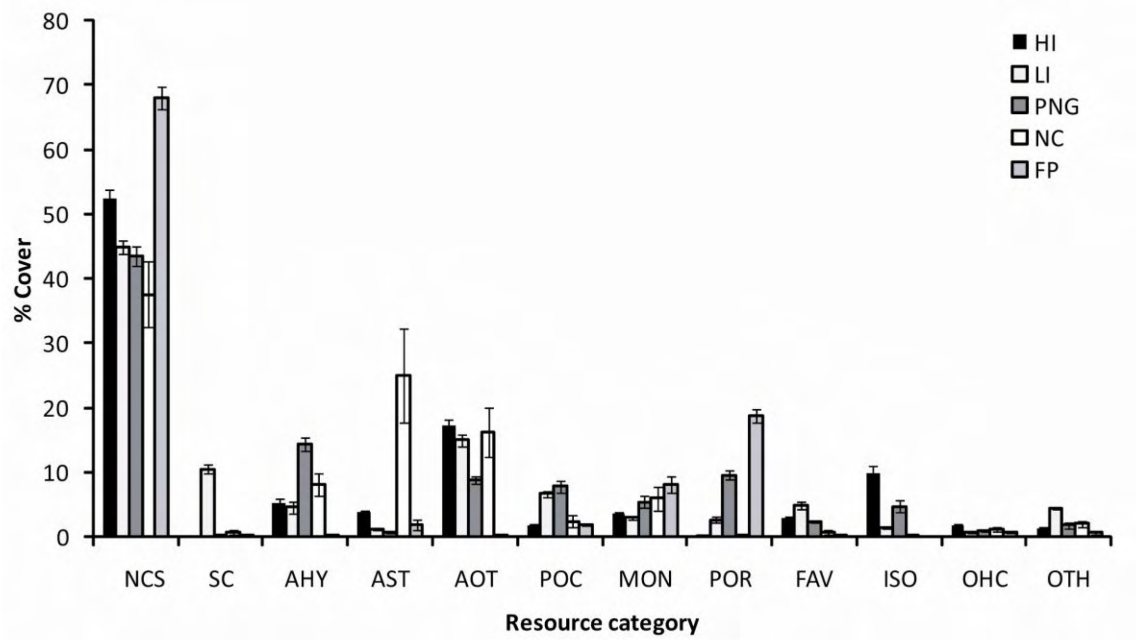

Figure 3.2 Mean (± S.E.) percent cover of twelve resource categories at five locations. Location abbreviations follow Fig 3.1. NCS: non-coral substrate, SC: soft coral, AHY: *Acropora hyacinthus*; AST: Staghorn *Acropora*, AOT: Other *Acropora*, POC: *Pocillopora* sp.; MON: *Montipora* sp.; POR: *Porites* sp.; FAV: Favidae; ISO: *Isopora* sp.; OHC: Other hard corals; OTH: Other.

3.4.2 Dietary composition and specialisation

Chaetodon vagabundus

Chaetodon vagabundus took at least 90% of all bites on non-coral substrates at Lizard Island, Heron Island and French Polynesia, but in New Caledonia and Papua New Guinea this figure dropped to 72.4% (±14 S.E.) and 61.1% (±6 S.E.) respectively (Table 3.2). A large number of bites were taken on hard corals in Papua New Guinea (32.0% ±5.2 S.E.) compared to other locations (less than 15%). Dietary composition varied significantly among locations (nested MANOVA, Pillai's trace=0.633, df = 48,1204 *P*<0.001) and sites nested within locations (nested MANOVA, Pillai's trace=0.681, df = 120,3070 *P*<0.001). Proportional consumption of non-coral substrates, *Pocillopora sp., Montipora sp., Porites sp.* ,Favidae and 'Other' varied significantly among locations and proportional consumption of non-coral substrates, *Montipora sp.* and 'Other' also varied significantly among sites nested within locations (Table 3.2). Dietary niche breadth was relatively high, ranging from 0.66 (±0.14 S.E.) in New Caledonia to 0.92 (±0.03

S.E.) in French Polynesia (Fig 3.3), and did vary not significantly among locations (one way ANOVA, $F_{4,10}$=2.606, *P*=0.10). Niche overlap between locations was also high, ranging from 0.89 to 1.00 (Table 3.3). Resource selections functions indicated that non-coral substrates were positively selected at all but one site, but selectivity for other dietary resources was much more variable among locations (Table 3.4). Different resource categories were selected or avoided in each location and, in some cases, selectivity for particular resource categories differed among sites within a location (e.g. *Porites sp.* in New Caledonia).

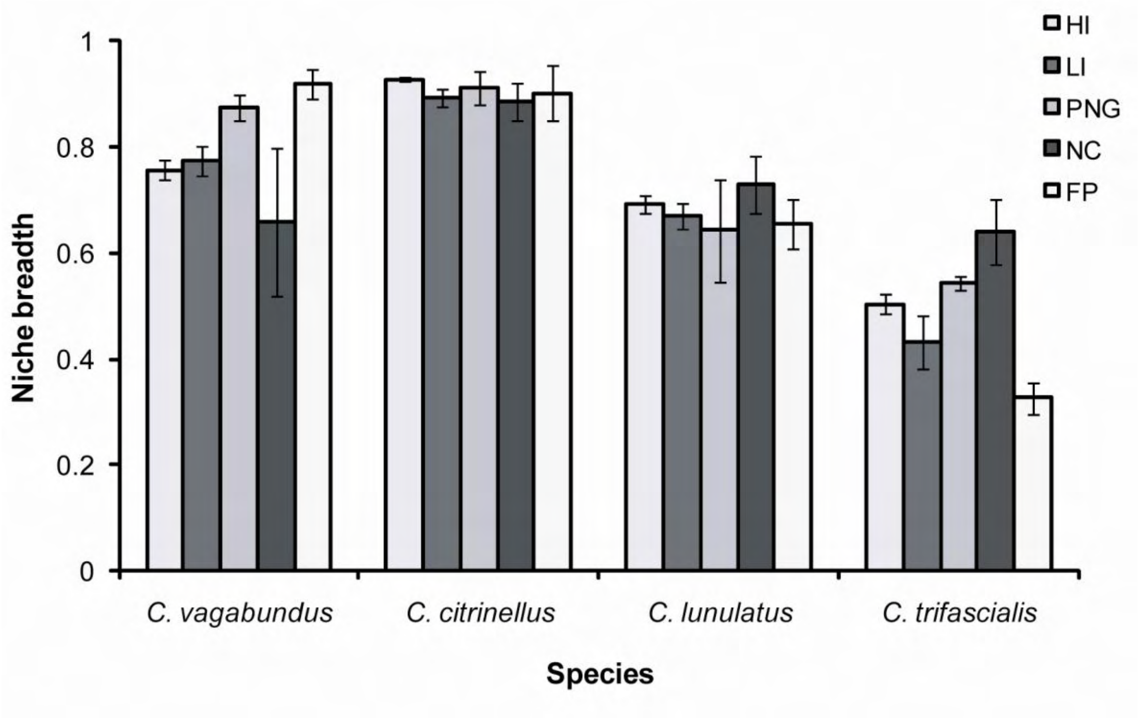

Figure 3.3 Mean (± S.E.) dietary niche breadth (*FT)* of four butterflyfish species at five locations. Location abbreviations follow Fig 3.1.

Table 3.2 Proportional consumption of 12 resource categories by four butterflyfishes across five locations. Data are pooled across *n* replicate feeding observations for each species of butterflyfish. Location abbreviations follow Fig 3.1.

Location	Site	*n*	Non-coral substrate	Soft coral	*A. hyacinthus*	*Staghorn Acropora*	*Other Acropora*	*Pocillopora sp.*	*Montipora sp.*	*Porites sp.*	*Favidae*	*Isopora sp.*	Other hard corals	Other
C. vagabundus														
HI	Blue Pools	22	98.7	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.4	0.4	0.0	0.0
	North Wistari	22	87.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	1.1	11.5
	2nd Point	22	95.8	0.0	0.0	0.0	0.6	0.3	0.0	0.3	0.0	0.0	0.0	2.9
LI	Bird Islet	20	91.4	0.0	0.5	0.3	6.8	0.0	0.0	0.0	1.0	0.0	0.0	0.0
	Lizard Head	31	95.0	1.5	0.5	0.0	0.3	0.8	0.0	0.3	0.8	0.0	0.0	1.0
	South Island	22	93.8	0.0	1.0	0.5	0.0	0.0	0.0	0.0	1.0	0.0	1.0	2.6
PNG	Christines	20	62.5	0.0	1.4	0.0	0.3	2.8	7.6	10.4	3.5	0.0	0.0	11.5
	Lubaluba	23	70.0	0.0	2.0	0.0	0.0	10.8	4.0	8.1	0.3	0.0	2.7	2.0
	Susans	21	50.0	0.0	1.4	0.0	2.5	5.2	22.4	6.0	4.4	0.3	0.3	7.7
NC	Ilot Nge	20	71.3	0.0	2.5	0.3	7.0	9.3	2.5	0.3	0.0	0.0	2.0	4.8
	Recif Senez	20	97.1	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	1.6
	Seche Croissant	20	48.8	0.0	0.0	0.3	0.3	8.2	0.0	1.5	0.9	0.0	3.2	36.8
FP	Motu Ahi	21	94.7	0.0	0.0	0.0	0.0	0.5	3.9	0.5	0.0	0.0	0.0	0.5
	Temea	20	89.8	0.0	0.0	0.0	0.0	2.5	2.5	5.3	0.0	0.0	0.0	0.0
	Tiahura	20	93.3	0.0	0.0	0.0	0.0	0.0	5.0	1.7	0.0	0.0	0.0	0.0
C. citrinellus														
HI	Blue Pools	24	63.0	0.0	6.6	0.9	1.7	3.2	4.6	0.9	4.9	7.2	5.2	2.0
	North Wistari	22	35.0	0.0	3.4	2.1	45.7	3.0	3.9	0.7	0.7	4.6	0.7	0.2
	2nd Point	20	35.9	0.2	5.5	7.6	26.8	8.4	1.1	0.4	0.0	6.5	0.4	7.2
LI	Bird Islet	20	21.1	1.1	16.7	1.8	8.8	31.4	7.5	1.0	4.1	3.7	0.3	2.4
	Lizard Head	20	34.2	6.8	11.4	0.0	15.6	23.5	1.8	0.5	1.4	1.1	0.6	3.1
	South Island	20	21.3	1.3	11.5	0.4	12.9	30.9	5.0	0.6	6.5	4.0	3.1	2.5
PNG	Christines	21	14.6	0.0	11.0	0.0	6.2	22.2	8.7	19.2	5.0	8.5	0.0	4.6
	Lubaluba	21	57.0	0.0	9.6	0.0	8.8	5.8	6.7	5.3	5.6	0.0	0.3	0.9
	Susans	20	11.5	0.0	16.8	0.0	8.1	32.4	21.0	6.4	1.5	0.5	1.7	0.0
NC	Ilot Nge	20	36.8	0.0	5.9	2.9	31.6	17.3	1.1	1.1	3.1	0.0	0.2	0.0
	Recif Senez	20	67.2	0.0	12.8	13.5	1.0	4.6	0.2	0.0	0.0	0.0	0.0	0.7
	Seche Croissant	20	55.9	0.0	2.0	2.6	9.3	2.6	19.8	0.2	0.0	0.0	0.2	7.6
FP	Motu Ahi	20	23.7	0.0	0.0	0.0	0.5	25.1	45.7	4.8	0.0	0.0	0.2	0.0
	Temea	21	75.8	0.0	0.8	0.0	0.0	7.7	7.1	7.9	0.5	0.0	0.0	0.2
	Tiahura	20	81.6	0.0	0.0	0.0	0.7	1.6	8.4	7.1	0.2	0.0	0.4	0.0

Table 3.2 cont.

Location	Site	*n*	Non-coral substrate	Soft coral	*A. hyacinthus*	*Staghorn Acropora*	*Other Acropora*	*Pocillopora sp.*	*Montipora sp.*	*Porites sp.*	*Favidae*	*Isopora sp.*	Other hard corals	Other
C. lunulatus														
HI	Blue Pools	21	2.7	0.0	15.5	4.6	35.8	3.1	2.7	7.0	0.5	16.7	10.9	0.5
	North Wistari	24	1.1	0.0	6.3	13.6	10.3	8.5	3.7	19.3	0.2	29.5	7.4	0.0
	2nd Point	20	0.3	0.0	31.2	13.3	5.9	1.3	1.2	4.4	3.4	38.7	0.3	0.0
LI	Bird Islet	21	0.5	0.4	13.3	22.3	8.0	7.3	11.5	1.9	8.0	22.7	3.7	0.5
	Lizard Head	23	0.8	0.0	19.9	29.1	8.7	2.5	4.6	2.6	0.0	30.3	1.5	0.0
	South Island	23	0.8	0.2	31.3	28.2	3.7	4.5	5.1	2.2	1.8	20.4	1.6	0.0
PNG	Christines	21	0.0	0.0	14.4	9.4	16.9	27.3	3.9	14.1	0.3	9.7	3.3	0.8
	Lubaluba	23	0.2	0.0	0.0	1.4	9.7	32.9	3.1	0.5	0.5	8.5	42.2	0.9
	Susans	22	0.0	0.0	18.2	25.1	14.9	17.7	1.6	1.6	9.0	11.0	0.9	0.0
NC	Ilot Nge	20	1.4	0.0	19.5	35.0	9.5	14.9	1.9	0.0	3.5	13.3	1.1	0.0
	Recif Senez	20	0.3	0.0	51.2	1.6	8.6	0.0	0.0	0.0	33.9	4.4	0.0	0.0
	Seche Croissant	20	0.9	0.0	9.1	7.3	42.6	6.8	0.0	0.0	8.0	20.9	4.5	0.0
FP	Motu Ahi	21	3.0	0.0	0.0	4.9	38.5	46.2	0.0	0.0	0.0	3.0	4.3	0.0
	Temea	20	0.9	0.0	0.6	8.8	36.9	52.9	0.0	0.0	0.0	0.0	0.0	0.0
	Tiahura	20	5.7	0.0	0.0	0.3	21.9	65.6	0.5	0.0	0.0	0.0	6.2	0.0
C. trifascialis														
HI	Blue Pools	26	0.0	0.0	57.3	1.8	36.1	0.0	4.1	0.0	0.0	0.6	0.0	0.0
	North Wistari	26	0.0	0.0	23.5	11.5	63.5	0.0	0.9	0.0	0.5	0.2	0.0	0.0
	2nd Point	21	0.0	0.0	72.0	5.1	22.0	0.4	0.0	0.0	0.5	0.0	0.0	0.0
LI	Bird Islet	20	0.0	0.0	77.7	5.0	10.0	7.3	0.0	0.0	0.0	0.0	0.0	0.0
	Lizard Head	23	0.6	0.0	76.3	0.2	18.3	4.6	0.0	0.0	0.0	0.0	0.0	0.0
	South Island	21	0.0	0.0	64.7	3.7	21.9	9.6	0.0	0.0	0.0	0.0	0.0	0.0
PNG	Christines	21	0.0	0.0	89.6	0.7	6.3	2.5	0.4	0.2	0.0	0.4	0.0	0.0
	Lubaluba	20	0.0	0.0	83.4	0.0	8.4	7.7	0.0	0.5	0.0	0.0	0.0	0.0
	Susans	20	0.0	0.0	72.9	0.0	14.7	11.4	0.5	0.5	0.0	0.0	0.0	0.0
NC	Ilot Nge	20	0.0	0.0	42.6	27.9	27.7	0.0	0.7	0.0	0.0	1.1	0.0	0.0
	Recif Senez	20	0.0	0.0	75.2	12.4	12.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
	Seche Croissant	20	0.0	0.0	10.0	21.6	64.2	0.0	4.2	0.0	0.0	0.0	0.0	0.0
FP	Motu Ahi	20	0.0	0.0	0.7	0.0	42.6	26.7	24.8	5.3	0.0	0.0	0.0	0.0
	Temea	20	0.0	0.0	22.6	1.0	36.3	28.1	8.9	3.1	0.0	0.0	0.0	0.0
	Tiahura	20	0.0	0.0	2.2	16.6	47.8	19.9	9.7	3.0	0.0	0.0	0.8	0.0

Table 3.3 Dietary overlap (C_λ) among five locations of four butterflyfish species. Location abbreviations follow Fig 3.1.

	LI	PNG	NC	FP
C. vagabundus				
HI	1.00	0.89	0.98	1.00
LI		0.89	0.98	1.00
PNG			0.94	0.90
NC				0.98
C. citrinellus				
HI	0.74	0.69	0.90	0.78
LI		0.93	0.71	0.65
PNG			0.69	0.68
NC				0.94
C. lunulatus				
HI	0.85	0.66	0.78	0.28
LI		0.64	0.75	0.24
PNG			0.64	0.71
NC				0.37
C. trifascialis				
HI	0.84	0.77	0.96	0.70
LI		0.99	0.82	0.38
PNG			0.74	0.29
NC				0.66

Chaetodon citrinellus

Chaetodon citrinellus fed predominantly on hard corals at Lizard Island and Papua New Guinea (68.7% ±6 S.E. and 60.3% ±15 S.E. of all bites respectively), while in New Caledonia and French Polynesia the majority of bites were taken on non-coral substrates (53.3% ±9 S.E. and 60.4% ±18 S.E. respectively) (Table 3.2). *Chaetodon citrinellus* fed across a range of different hard coral resource categories in all locations. Roughly half of all bites on hard corals were taken on *Montipora sp.* in French Polynesia and 'Other *Acropora'* in Heron Island, while at Lizard Island *Pocillopora sp*. accounted for nearly 40% of all bites on hard corals on average. In contrast, in both New Caledonia and Papua New Guinea, bites were spread reasonably evenly between all hard coral resource categories. Dietary composition varied significantly among locations (nested MANOVA, Pillai's trace=1.109, df = 48,1144, $P<0.001$) and sites nested within locations (nested MANOVA, Pillai's trace=1.453, df = 120,2920, $P<0.001$). Proportional consumption of all individual resource categories except other hard corals and 'other' varied significantly among locations, while proportional consumption of non-coral substrates, 'Staghorn *Acropora', Pocillopora sp., Montipora sp., Porites sp.* and 'Other' varied significantly among sites nested within locations (Table 3.2). Niche breadth ranged from 0.89 (±0.04 S.E.) in New Caledonia to 0.93 (±0.01 S.E.) in Heron Island (Fig 3.3) and did not vary significantly among locations (one way ANOVA, $F_{4,10}$=0.285, *P*=0.88). Niche overlap was variable between locations, ranging from 0.65 to 0.94, however there was no clear pattern in similarity between locations (Table 3.3). Resource selection functions indicated that *C. citrinellus* was a highly generalised feeder at local and regional scales. Significant selectivity or avoidance was only shown for a few resource categories and most categories were consumed in proportion to their availability across all locations (Table 3.4).

Chaetodon lunulatus

Chaetodon lunulatus fed almost exclusively on hard corals, taking at least 97% of all bites on hard corals at all locations (Table 3.2). Bites were taken on at least 7 of the 9 hard coral resource categories in each location, with the majority of bites taken on 'Staghorn *Acropora',*' 'Other *Acropora', Pocillopora sp.* or *Montipora sp.*. Dietary composition varied significantly among locations (nested MANOVA, Pillai's trace=1.334, df = 48,1184, *P*<0.001) and sites nested within locations (nested MANOVA, Pillai's trace=1.464, df = 120,3020, *P*<0.001). Proportional consumption of all individual resource categories except non-coral substrates, soft corals and 'Other' varied significantly among locations and sites nested within locations; proportional consumption of Favidae and 'Other *Acropora'* also varied significantly among sites nested within locations (Table 3.2). Dietary niche breadth ranged from 0.64 (±0.10 S.E.) in Papua New Guinea to 0.73 (±0.05 S.E.) in New Caledonia (Fig 3.3), and did not vary significantly among locations (one way ANOVA, $F_{4,10}$=0.403, *P*=0.80). However, niche overlap was highly variable between locations (Table 3.3). Dietary composition was most similar between Heron

Island and Lizard Island (overlap: 0.85) and least similar between French Polynesia and all other sites except Papua New Guinea (overlap of 0.28, 0.24 and 0.37 for Heron Island, Lizard Island and New Caledonia respectively). Resource selection functions indicated that *C. lunulatus* had very generalised feeding preferences across all locations, with most resource categories consumed in proportion to their availability (Table 3.4).

Chaetodon trifascialis

Chaetodon trifascialis also fed exclusively on hard corals, taking 100% of bites on hard corals at all locations (Table 3.2). With the exception of French Polynesia, over 90% of all bites were taken on *Acropora* coral resource categories (*A. hyacinthus,* 'Staghorn *Acropora'* and 'Other *Acropora'*) in each location on average, and between 42.6% (±0.9 S.E., New Caledonia) and 82.0% (±0.2 S.E., Papua New Guinea) of all bites were taken on *A. hyacinthus* (Table 3.2). In French Polynesia only 56.6% (±4.0 S.E.) of all bites were taken on *Acropora* coral resource categories, and instead *C. trifascialis* also fed on *Montipora sp.* and *Pocillopora sp.* corals. Dietary composition varied significantly among locations (nested MANOVA, Pillai's trace=1.016, df = 40,1164, *P*<0.001) and sites nested within locations (nested MANOVA, Pillai's trace=0.70, df = 100,2970, *P*<0.001). Proportional consumption of *A. hyacinthus, '*Staghorn *Acropora'* and 'Other *Acropora'* varied significantly among locations and sites nested within locations; proportional consumption of *Pocillopora sp., Porites sp.* and *Montipora sp.* also varied significantly among sites nested within locations (Table 3.2). Dietary niche breadth varied significantly among locations (one way ANOVA, $F_{4,10}$=8.375, *P*=0.03), ranging from 0.33 (±0.03 S.E.) in French Polynesia to 0.64 (±0.06 S.E.) in New Caledonia (Fig 3.3). Niche overlap was reasonably high between all locations (Table 3.3) except French Polynesia and Lizard Island, and French Polynesia and Papua New Guinea (overlap of 0.29 and 0.38 respectively). Resource selection functions indicated that *C. trifascialis* was a highly specialised feeder, with

Table 3.4 Dietary selectivity of four butterflyfishes at five locations on 12 resource categories. +: category used significantly more than expected (selected); =: category used in proportion to availability; -: category used significantly less than expected (avoided); 0: category unused (strongly avoided); NA: category not available. Location abbreviations follow Fig 3.1.

Location	Site	Reef substrate	Soft coral	*A. hyacinthus*	*Staghorn Acropora*	*Other Acropora*	*Pocillopora sp.*	*Montipora sp.*	*Porites sp.*	*Favidae*	*Isopora sp.*	Other hard corals	Other
C. vagabundus													
HI	Blue Pools	+	0	0	0	0	-	0	0	0	0	=	=
	North Wistari	+	NA	0	0	=	-	0	=	0	0	0	=
	2nd Point	+	NA	0	0	0	=	0	0	=	-	0	0
LI	Bird Islet	+	0	=	-	=	0	0	0	=	0	0	0
	Lizard Head	+	-	=	0	-	-	0	-	-	0	0	=
	South Island	+	0	-	-	0	0	0	0	-	0	=	=
PNG	Christines	+	0	-	0	-	=	=	=	=	0	0	+
	Lubaluba	+	NA	-	0	0	=	=	=	=	0	=	=
	Susans	=	NA	-	0	-	=	=	=	=	-	=	+
NC	Ilot Nge	+	0	-	-	=	=	+	+	0	0	=	+
	Recif Senez	+	NA	0	0	0	0	=	0	NA	NA	NA	=
	Seche Croissant	+	0	0	-	-	=	0	=	NA	0	=	+
FP	Motu Ahi	+	NA	NA	NA	0	=	-	-	0	NA	0	=
	Temea	+	NA	0	0	0	=	=	-	0	NA	0	0
	Tiahura	+	NA	NA	0	0	0	-	-	0	NA	0	0
C. citrinellus													
HI	Blue Pools	=	0	=	=	=	=	=	=	=	=	-	-
	North Wistari	=	NA	=	=	=	=	=	=	0	=	=	=
	2nd Point	+	NA	=	=	-	=	=	=	=	=	=	=
LI	Bird Islet	-	-	=	=	=	+	=	=	=	=	=	=
	Lizard Head	=	=	=	0	=	+	=	-	-	=	=	=
	South Island	-	-	=	=	=	+	=	-	=	=	=	=
PNG	Christines	-	0	-	0	=	+	=	=	=	=	0	=
	Lubaluba	=	NA	=	0	=	=	=	=	=	0	=	-
	Susans	-	NA	=	0	=	+	+	-	=	-	=	0
NC	Ilot Nge	+	0	=	=	=	=	=	=	=	0	=	0
	Recif Senez	+	NA	=	=	-	=	=	0	NA	NA	NA	=
	Seche Croissant	+	0	=	=	=	=	=	=	NA	0	=	=
FP	Motu Ahi	-	NA	NA	NA	=	+	+	-	0	NA	=	0
	Temea	=	NA	=	0	0	=	=	-	=	NA	0	=
	Tiahura	+	NA	NA	0	=	=	=	-	=	NA	=	0

Table 3.4 cont.

Location	Site	Reef substrate	Soft coral	*A. hyacinthus*	*Staghorn Acropora*	*Other Acropora*	*Pocillopora sp.*	*Montipora sp.*	*Porites sp.*	*Favidae*	*Isopora sp.*	Other hard corals	Other
C. lunulatus													
HI	Blue Pools	-	0	=	=	=	+	=	=	=	=	=	=
	North Wistari	-	NA	+	=	=	=	=	=	=	=	=	=
	2nd Point	=	NA	=	=	+	=	+	=	=	=	+	-
LI	Bird Islet	-	-	+	=	=	+	=	=	=	=	=	-
	Lizard Head	-	0	=	0	+	+	=	=	=	=	=	0
	South Island	-	-	+	=	=	+	=	=	=	=	=	0
PNG	Christines	0	0	=	=	=	=	+	+	=	=	=	=
	Lubaluba	-	NA	0	=	=	-	=	+	=	=	+	-
	Susans	0	NA	=	=	=	+	=	=	=	=	=	0
NC	Ilot Nge	-	0	+	=	=	+	=	+	=	0	=	0
	Recif Senez	-	NA	+	=	=	=	=	0	NA	NA	NA	0
	Seche Croissant	-	0	+	=	=	=	+	+	NA	0	=	0
FP	Motu Ahi	-	NA	NA	NA	=	=	+	+	0	NA	=	0
	Temea	-	NA	=	0	0	=	+	+	0	NA	0	0
	Tiahura	-	NA	NA	0	0	-	+	+	=	NA	=	0
C. trifascialis													
HI	Blue Pools	0	0	+	=	+	0	-	0	-	=	0	0
	North Wistari	0	NA	=	=	=	-	0	0	-	0	0	0
	2nd Point	0	NA	+	=	+	0	=	0	0	-	0	0
LI	Bird Islet	0	0	+	=	=	=	0	0	0	0	0	0
	Lizard Head	0	0	+	-	=	=	0	0	0	0	0	0
	South Island	0	0	+	=	=	=	0	0	0	0	0	0
PNG	Christines	0	0	+	=	=	=	-	-	0	-	0	0
	Lubaluba	0	NA	+	0	=	=	0	-	0	0	0	0
	Susans	0	NA	+	0	=	=	-	-	0	0	0	0
NC	Ilot Nge	0	0	+	+	+	0	=	0	0	=	0	0
	Recif Senez	0	NA	+	=	+	=	0	0	NA	NA	NA	0
	Seche Croissant	0	0	+	+	+	0	-	0	NA	0	0	0
FP	Motu Ahi	0	NA	NA	NA	+	+	=	=	0	NA	0	0
	Temea	0	NA	+	=	+	+	=	-	0	NA	0	0
	Tiahura	0	NA	NA	=	+	=	=	-	0	NA	=	0

similar patterns of selectivity recorded in each location (Table 3.4). *Acropora hyacinthus* was positively selected at all sites where it was available, except one site (North Wistari) at Heron island where it was consumed in proportion to availability. Furthermore, with the exception of two sites in French Polynesia, significant selectivity was only shown for *Acropora* coral resource categories.

3.5 DISCUSSION

Despite varying resource availability, the level of dietary specialisation shown by each of the four species of butterflyfishes varied little among geographically separated locations. Species using a high number of resources locally did so across all locations and varied patterns of resource use with varying resource availability. In contrast, species using a low number of resources locally used the same resources in each location, regardless of their availability. Similarities between local and regional patterns of dietary specialisation suggest that the dietary niche of coral-feeding butterflyfishes is not constrained at the locations studied here.

Analyses indicated that *C. vagabundus, C. citrinellus* and *C. lunulatus* had low levels of dietary specialisation and varying patterns of resource use in each location. These findings are in agreement with previous studies showing that these species feed on a large range of dietary resources across multiple locations (e.g. Motta 1988; Harmelin-Vivien 1989; Cox 1994; Pratchett 2007a) and suggest that they have wide dietary niche breadths. Most likely, the same factors that allow these species to use a wide range of dietary resources locally also allow them to substitute those resources between locations (Krasnov et al. 2008). In contrast, *C. trifascialis* used very similar resources and had high levels of dietary specialisation in each location. *Acropora* corals dominated its diet, accounting for 57% of dietary composition in French Polynesia, despite very low availability (<2% total cover), and >90% of dietary composition at all other locations. *Chaetodon trifascialis* is widely known to preferentially feed on *Acropora* corals throughout its geographic range, showing high selectivity for these corals regardless of their availability (Reese 1981; Alwany et al. 2003; Graham 2007; Pratchett 2007a). For example, even though *Acropora* corals comprised less than 0.5% of the total coral cover at Johnston Atoll, *C. trifascialis* still took 83% of all bites on these corals (Irons 1989). This high dietary specialisation, and selective use of the same resources across locations despite varying resource availability, suggests that *C. trifascialis* has a very narrow dietary niche breadth.

The inferred dietary niche breadths for these species are supported by their response to localised coral loss on reefs. Consistent with a conclusion of wide dietary niche breadths, multiple studies have shown that *C. vagabundus, C. citrinellus* and *C. lunulatus* do not decline in abundance following moderate coral loss (e.g. Williams 1986; Halford et al. 2004; Pratchett et al. 2006), or have smaller relative declines in abundance compared to other more specialised species (Bouchon-Navaro et al. 1985; Berumen and Pratchett 2006b). Furthermore, *C. lunulatus* has also been shown to alter its diet and increase feeding on previously non-preferred coral species following a bleaching event resulting in a 55% decline in total coral cover and a loss of some coral taxa (Pratchett et al. 2004). In contrast, *C. trifascialis* is often one of the worst affected of all coral-feeding butterflyfishes by coral loss (Wilson et al. 2006; Pratchett et al. 2008b). Consistent with a conclusion of narrow dietary niche breadth, the abundance of *C. trifascialis* has declined severely following coral loss across multiple locations (e.g. Halford et al. 2004; Graham et al. 2006; Pratchett et al. 2006; Wilson et al. 2006) and at some sites possible local extinctions of this species have been recorded (Berumen and Pratchett 2006b).

Although *C. trifascialis* is undoubtedly vulnerable to coral loss, the results of this study suggest that it is more versatile and thus, less vulnerable to coral loss than has been previously suggested. *Chaetodon trifascialis* has been characterised as an extreme specialist (e.g. Pratchett et al. 2008b) as it feeds almost exclusively on tabular *Acropora* corals, such as *A. hyacinthus*, in a number of locations (Reese 1981; Irons 1989; Pratchett 2005; Berumen and Pratchett 2008). In the current study, *A. hyacinthus* accounted for less than 50% of dietary composition at some sites (e.g. Ilot Nge, Seche Croissant, North Wistari), and at many sites staghorn *Acropora* and other *Acropora* corals were also consumed in significant quantities. Furthermore, as was apparent in French Polynesia in the current study, there is some evidence that *C. trifascialis* increases consumption of other coral taxa when abundance of *Acropora* corals is very low. *Chaetodon trifascialis* has also been observed to increase feeding on *Pocillopora* corals at sites in the Seychelles where *Acropora* corals were scarce (Graham 2007). These recent demonstrations of feeding plasticity suggest that *C. trifascialis* may have a lower dependence on *Acropora* corals, and *A. hyacinthus* in particular, than has previously been assumed. But while increased use of alternative coral taxa may enable *C. trifascialis* to persist through periods of coral loss in the short term, it may also have significant sub-lethal effects on growth and condition. In a tank experiment, *C. trifascialis* juveniles maintained on an exclusive diet of non-preferred corals rapidly lost weight, despite actively feeding each day (Berumen and Pratchett 2008). Likewise, liver lipid reserves (an indicator of physiological condition) of *C. lunulatus* and *C. baronessa* were found to be significantly lower at sites where the abundance of preferred corals was low, even though feeding rates were maintained (Berumen et al. 2005). If use of non-preferred coral resources is continuous or prolonged, then sub-lethal effects may accumulate over time, potentially decreasing reproductive output and reducing survival. Such a situation may already have occurred at some sites in Moorea, French Polynesia, where the abundance of *C. trifascialis* has declined by almost 100% following a shift in coral composition from assemblages dominated by *Acropora* sp. to assemblages dominated by *Pocillopora* sp. as a result of recurrent disturbances (Berumen and Pratchett 2006b).

Interspecific interactions such as competition and predation are often cited as a key constraint on resource use (Colwell and Fuentes 1975). Competitive interactions between species can restrict the use of mutually preferred resources by subordinate competitors (Abramsky et al. 1990; Connell 1983; Young 2004; Bonin et al. 2009). Clear dominance hierarchies have been demonstrated for butterflyfishes and some species are known to aggressively defend territories containing the coral *A. hyacinthus* (Berumen and Pratchett 2006a). However, the only species in this study with locally restricted use of resources, *C. trifascialis*, is competitively dominant (Berumen and Pratchett 2006a). Consequently, coral resource use by *C. trifascialis* is unlikely to be restricted by competitive interactions with other butterflyfish species. An alternative possibility is that competitive interactions may actually result in an expansion of dietary niche breadth for some subordinate butterflyfishes, whereby dominant competitors limit access to reef habitats with high abundance of preferred coral resources but are unable to completely monopolise specific prey types (Pratchett 2005). Aside from competition, predation (or more specifically, the risk of predation) can moderate patterns of prey and habitat use (Werner et al. 1983; Gotceitas and Colgan 1990; Creel et al. 2005). Predation is generally thought to be very low for coral-feeding butterflyfishes (Cole et al. 2008), although further research is needed to explicitly quantify predation risk for adult butterflyfishes and the influence of predation risk on patterns of prey and habitat use. It is possible that resource availability was limiting resource use at some sites. However, despite varying resource availability among both sites and locations, *C. trifascialis* used the same restricted range of resources (mostly *Acropora* corals) across all sites and locations. This finding reinforces experimental studies conducted by Berumen and Pratchett (2008) showing that *C. trifascialis* is a fundamental dietary specialist. In contrast, *C. vagabundus, C. citrinellus* and *C. lunulatus* all varied patterns of resource use in each location and used a wide range of resources across all locations.

It has long been assumed that localised patterns of resource use are constrained for many organisms (Hutchinson 1957). This assumption is supported by numerous studies which have experimentally demonstrated an expansion of niche breadth for a wide range of organisms following a release from interspecific competition or predation pressure (reviewed by Colwell and Fuentes 1975). However, in combination with recent studies failing to detect an expansion of niche breadth in the absence of competition (Arlettaz et al. 1997; Mesquita et al. 2007; but see Costa et al. 2008), the findings of this study question this assumption and suggest that interspecific interactions may not be the primary determinant of niche breadth for some species (Manthey et al. 2011). Furthermore, this study suggests that the dietary niche breadth of coral feeding butterflyfishes is unlikely to be much wider if considered on a regional rather than a local scale. A similar conclusion can be inferred from a recent study of host specificity in parasitic fleas, which found that host specialisation was scale invariant, such that species that were either specialised or generalised at a local scale, were also specialised or generalised across their entire geographic range (Krasnov et al. 2008). These findings suggest that local resource use will not always be constrained. As a result, researchers should be wary of expecting the niche breadth of organisms to expand if the spatial scale of analysis is increased.

3.5.1 Conclusions

Although previous studies have emphasized the vulnerability of specialised coral feeding fishes to coral loss based on their inability to use non-preferred resources (e.g. Pratchett et al. 2008b), there has been little understanding of whether particular butterflyfish species are fundamentally specialised or locally adapted to take advantage of dominant coral taxa. This study shows that relative levels of dietary specialisation among different butterflyfishes do hold at larger spatial scales, but the finding of geographical variation in the dietary composition of all butterflyfishes shows that prey availability has a fundamental influence on dietary composition. The similarity between local versus regional patterns of prey use was highest for *C. trifascialis*, which relies on coral taxa (mostly *Acropora* spp) that are highly vulnerable to an increasing array of different disturbances (Pratchett et al. 2008b). With coral loss and degradation of reef ecosystems predicted to increase (Hoegh-Guldberg et al. 2007), this species is likely to be at a high risk of extinction. However, the increased feeding plasticity observed here suggests that *C. trifascialis* may have a greater capacity to respond to coral loss than previously assumed from single region assessments. These findings reinforce the importance of considering patterns of specialisation across a broad geographic scale when assessing vulnerability.

Chapter 4: Influence of dietary specialisation and resource availability on geographical variation in the abundance of butterflyfishes [§]

4.1 ABSTRACT

Empirical evidence indicates that both niche breadth and resource availability are key drivers of a species' local abundance and distribution patterns. However, most studies have considered the influence of either niche breath or resource availability in isolation, while it is the interactive effects that are likely to influence local abundance. This study examined geographic variation in the feeding ecology and distribution of butterflyfishes to determine the influence of dietary specialisation and dietary resource availability on their local abundance. Dietary composition and abundance of five butterflyfish species and coral dietary resource availability were determined at 45 sites across five geographic locations (Lizard Island and Heron Island, Great Barrier Reef, Australia; Kimbe Bay, Papua New Guinea; Noumea, New Caledonia; and Moorea, French Polynesia). Multiple regression models using variables representative of total dietary resource availability, availability of specific dietary resources and interspecific competition were used to determine the best predictors of local abundance across all sites and locations for each of the five species. Factors influencing local abundance varied between butterflyfishes with specialised and generalised diets. Dietary resource availability had the strongest influence on the abundance of *C. trifascialis* - the species with the most specialised diet. Local abundance of *C. trifascialis* was best predicted by availability of the Acropora corals that it preferentially feeds on. In contrast, abundance of generalist butterflyfishes was poorly described by variation in availability of specific dietary resources.

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Rather, it was indices of total dietary resource availability (coral species diversity/richness) that best predicted their abundance. Overall, multiple regression models only explained a small proportion of the variation in local abundance for all five species. Despite their relatively specialised diets, dietary resource availability has limited influence on the local abundance of butterflyfishes. Only the most specialised species appear to be consistently limited by prey availability. However, this study challenges the assumption that specialist species are locally rare and therefore more vulnerable compared to generalist counterparts. Local and total abundance of species are influenced by a wide range of different factors and there is definite need to conduct independent species assessments, rather than assuming vulnerability status based on general biological or ecological attributes.

4.2 INTRODUCTION

Many macroecological studies have sought to understand what determines a species' patterns of abundance (Brown 1984; Gregory and Gaston 2000). Niche breadth is often invoked as a key determinant following Brown's (1984) niche breadth hypothesis, which predicts that generalist species will be locally abundant as they are able to exploit a wide range of environmental conditions and resources, while specialist species will be locally rare (Brown 1984; Brown et al. 1995). However, the link between niche breadth and abundance remains unclear, with studies both supporting (Pyron 1999; Harcourt et al. 2002) and failing to find (Gaston et al. 1997; Gregory and Gaston 2000; Brandle et al. 2002) a relationship. These contrasting results may in part be due to resource availability - specialist species may attain high local abundance if their preferred resources are also locally abundant. Resource availability has been identified as a key determinant of local abundance patterns in multiple studies across a range of taxa (e.g. fish: Holbrook et al. 2000; birds: Tellería and Pérez-Tris 2003; mammals: Womble and Sigler 2006; bees: Roulston and Goodell 2011). But despite the recognised importance of both niche breadth and resource availability in determining local abundance (Munday 2002), most studies have considered these factors in isolation and the interactive effects between them remain largely unstudied.

Local abundance is likely to be influenced by both niche breadth and resource availability, such that at a given location, local abundance will be determined by not only by the availability of resources but also by an organism's ability to utilise those resources. As generalist species are able to utilise a wide range of resources, their local abundance should be largely unaffected by differences in the availability of specific resources, as long as total resource availability remains constant. In contrast, specialist species are expected to be limited by the availability of critical resources (Brown 1984). Accordingly, their local abundance is more likely to be correlated with the abundance of the specific resources they specialise on, rather than total resource availability (Munday 2002; Pratchett and Berumen 2008), and will therefore be more variable than that of generalist species. Indirect evidence for these predictions comes from several sources. Specialist species are more sensitive to changes in resource availability (e.g. Harcourt et al. 2002; Kotze and O'Hara 2003; Swihart et al. 2003; Julliard et al. 2004; Aitken and Martin 2008) and can also have more restricted distributions across habitats with varying resource availability (Ostergard et al. 2009) compared to generalist counterparts. Furthermore, the abundance of some specialist species can vary significantly between sites with similar levels of total resource availability, but differing availability of specific resources (Graham 2007). These findings suggest that overall indices of resource availability will not provide an accurate reflection of resource availability for specialist species, and as such, these indices may not be the best predictors of their local abundance. However, the relative importance of total resource availability versus the availability of specific resources as determinants of local abundance for specialist species has rarely been examined.

Butterflyfishes (Genus Chaetodon) provide an ideal model group to investigate the influence of resource availability on the local abundance of specialist versus generalist species. The dietary composition and level of dietary specialisation of species within this genus vary considerably, ranging from generalist species such as *Chaetodon citrinellus*, which feed on a broad range of hard coral species as well as soft corals and other reef macro-invertebrates, to highly specialised species such as *C. trifascialis* which feed on only a small number of hard coral species (Pratchett 2005; Lawton et al. In press-b). The composition and abundance of hard coral species, the key dietary resource of these fish, also vary markedly at both a local (e.g. between reefs within a single location) and geographical scale (Edmunds and Bruno 1996; Veron 2000; Berumen et al. 2005). There is also evidence that the local abundance of coral-feeding butterflyfishes is related to the availability of coral dietary resources. Numerous studies have found a strong link between total hard coral cover and butterflyfish abundance (Bell and Galzin 1984; Bouchon-Navaro et al. 1985; Bozec et al. 2005; Pratchett and Berumen 2008; Emslie et al. 2010; but see Bell et al. 1985; Fowler 1990) and many butterflyfishes have been observed to decline in abundance following coral loss (e.g. Sano et al. 1987; McClanahan et al. 2002; Halford et al. 2004; Pratchett et al. 2006; Graham 2007). Furthermore, predation on coral-feeding butterflyfishes is generally thought to be very low (Cole et al. 2008) and their local abundance tends to be fairly stable in the absence of changes in coral availability (Halford et al. 2004), implying that availability of coral dietary resources, rather than predation or recruitment-driven processes, is likely to be a primary driver of local abundance patterns for these fishes. Empirical data indicates that butterflyfishes with specialised diets are more susceptible to coral loss than generalist feeders (Pratchett et al. 2006; Graham 2007; Pratchett et al. 2008b), suggesting that different factors are likely to determine the local abundance of specialist and generalist butterflyfish species. These characteristics make butterflyfishes ideal candidates to explore the links between ecological versatility, resource availability and local abundance.

Coral-feeding butterflyfishes have been identified as one of the most vulnerable groups of reef fishes to the combined effects of ongoing global coral loss and degradation of coral reef habitats (Wilson et al. 2006; Pratchett et al. 2008b). Identifying key drivers of their local abundance has important implications for understanding how butterflyfishes are likely to be impacted by climate change. Many species preferentially feed on corals from the genus *Acropora* (Pratchett 2005; Cole et al. 2008) which are themselves vulnerable to a range of disturbances on reefs (Marshall and Baird 2000; Madin and Connolly 2006; Pratchett 2010). If local abundance of butterflyfishes, particularly specialist species, is also linked to these corals, then their vulnerability to global climate change is likely to be greatly increased. Although variation in butterflyfish abundance and the role of hard coral cover as a driver of local abundance patterns have been previously investigated at a number of spatial scales (e.g. geographic regions: Findley and Findley 2001; reefs: Bozec et al. 2005; physiognomic reef zones: Pratchett and Berumen 2008) the influence of specific dietary resources on abundance patterns is yet to be examined. Comparisons of local abundance and coral resource availability at replicate sites within different locations will help identify the spatial scale at which these factors are influencing populations (Underwood and Chapman 1996; Hughes et al. 1999; Munday 2002).

Although a wide range of factors can potentially influence the abundance of reef fishes, we focus here on the influence of coral dietary resources due to the strong reliance of many butterflyfishes on corals which are highly vulnerable to the impacts of global climate change. Therefore, the objective of this study was to investigate the influence of dietary specialisation and coral dietary resource availability on the local abundance of butterflyfishes. The specific aims were to (i) determine the dietary composition, level of dietary specialisation and local abundance of five butterflyfishes across five geographically separated locations; (ii) compare the local abundance of each species to the availability of dietary resources at each location; and (iii) determine the best predictors of local abundance for each species across all locations. It was expected that local abundance of dietary specialists would be best predicted by the availability of their preferred coral resources, whereas the local abundance of dietary generalists would be best predicted by total dietary resource availability. Local abundance of butterflyfishes may also be modified by interspecific competition and the presence of other butterflyfish species. Butterflyfishes are known to aggressively defend territories and dominant competitors have been observed to restrict the access of subordinates to habitats containing preferred corals (Crosby and Reese 2005; Berumen and Pratchett 2006a). Therefore, the influence of interspecific competition was also considered as a possible determinant of local abundance.

4.3 METHODS

4.3.1 Study sites and species

This study investigated local abundance patterns of five common and widespread species of butterflyfishes - *Chaetodon auriga, C. vagabundus, C. citrinellus, C. lunulatus* and *C. trifascialis*. *Chaetodon auriga, C. vagabundus* and *C. citrinellus* are all facultative corallivores – consuming hard corals as well as other small motile invertebrates and soft corals; while *C. lunulatus* and *C. trifascialis* are both obligate corallivores, feeding almost exclusively on hard corals (Pratchett 2005; Cole et al. 2008; Lawton et al. In press-b). Sampling was conducted at five geographically separated locations throughout the Pacific: i) Lizard Island, Northern Great Barrier Reef; ii) Heron Island, Southern Great Barrier Reef; iii) Kimbe Bay, Papua New Guinea; iv) Noumea, New Caledonia; v) Moorea, French Polynesia (Fig. 3.1). These sites are separated by 1100km to 6600km and distributed along known diversity gradients (Bellwood and Hughes 2001). At each location, nine distinct sites across a range of habitats (e.g. exposed front reef, sheltered back reef, fringing reef, shallow water patch reef) were sampled to determine butterflyfish abundance. At three of these sites, feeding observations were conducted to determine the dietary composition of the five focal species in each location.

4.3.2 Butterflyfish abundance and coral composition

The abundance of butterflyfishes (focal species as well as all other congenerics) was determined using underwater visual census. At each site, 50 x 4m belt transects were laid parallel to the reef crest. Transects were delineated using a 50m fibreglass tape and the number of individual butterflyfishes >50mm total length located within 2m of either side of the tape were recorded to species level. A total of five replicate transects were surveyed at each site, giving a total of 225 transects across all locations. To allow butterflyfish abundance to be directly related to coral cover and dietary resource availability at each site, coral composition on each of the five transects used to census butterflyfish abundance was determined using 50m point intercept transects. Along each transect, the substrate directly beneath 200 uniform sampling points (spaced every 25cm) was recorded to species level for hard corals, and to broad categories for all other substrate types (e.g. non-coral substrate, macroalgae). To provide an index of coral species richness, the total number of different hard coral species detected on each individual transect was determined. The Shannon-Wiener *J'* index was calculated for each individual transect following Zar (1999) as an index of coral species diversity.

4.3.3 Dietary composition

Field observations of feeding behaviour at three sites in each location were conducted to determine the dietary composition of each of the five focal species. Individual adult butterflyfishes were randomly selected and followed at a distance of 2 to 5 metres for 3-minutes, following Pratchett (2005). Every effort was made to ensure individual fish were not observed more than once. At least 20 observations for each species were conducted throughout the day at each site, giving a total of at least 60 observations at each location for each species. During each observation the total number of bites taken on each of six coral taxa groupings (*Acropora, Montipora, Pocillopora, Porites*, Favidae, Other hard corals), non-coral substrates (e.g. sand, rubble, pavement) and any other items (e.g. algae, non-coral macro-invertebrates) was recorded, following Pratchett (2005). Smith's measure of niche breadth (FT) was used to determine the relative degree of dietary specialisation for each species at each site (Smith 1982). This measure takes into account resource availability and is less sensitive to the use of rare resources compared to other niche breadth measures (Krebs 1999). FT is a standardised measure, ranging from 0 (most specialised) to 1 (least specialised), therefore allowing comparison of the level of specialisation between sites, locations and species.

4.3.4 Statistical analyses

Variation in the abundance of the five focal butterflyfish species and coral assemblage composition among locations and sites was assessed using multivariate analyses of variance (MANOVA) comparing the mean abundance of butterflyfishes and mean percent cover of corals (grouped into six taxa, plus non-coral substrates and other items) among nine sites nested within each of the five geographically-separated locations. Abundance data were log10 transformed and coral cover data were arc-sine transformed to satisfy assumptions of multivariate homogeneity and normality. Pillai's trace statistic was used to determine the significance of MANOVA results. Patterns in butterflyfish abundance and coral composition at each site were explored using canonical discriminant analyses (CDA). To assist with interpretation of the CDA, structural co-efficients of the butterflyfish species and coral taxa were plotted as vectors to indicate the predominant species and taxa at each site. To explore inter-specific differences in the relative importance of different spatial scales of comparison, variance in the abundance of each focal species was partitioned among locations, sites and transects, using the mean squares ratios of univariate F values from independent nested ANOVAs. To explore the relationship between niche breadth and local abundance, the average niche breadth of each species was calculated for each location and plotted again the average abundance of each species in each location. Due to the small number of data points, a formal quantitative analysis of this relationship was not undertaken.

Separate multiple linear regressions were run for each of the five focal species to identify factors significantly contributing to their local abundance. Data collected on each transect was treated as an individual replicate. An initial multiple regression analysis was run for each species with their abundance as the dependent variable and a standard set of predictor variables entered into the model simultaneously. Predictor variables with non-significant beta co-efficients in this initial model were discarded. The model was then rerun using the remaining predictor variables, which were entered hierarchically in order of their decreasing contribution to the initial model. Only predictor variables resulting in a significant change in the R^2 value on this second model (based on an F-ratio test conducted in SPSS) were retained and used in the final model. Residual plots, homogeneity tests and the Durbin-Watson test were used to ensure assumptions were met. Predictor variables used for each species in the initial model were as follows: hard coral species richness, hard coral species diversity, percent total hard coral cover, the percent cover of any dietary category comprising more than 1% of total diet across all locations, and the ratio of total hard coral cover to total abundance of all congeneric butterflyfishes. Predictor variables were chosen to be representative of the influence of total dietary resource availability (coral species richness and diversity indices, percent total hard coral cover), availability of specific dietary resources (percent cover of dietary categories) and interspecific competition (ratio of total coral cover to total abundance of all congeneric butterflyfishes). Predictor variables used for each species in each stage of the analysis are given in Table 4.1.

4.4 RESULTS

4.4.1 Butterflyfish assemblages

A total of 2440 individual butterflyfishes were recorded across all 225 transects sampled, corresponding to an average of 10.8 (± 0.4 S.E.) fishes per transect. There was no consistent pattern with longitude in either abundance (Fig. 4.1a) or diversity (Fig. 4.1b). The five focal butterflyfish species accounted for 47% of the total number of butterflyfishes recorded across all locations. The abundance of the five focal species was highest at Lizard Island (8.2 fishes per transect ± 0.7 S.E.) and was lowest in Papua New Guinea (2.8 fishes per transect ± 0.4 S.E.). Abundance of the five focal species varied significantly among locations (nested MANOVA, Pillai's trace=1.019, df = 20,716, $P<0.001$) and sites nested within locations (nested MANOVA, Pillai's trace=1.8768, df = 200,900, $P<0.001$). There was some partitioning of site centroids by location in the CDA, however there was considerable overlap of site centroids from different locations, inferring that the butterflyfish assemblages were generally similar between sites and locations (Fig. 4.2a). Structural co-efficients indicated that sites in French Polynesia and Lizard Island were characterised by a high abundance of *C. vagabundus* and *C. lunulatus* (Fig. 4.2a). Variance components indicated that for all species except *C. trifascialis*, most of the variation in abundance was attributable to variation among locations, rather than sites or transects. In contrast, variation in abundance was similar at both sites and locations for *C. trifascialis* (Fig. 4.3).

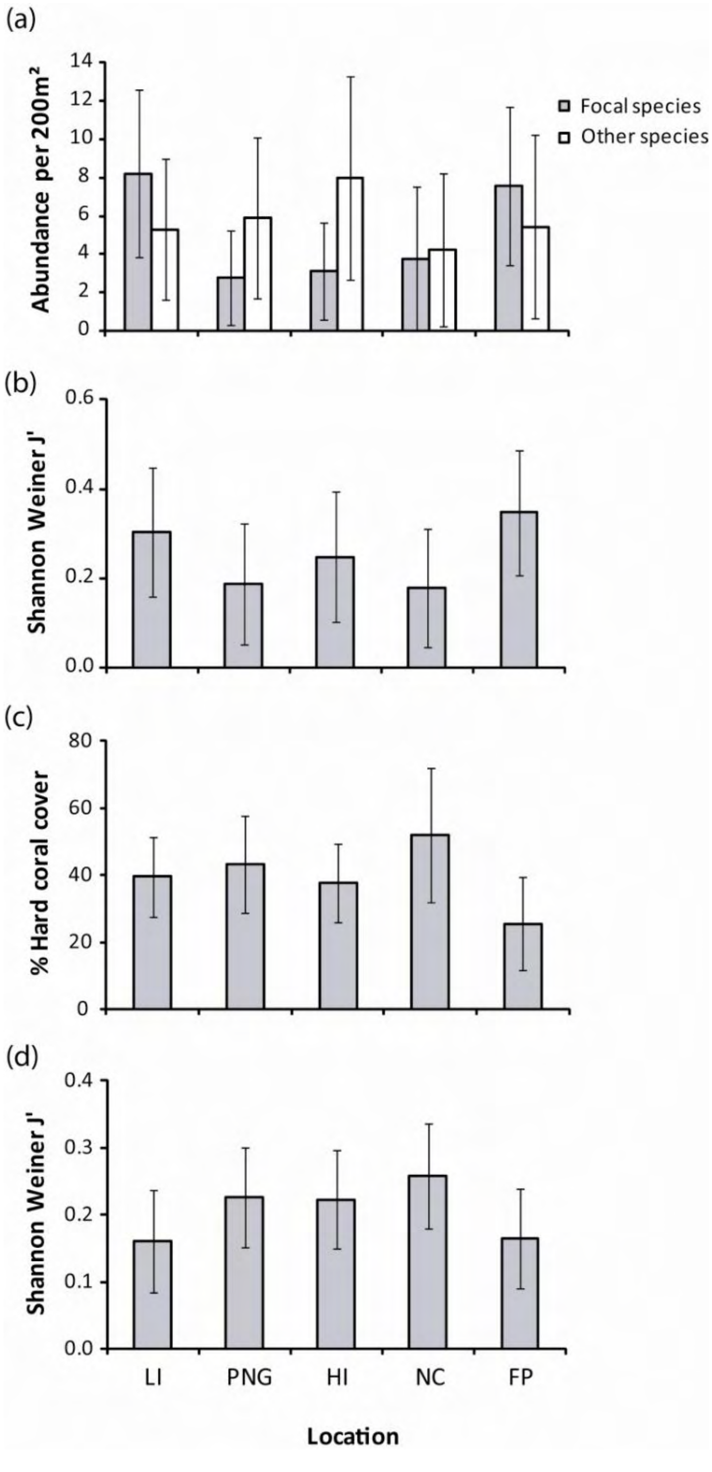

Figure 4.1 Characteristics of butterflyfish assemblages and coral communities at five locations. (a) Mean (+S.E.) abundance per transect of focal species and other butterflyfish species; (b) mean (+S.E.) species diversity (Shannon Weiner J') of all butterflyfishes; (c) mean (+S.E.) percent hard coral cover; and (d) mean (+S.E.) species diversity (Shannon Weiner J') of hard corals. Heron Island (HI); Lizard Island (LI); Papua New Guinea (PNG); New Caledonia (NC) and French Polynesia (FP).

4.4.2 Coral composition

Both total hard coral cover and hard coral species diversity (measured by the Shannon Weiner J' index) were highest in New Caledonia (coral cover: 53.2% ± 2.9 S.E., species diversity: 0.26 ± 0.01 S.E.), but the total number of different hard coral species recorded on each transect was highest in Papua New Guinea (18.1 species ± 0.8 S.E.) (Figs 4.1c & 4.1d). Total hard coral cover, hard coral species diversity and the number of hard coral species detected on each transect were all lowest in French Polynesia (coral cover: 25.5% ± 2.0 S.E., species diversity: 0.16 ± 0.01 S.E., coral species detected: 4.7 ± 0.3 S.E.). Coral assemblage composition varied significantly between locations (nested MANOVA, Pillai's trace=2.634, df = 32,704, $P<0.001$) and sites nested within locations (nested MANOVA, Pillai's trace=4.538, df = 320,1440, $P<0.001$). The groupings of site centroids in the CDA indicated that coral assemblages at each location were more distinct than butterflyfish assemblages (Fig. 4.2b). Fewer site centroids from different locations overlapped with each other in the coral CDA and, in contrast to the butterflyfish CDA, centroids from Lizard Island and French Polynesia sites were completely separated from each other. Structural co-efficients indicated that sites in French Polynesia were characterised by a high abundance of non-coral substrates, reflecting the low total hard coral cover at this location. Coral assemblages at Heron Island, New Caledonia and Lizard Island were dominated by *Acropora* corals, with this taxon comprising more than 74%, 63% and 56% respectively of the total hard coral cover at these locations. French Polynesia sites were dominated by *Porites* and *Montipora* corals – these two taxa accounting for >80% of the total coral cover in this location. In contrast, cover of different coral taxa was variable at sites in Papua New Guinea, with no one taxa dominating assemblages in this location.

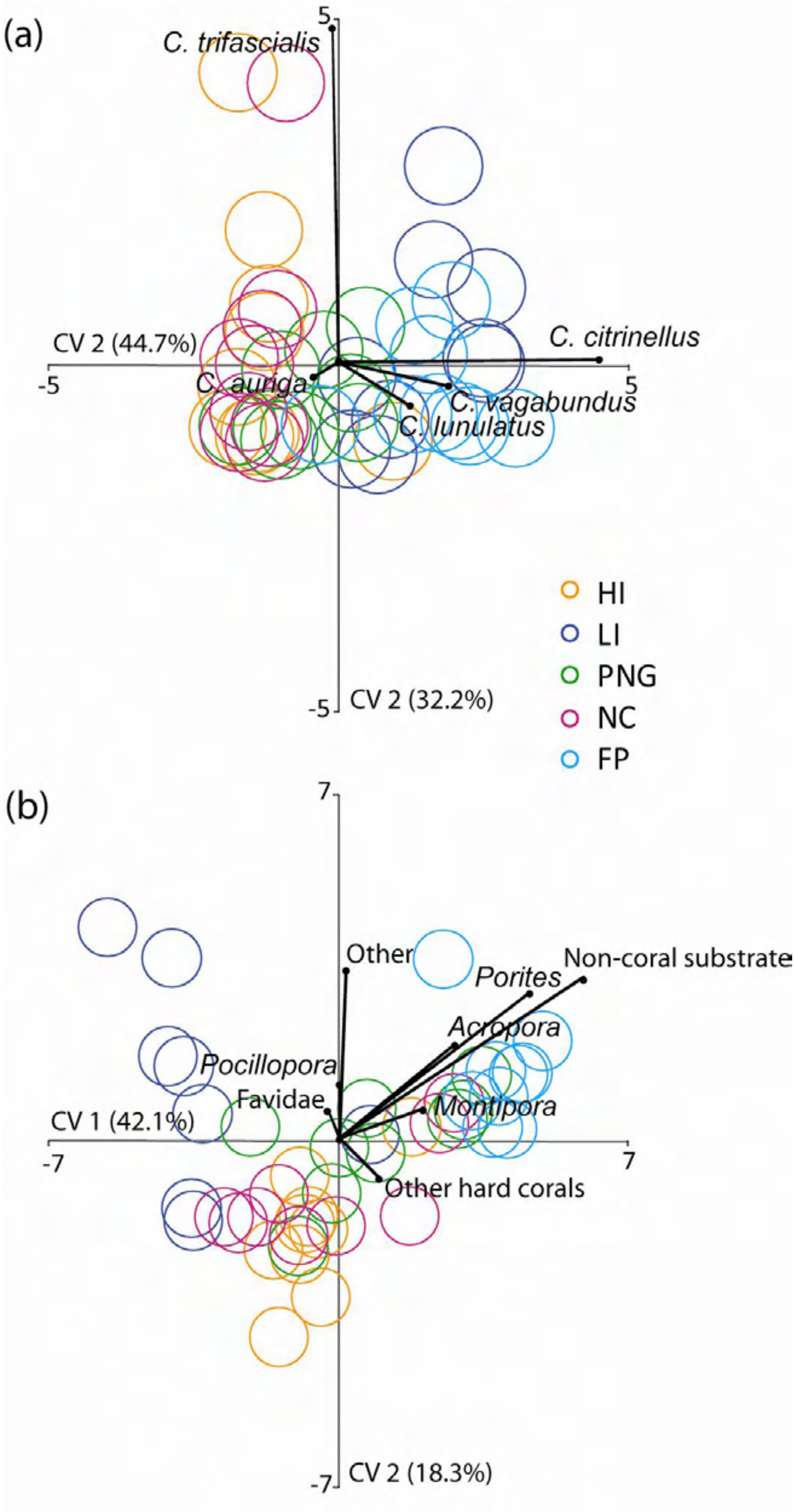

Figure 4.2 Canonical discriminant analyses of (a) butterflyfish communities and (b) coral assemblages at nine sites in each of five locations (HI, LI, PNG, NC, FP). Location abbreviations follow Fig. 4.1. Vectors are structural co-efficients indicating the relative abundance of butterflyfish species (a) and coral taxa (b).

Table 4.1 Predictor variables used in multiple regression analyses for five species of butterflyfishes.

Species	Dietary categories	Significant variables	Final model
C. auriga	Non-coral substrate, *Acropora* , Other hard corals, Other	*Acropora*	-[1]
C. vagabundus	Non-coral substrate, *Acropora, Pocillopora, Montipora, Porites*, Other	*Pocillopora,* Hard coral species diversity	*Pocillopora,* Hard coral species diversity
C. citrinellus	Non-coral substrate, *Acropora, Pocillopora, Montipora, Porites*, Favidae, Other hard corals, Other	Number of hard coral species, Hard coral species diversity, Total coral cover/abundance congenerics	Number of hard coral species, Total coral cover/abundance congenerics
C. lunulatus	Non-coral substrate, *Acropora, Pocillopora, Montipora, Porites*, Favidae, Other hard corals,	Non-coral substrate, Total coral cover/abundance congenerics, Number coral species	Non-coral substrate, Total coral cover/abundance congenerics, Number coral species
C. trifascialis	*Acropora, Pocillopora, Montipora*	*Acropora,* Total coral cover/abundance congenerics, *Montipora*	*Acropora,* Total coral cover/abundance congenerics

[1] Final model was not significant.

Data displayed are any dietary items comprising more than 1% of total diet across all locations (dietary categories), significant predictor variables in the initial model (significant variables) and predictor variables included in the final model (final model). Significant variables are listed in order of their decreasing contribution to the initial model. See methods section for more details.

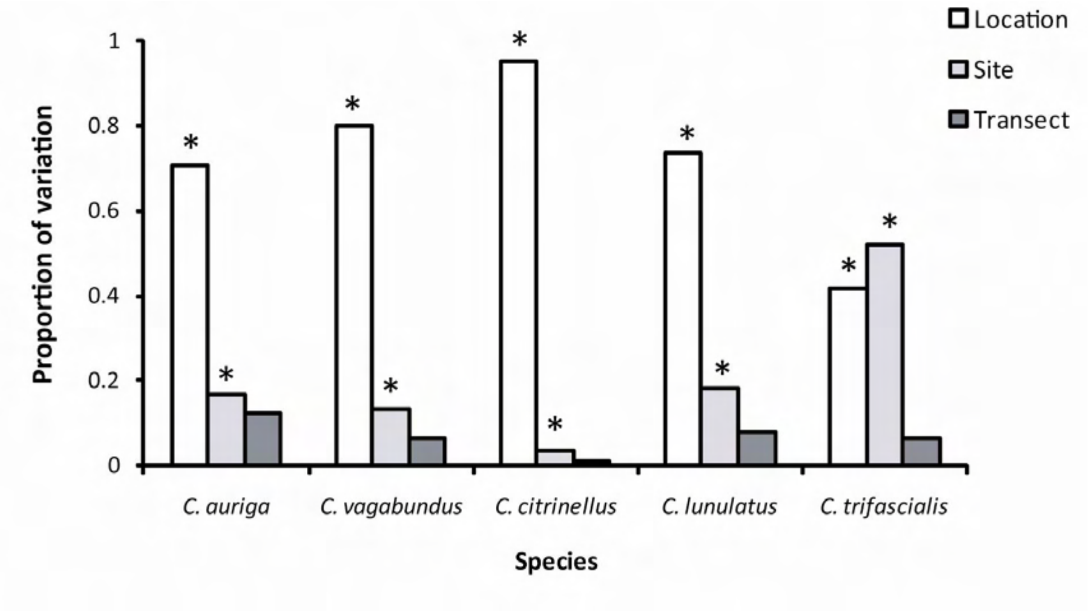

Figure 4.3 Proportion of variation in abundance of butterflyfish assemblages occurring among locations, sites and transects. * $P < 0.05$ (ANOVA Bonferroni-corrected significance levels).

4.4.3 Dietary composition and specialisation

Feeding observations were completed for a total of 1,506 individual fishes (Table 4.2). All butterflyfishes studied fed from the surface of live corals, but the proportional feeding on corals versus non-coral substrates varied greatly. *Chaetodon auriga* took at least 85% of all bites on non-coral substrates at each location (Table 4.2). *Chaetodon vagabundus* also fed predominantly on non-coral substrates, taking at least 90% of all bites on this category at Lizard Island, Heron Island and French Polynesia, and more than 60% of all bites on this category in New Caledonia and Papua New Guinea respectively (Table 4.2). Hard corals contributed significantly to the diet of *C. vagabundus* in Papua New Guinea, accounting for 32.0% (±5.2 S.E.) of all bites, most of which were taken on *Montipora, Pocillopora* and *Porites* corals. Both *C. auriga* and *C. vagabundus* had relatively high niche breaths (Fig. 4.4), indicating that they were both generalist feeders. *Chaetodon citrinellus* fed across a broad range of hard coral taxa, non-coral substrates and other dietary items and diet was variable among locations (Table 4.2). Between 11% and 81% of all bites were taken on non-coral substrates at each site,

Table 4.2 Proportional consumption of eight dietary categories by five butterflyfishes across five locations. Data are pooled across *n* replicate feeding observations for each species of butterflyfish. Location abbreviations follow Fig 4.1. ACR: *Acropora,* POC: *Pocillopora*, MON: *Montipora*, POR: *Porites*, FAV: Favidae, OHC: other hard corals, NCS: non-coral substrates, OTH: other. *C. auriga* not present at sampling sites in PNG.

Location	Site	*n*	ACR	POC	MON	POR	FAV	OHC	NCS	OTH
C. auriga										
HI	Blue Pools	20	0.0	0.0	0.0	0.0	0.0	0.0	99.3	0.7
	North Wistari	20	1.2	0.0	0.0	0.0	0.0	0.0	94.0	4.8
	2nd Point	21	0.0	0.0	0.0	0.0	0.0	0.0	95.8	4.2
LI	Bird Islet	20	0.0	1.6	0.0	0.0	0.0	0.0	98.4	0.0
	Lizard Head	20	0.0	2.1	0.0	0.0	0.0	0.4	96.3	1.2
	South Island	21	8.7	2.5	0.4	0.0	3.7	0.4	83.9	0.4
NC	Ilot Nge	20	6.5	2.4	0.0	0.0	0.0	0.0	86.2	4.9
	Recif Senez	20	0.7	0.0	0.2	0.0	0.0	0.0	99.1	0.0
	Seche Croissant	20	0.4	0.0	1.6	1.2	0.0	12.5	69.1	15.2
FP	Motu Ahi	20	0.0	0.0	0.0	1.0	0.0	0.0	99.0	0.0
	Temea	20	0.0	0.0	3.2	10.4	0.0	0.0	86.4	0.0
	Tiahura	20	0.0	0.0	1.0	2.1	0.0	0.0	96.9	0.0
C. vagabundus										
HI	Blue Pools	22	0.0	0.4	0.0	0.0	0.0	0.0	86.2	13.5
	North Wistari	22	0.6	0.3	0.0	0.3	0.0	0.3	95.7	2.8
	2nd Point	22	0.0	0.4	0.0	0.0	0.4	0.4	98.3	0.4
LI	Bird Islet	20	7.7	0.0	0.0	0.0	0.3	0.0	92.1	0.0
	Lizard Head	31	0.7	0.5	0.3	0.2	0.5	0.0	95.9	2.0
	South Island	22	1.5	0.0	0.0	0.0	2.0	1.0	94.0	1.5
PNG	Christines	20	1.7	2.8	7.6	10.4	3.8	0.0	62.5	11.1
	Lubaluba	23	2.0	10.5	3.9	7.9	0.3	2.6	70.7	2.0
	Susans	21	4.0	5.3	21.9	6.4	4.3	0.5	50.1	7.5
NC	Ilot Nge	20	9.9	9.3	2.5	0.3	0.0	2.0	71.3	4.8
	Recif Senez	20	0.0	0.0	1.3	0.0	0.0	0.0	97.1	1.6
	Seche Croissant	20	0.6	8.2	0.0	1.5	0.9	3.2	48.8	36.8
FP	Motu Ahi	21	0.0	0.5	3.9	0.5	0.0	0.0	94.7	0.5
	Temea	20	0.0	2.5	2.5	5.3	0.0	0.0	89.8	0.0
	Tiahura	20	0.0	0.0	5.0	1.7	0.0	0.0	93.3	0.0
C. citrinellus										
HI	Blue Pools	24	51.1	3.0	3.9	0.7	0.7	5.3	35.3	0.2
	North Wistari	22	39.8	8.4	1.1	0.4	0.0	6.9	35.8	7.6
	2nd Point	20	8.2	2.8	4.1	0.8	3.4	13.1	65.7	1.8
LI	Bird Islet	20	27.3	31.4	7.5	1.0	4.1	4.1	21.1	3.6
	Lizard Head	20	27.0	23.5	1.8	0.5	1.4	1.8	34.2	9.8
	South Island	20	24.8	30.9	5.0	0.6	6.5	7.1	21.3	3.8

Table 4.2 cont.

Location	Site	*n*	ACR	POC	MON	POR	FAV	OHC	NCS	OTH
PNG	Christines	21	17.3	22.5	8.6	19.1	5.0	8.4	14.5	4.5
	Lubaluba	21	18.3	5.7	6.6	5.2	5.4	0.3	57.6	0.9
	Susans	20	24.9	32.4	21.0	6.4	1.5	2.2	11.5	0.0
NC	Ilot Nge	20	40.4	17.3	1.1	1.1	3.1	0.2	36.8	0.0
	Recif Senez	20	27.3	4.6	0.2	0.0	0.0	0.0	67.2	0.7
	Seche Croissant	20	13.8	2.6	19.8	0.2	0.0	0.2	55.9	7.6
FP	Motu Ahi	20	0.5	25.1	45.7	4.8	0.0	0.2	23.7	0.0
	Temea	21	0.8	7.7	7.1	7.9	0.5	0.0	75.8	0.2
	Tiahura	20	0.7	1.6	8.4	7.1	0.2	0.4	81.6	0.0
C. lunulatus										
HI	Blue Pools	21	35.7	13.5	9.8	8.1	3.5	27.8	1.7	0.0
	North Wistari	24	73.3	13.3	5.9	1.3	1.2	4.7	0.3	0.0
	2nd Point	20	32.5	4.5	35.8	3.1	2.6	18.4	2.6	0.5
LI	Bird Islet	21	44.2	22.2	7.9	7.2	11.4	5.6	0.5	0.9
	Lizard Head	23	53.7	27.8	7.5	2.1	4.5	3.8	0.7	0.0
	South Island	23	56.3	25.0	3.2	5.2	6.3	3.4	0.7	0.0
PNG	Christines	21	23.7	9.2	16.4	29.1	3.8	17.0	0.0	0.8
	Lubaluba	23	8.2	1.3	9.0	31.7	8.8	39.9	0.2	0.8
	Susans	22	37.3	25.9	15.3	17.5	1.6	2.4	0.0	0.0
NC	Ilot Nge	20	36.3	35.0	9.5	14.9	1.9	1.1	1.4	0.0
	Recif Senez	20	89.5	1.6	8.6	0.0	0.0	0.0	0.3	0.0
	Seche Croissant	20	38.0	7.3	42.6	6.8	0.0	4.5	0.9	0.0
FP	Motu Ahi	21	3.0	4.9	38.5	46.2	0.0	4.3	3.0	0.0
	Temea	20	0.6	8.8	36.9	52.9	0.0	0.0	0.9	0.0
	Tiahura	20	0.0	0.3	21.9	65.6	0.5	6.2	5.7	0.0
C. trifascialis										
HI	Blue Pools	26	98.5	0.2	0.8	0.0	0.0	0.6	0.0	0.0
	North Wistari	26	99.1	0.4	0.0	0.0	0.5	0.0	0.0	0.0
	2nd Point	21	95.5	0.0	3.8	0.0	0.0	0.8	0.0	0.0
LI	Bird Islet	20	92.7	7.3	0.0	0.0	0.0	0.0	0.0	0.0
	Lizard Head	23	94.8	4.6	0.0	0.0	0.0	0.0	0.6	0.0
	South Island	21	90.8	9.2	0.0	0.0	0.0	0.0	0.0	0.0
PNG	Christines	21	96.7	2.4	0.3	0.2	0.0	0.3	0.0	0.0
	Lubaluba	20	91.8	7.7	0.0	0.5	0.0	0.0	0.0	0.0
	Susans	20	87.6	11.4	0.5	0.5	0.0	0.0	0.0	0.0
NC	Ilot Nge	20	98.3	0.0	0.7	0.0	0.0	1.1	0.0	0.0
	Recif Senez	20	99.6	0.4	0.0	0.0	0.0	0.0	0.0	0.0
	Seche Croissant	20	95.8	0.0	4.2	0.0	0.0	0.0	0.0	0.0
FP	Motu Ahi	20	43.2	26.7	24.8	5.3	0.0	0.0	0.0	0.0
	Temea	20	59.9	28.1	8.9	3.1	0.0	0.0	0.0	0.0
	Tiahura	20	66.6	19.9	9.7	3.0	0.0	0.8	0.0	0.0

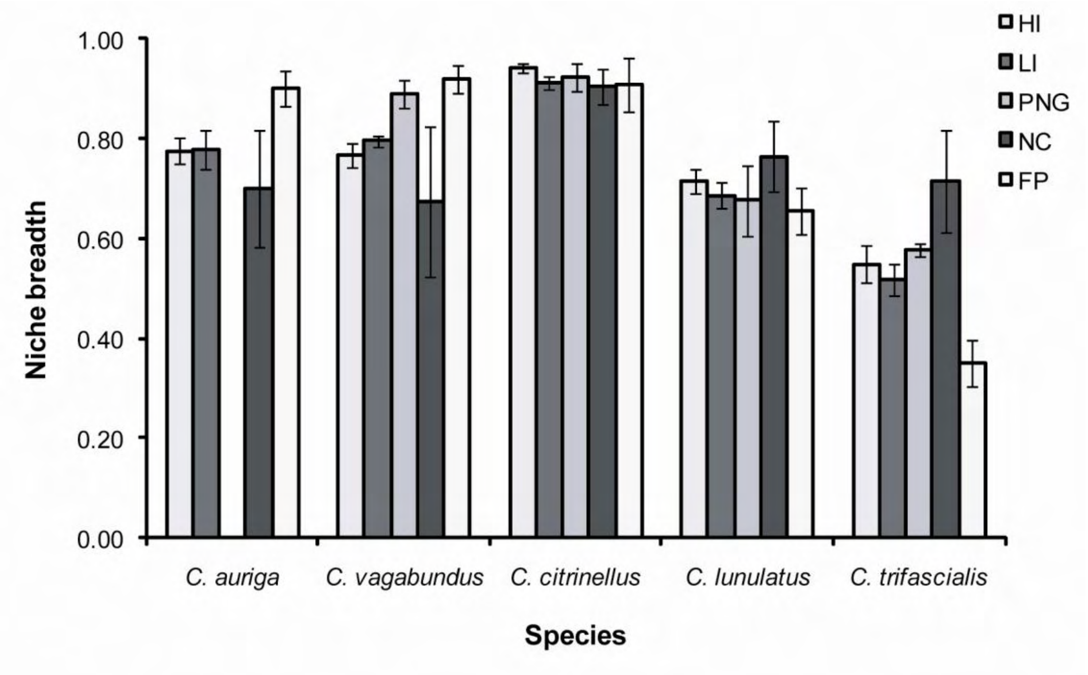

Figure 4.4 Mean (± S.E.) dietary niche breadth (FT) of five butterflyfish species at five locations. Location abbreviations follow Fig 4.1.

with the majority of bites at New Caledonia and French Polynesia taken on this category (53.3% +9 S.E. and 60.4% +18 S.E. respectively). Diet was dominated by *Acropora* corals at Heron Island, with roughly half of all bites on hard corals taken on this taxon, while at Lizard Island *Pocillopora* corals accounted for nearly 40% of all bites on hard corals on average. In contrast, in both New Caledonia and Papua New Guinea, bites were spread reasonably evenly between all hard coral resource categories. *Chaetodon citrinellus* was the most generalised of all species, with a high dietary niche breadth in all locations (Fig. 4.4). *Chaetodon lunulatus* took at least 97% of all bites on hard corals at all locations (Table 4.2). At each site, bites were spread across all hard coral resource categories, with the exception of French Polynesia where diet was dominated by *Montipora* and *Porites* corals (at least 80% of all bites). Niche breadth was reasonably high, indicating that *C. lunulatus* had a fairly generalised diet (Fig. 4.4). *Chaetodon trifascialis* took 100% of bites on hard corals at all locations (Table 4.2) and had a much more specialised diet than the other species. Diet was dominated by *Acropora* corals (>90% of all bites) in all locations except French Polynesia where *Montipora* and *Pocillopora* corals were also fed on, albeit in relatively low proportions (<30% of bites). *Chaetodon trifascialis* was the most specialised of all species, with a low to moderate niche breadth in each location (Fig. 4.4).

4.4.4 Niche breadth and local abundance

Plots of the average niche breadth and local abundance of each species at each of the five study locations were variable in pattern. Overall, there was no strong trend towards a positive or negative relationship between these factors (Fig. 4.5).

4.4.5 Regression models

Multiple linear regression analyses indicated that the local abundance of each of the five focal species was explained by a different set of variables. Availability of specific resource categories were significant predictors of abundance for three of the study species (Tables 4.1 & 4.3), but not for *C. auriga* or *C. citrinellus*. In particular, the abundance of the dietary specialist *C. trifascialis* was best predicted by *Acropora* corals, it's preferred coral prey (Table 4.3). The abundance of *C. vagabundus* was positively correlated with the availability of *Pocillopora* corals, while the abundance of *C. lunulatus* was negatively correlated with the availability of non-coral substrates (Table 4.3). The index of interspecific competition (the ratio of total hard coral cover to total abundance of all congeneric butterflyfishes) was negatively correlated with the abundance of *C. citrinellus, C. lunulatus* and *C. trifascialis*, while indices of coral species richness and diversity were a significant predictor of abundance for *C. vagabundus, C. citrinellus* and *C. lunulatus* (Table 4.3). Overall regression models and individual predictor variables were highly significant for all species except *C. auriga*, however, the models only explained a low proportion of the variation in abundance for each species, ranging from 11.5% (adjusted R^2) for *C. vagabundus* to 20.8% for *C. trifascialis* (Table 4.4).

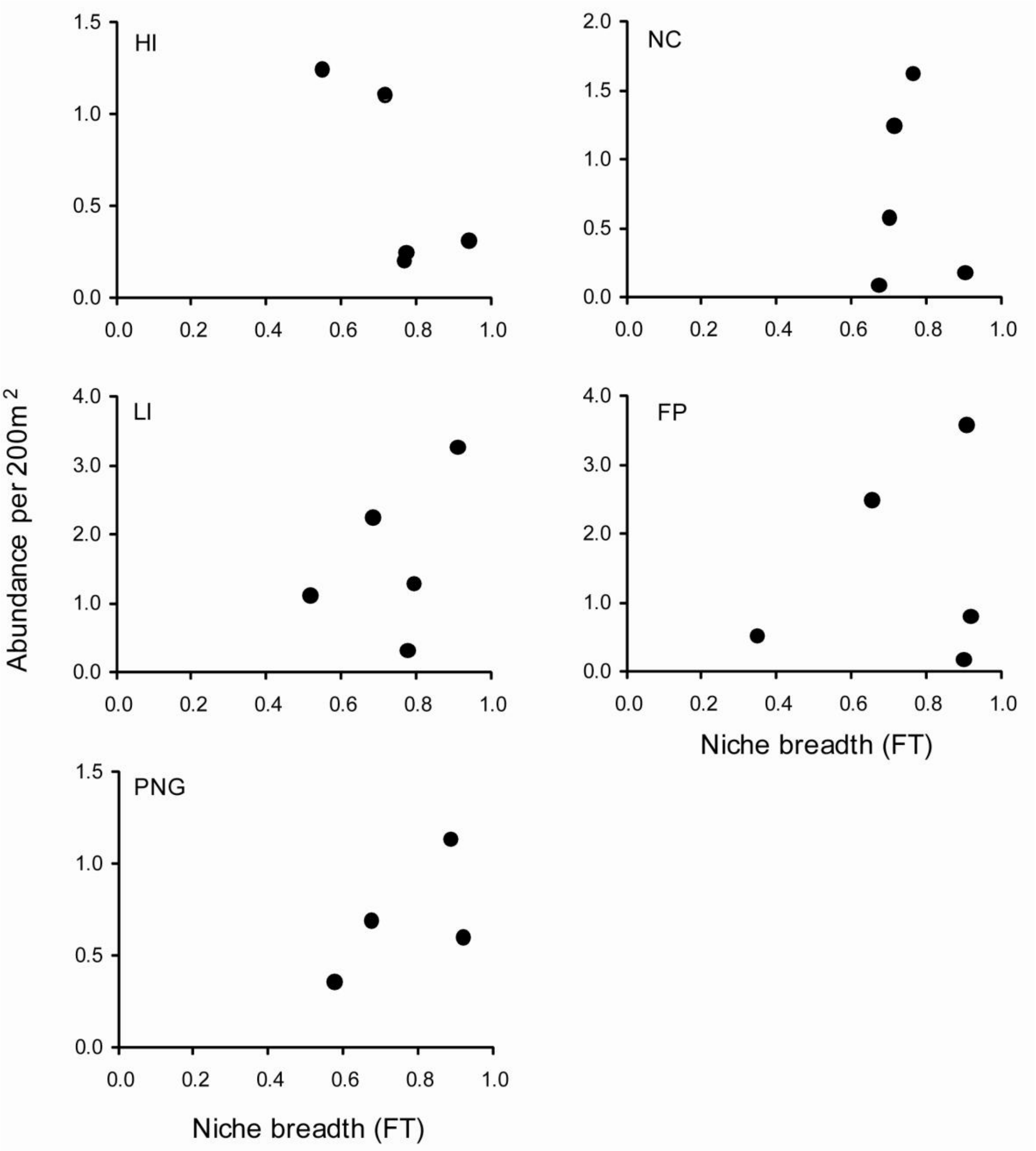

Figure 4.5 Average niche breadth (FT) and Abundance per 200m^2 of 5 species of coral feeding butterflyfishes across 5 geographic locations. Location abbreviations follow Fig 1.

Table 4.3 Co-efficients of multiple regression models for four species of butterflyfishes.

Species	Final predictors	*B*	S.E. *B*	β
C. vagabundus	*Pocillopora*	2.354	0.437	0.344***
	Hard coral diversity	-0.442	0.181	-0.156*
C. citrinellus	Number of coral species	-0.15	0.003	-0.280***
	Total coral cover/abundance congenerics	-1.201	0.292	-0.256***
C. lunulatus	Non-coral substrate	-0.394	0.086	-0.306***
	Total coral cover/abundance congenerics	-0.897	0.252	-0.226***
	Number coral species	-0.015	0.003	-0.320***
C. trifascialis	*Acropora*	0.590	0.077	0.485***
	Total coral cover/abundance congenerics	-0.769	0.201	-0.242***

The unstandardised beta co-efficients (*B*), their standard errors (S.E. *B*) and the standardised beta co-efficients (β) for the predictor variables included in the final regression model for each species are presented. * *P*<0.05, ***P*<0.01, ****P*<0.001.

Table 4.4 Final multiple regression results for abundance of five species of butterflyfishes.

Species	Adjusted R^2	Sum of Squares	df	Mean Square	*F*	Significance
C. auriga	-0.004	0.00	1, 224	0.000	0.020	0.889
C. vagabundus	0.115	1.546	2, 224	0.773	15.550	<0.001
C. citrinellus	0.163	4.194	2, 224	2.097	22.751	<0.001
C. lunulatus	0.159	3.491	3, 224	1.164	15.114	<0.001
C. trifascialis	0.208	3.212	2, 224	1.606	30.340	<0.001

4.5 DISCUSSION

This study revealed that the factors influencing local abundance varied among butterflyfishes, with pronounced differences between specialist versus generalist species. Dietary resource availability had the strongest influence on abundance patterns for the most specialised species, *C. trifascialis*, with the final regression model explaining the highest proportion (20.8%) of variation in abundance for this species. The variance components analysis indicated that variation in the abundance of *C. trifascialis* among sites was as high as variation among locations, providing further support for the influence of dietary resource availability. Feeding observations conducted across five different geographical locations revealed that the diet of *C. trifascialis* is highly consistent among locations, whereby this species feeds predominantly on *Acropora* corals as shown previously in Lawton et al.(In press-b). Accordingly, the abundance of *C. trifascialis* was best predicted by a model that included the availability of *Acropora* corals rather than total dietary resource availability. In contrast, feeding observations indicated that *C. auriga, C. vagabundus, C. citrinellus* and *C. lunulatus* were all dietary generalists, and also altered their diets among locations in response to differing availability of certain prey (Lawton et al. In press-b). In contrast to *C. trifascialis*, the abundance of three of these species was best predicted by regression models that included indices of total dietary resource availability (coral species diversity/richness) and variation in their abundance among sites was much lower than variation among locations. However, the low proportion of variance explained by the multiple regression models for all five species indicates that the relationship between dietary resource availability and local abundance is not strong and suggests that other factors are likely to have an important influence on the local abundance of these butterflyfishes.

Contrary to numerous studies which have found a strong positive relationship between total hard coral cover and butterflyfish abundance (e.g. Bell and Galzin 1984; Bouchon-Navaro et al. 1985; Cadoret et al. 1999; Bozec et al. 2005; Pratchett and Berumen 2008; Emslie et al. 2010), this study indicates that total coral cover is not an important predictor of abundance for individual butterflyfish species. There are several possible reasons the same relationship between abundance and coral cover found in these previous studies was not apparent here. In contrast to the current study, most previous studies have only considered the influence of coral cover on the abundance of the entire butterflyfish assemblage or specific feeding guilds (e.g. obligate corallivores). However, relationships between the abundance of individual species and coral cover are likely to vary from that of the butterflyfish assemblage due to community level interactions. Biogeographical studies have shown that the abundance of individual butterflyfish species is negatively related to the abundance of the total butterflyfish community (Findley and Findley 2001), suggesting that factors such as interspecific competition and density compensation can strongly influence the abundance of individual species independently of total coral cover. The relationship between total coral cover and the abundance of individual butterflyfish species has only been investigated by Pratchett and Berumen (2008), who found a strong positive correlation for all obligate corallivore species at the scale of a single reef, Lizard Island. However, the total coral cover at sites sampled in their study ranged from roughly 2% to 30%. In comparison, total coral cover at sites in the current study ranged from 6% to 80%. The absence of total coral cover as a significant variable in our multiple regression models suggests that although total coral cover and abundance of individual butterflyfishes appear to be linearly related at low to moderate levels of coral cover (e.g. Pratchett and Berumen 2008), the overall relationship is more likely to be asymptotic, such that further increases in coral cover above a certain threshold (e.g. 40% coral cover) have limited influence on the abundance of individual butterflyfishes.

The relatively weak effect of dietary resource availability on variation in abundance of all five coral feeding butterflyfishes is also in contrast to previous studies of other coral reef fishes which have shown that that resource availability (specifically, coral cover) is a major determinant of abundance patterns for individual species at geographic spatial scales (e.g. gobies: Munday 2002; damselfishes: Holbrook et al. 2000). These contrasting results could be a result of several factors. For some of these butterflyfishes, it is possible that the resource categories used here were too poorly resolved to effectively assess variation in the abundance of key dietary components. This is likely to be the case for species such as *C. auriga*, for which small motile invertebrates comprise a significant proportion of diet (Anderson et al. 1981; Pratchett 2005). It was assumed that bites on non-coral substrates not obviously occupied by any macro-invertebrates were targeting these organisms as has been shown previously (Anderson et al. 1981). As their availability is extremely difficult to quantify in the field the resource category of ‘non-coral substrates’ was used as a proxy. However, the availability of non-coral substrates may not capture the true availability of small motile invertebrates. Obligate coral feeding species, such as *C. trifascialis* and *C. lunulatus*, exhibit strong preferences for specific coral species (Pratchett 2005). Availability of these individual coral species may vary significantly from the availability of coral taxa groupings that were used in this study. Consequently, categorisation of dietary resources at a finer taxonomic resolution may be necessary to reflect true dietary resource availability for these butterflyfishes.

A further possibility is that availability of dietary resources is not the primary driver of local abundance at a geographic scale for these butterflyfishes. The inclusion of the variable representing interspecific competition (the ratio of total coral cover to the total abundance of all congeneric butterflyfishes) in final regression models indicates that competitive interactions are likely to influence local abundance. Competitive interactions may influence the range of habitats used by a species and asymmetric competition between species can lead to the exclusion of subordinate competitors from mutually preferred habitats (Connell 1983; Abramsky et al. 1990; Young 2004; Bonin et al. 2009). Although the overall predictive power of final regression models was low, the highly significant negative correlation between our interspecific competition variable and abundance for three of the five focal species is supported by previous studies which have shown that abundance of individual species may increase in the absence of interspecific competitors (Schmitt and Holbrook 1990; Robertson 1996). Competitive interactions are likely to have the strongest influence on the local abundance of obligate coral feeding butterflyfishes as this variable was included in regression models for *C. citrinellus, C. lunulatus* and *C. trifascialis* - the three species with the highest proportional consumption of hard corals. In agreement with previous observational studies of competitive interactions between butterflyfishes (Berumen and Pratchett 2006a), this study suggests that defence of preferred coral resources by dominant competitors may be negatively influencing local abundance patterns of coral feeding butterflyfishes.

Larval supply and recruitment may also be a key determinant of butterflyfish abundance at large spatial scales. Both of these factors are widely acknowledged to be highly variable across both space and time in marine populations (Doherty 1991; Caley et al. 1996; Doherty 2002). Differences in adult abundance have been shown to be strongly related to prior levels of recruitment for some reef fishes (Victor 1983, 1986; Holbrook et al. 2000) and variable larval supply may be contributing to the local patterns of abundance for the butterflyfishes considered here (Bell et al. 1985; Pratchett and Berumen 2008). A further possibility is that both larval supply and resource availability may be constraining local abundance, as appears to be occurring in some other reef fish populations (e.g. Forrester 1995; Schmitt and Holbrook 1999; Holbrook et al. 2000), such that recruit abundance is initially determined by larval supply then consequently regulated by resource availability. Juvenile obligate coral-feeding butterflyfishes are consistently found in close association with hard coral colonies in the field (Cole and Pratchett 2011) and the distribution of several species corresponds closely to the distribution of preferred coral micro-habitats (Pratchett et al. 2008a). These observations suggest that the availability of coral resources for both settlement habitat and food strongly influences the abundance of juvenile coral-feeding butterflyfish and may override initial abundance patterns established at settlement (Booth 2002). Further research is necessary to determine both the influence of resource availability on the abundance and distribution of juvenile butterflyfishes, and the relationship between juvenile and adult abundance.

Theory predicts that the abundance of specialist species should be lower than that of generalist counterparts, due to increased limits imposed by a restricted set of critical resources

(Brown 1984). This study confirmed that dietary resource availability has a greater influence on the abundance of the most specialised species (*C. trifascialis*), but this species was generally more abundant, not less abundant, than generalist counterparts. This is probably due to the high abundance of *Acropora* corals at most locations. Consequently, it should not be assumed that specialists will always be rarer than generalists. Chaetodon *trifascialis* is frequently one of most abundant butterflyfishes throughout its geographic range (Jones et al. 2002), and is generally only rare where there has been systematic depletion of *Acropora* corals (Berumen and Pratchett 2006b). These results highlight the need to be wary of assigning specialised species high vulnerability status due to an assumed low abundance and resource dependence without conducting independent assessments. Supporting this, recent research has demonstrated that *C. trifascialis* has a greater level of feeding plasticity and therefore a greater capacity to respond to coral loss than previously assumed (Lawton et al. In press-b), while genetic evidence suggests there is a high potential for *C. trifascialis* to recover from population declines (Lawton et al. 2011). These findings indicate that the vulnerability of *C. trifascialis* to coral loss on reefs is likely to be lower than has been previously assumed.

Chapter 5: High gene flow across large geographic scales reduces extinction risk for a highly specialised coral feeding butterflyfish[**]

5.1 ABSTRACT

The vulnerability of ecologically specialised species to environmental fluctuations has been well documented. However, population genetic structure can influence vulnerability to environmental change and recent studies have indicated that specialised species may have lower genetic diversity and greater population structuring compared to their generalist counterparts. To examine whether there were differences in population genetic structure between a dietary specialist (*Chaetodon trifascialis*) and a dietary generalist (*C. lunulatus*) the demographic history and levels of gene flow of two related coral-feeding butterflyfishes was compared. Using allele frequencies of $\geq$11 microsatellite loci and >350 bases of mitochondrial control region sequence, analyses of *C. trifascialis* and *C. lunulatus* from five locations across the Pacific Ocean revealed contrasting demographic histories and levels of genetic structure. Heterozygosity excess tests, neutrality tests and mismatch distributions were all highly significant in the dietary specialist *C. trifascialis* (all $P<0.01$), suggesting genetic bottlenecks have occurred in all locations. In contrast, There was little evidence of genetic bottlenecks for the dietary generalist *C. lunulatus*. High gene flow and low genetic structuring was detected among locations for *C. trifascialis* (AMOVA: $R_{ST} = 0.0027$, $P=0.371$; $\Phi_{ST}=0.068$, $P< 0.0001$). Contrary to expectations, a greater level of genetic structuring between locations was detected for *C. lunulatus* (AMOVA: $R_{ST} = 0.0277$, $\Phi_{ST} = 0.166$, both $P< 0.0001$). These results suggest that dietary specialisation may affect demographic history through reductions in

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population size following resource declines, without affecting population structure through reductions in gene flow in the same way that habitat specialisation appears to. Although *C. trifascialis* is highly vulnerable to coral loss, the high gene flow detected here suggests populations will be able to recover from local declines through recolonisation from healthy source populations.

5.2 INTRODUCTION

Biodiversity is declining globally and an increasing number of species are threatened by the combined effects of habitat loss, climate change and other anthropogenic disturbances (Pimm et al. 1995; Vitousek et al. 1997; Thomas et al. 2004). Susceptibility to disturbance and overall extinction risk may be influenced by a range of factors (McKinney 1997; Purvis et al. 2000a; Dulvy et al. 2003). Ecological specialisation is often correlated with high vulnerability and extinction risk (McKinney 1997; Colles et al. 2009) because specialist species tend to be disproportionately affected by changes in resource availability. For example, greater declines in local abundance have been observed in specialised species of birds (Aitken and Martin 2008), mammals (Harcourt et al. 2002), amphibians (Swihart et al. 2003), marsupials (Fisher et al. 2003), coral reef fishes (Munday 2004), insects (Kotze and O'Hara 2003) and butterflies (Charrette et al. 2006) compared to generalist counterparts following declines in habitat availability. If all things are equal, then specialist species will be much more vulnerable to local and global extinction compared to generalist counterparts, but the risk of extinction may be moderated by a number of other biological attributes (Williams et al. 2006).

The genetic structure of species and populations can have large impacts on their vulnerability to environmental change and overall extinction risk. Substantial evidence suggests that genetic diversity is an important factor influencing population viability (Frankham 2005, 2010). Loss of genetic diversity can increase extinction risk as it reduces the ability of populations to evolve and deal with environmental change (Spielman et al. 2004; Frankham 2010). Gene flow and the level of connectivity between populations can also directly influence population persistence and stability (Hanski 1999). Low gene flow can lead to genetic drift and loss of genetic diversity (Keller and Waller 2002), reducing adaptive capacity and increasing the vulnerability of local populations to disturbance. In contrast, high gene flow and population connectivity may help guard against extinction as migration and dispersal can rescue declining populations and enable recolonisation of locations where species are extirpated (Hanski 1999; Pannell 2003; Jones et al. 2009). While there is a growing body of case studies documenting the demographic effects of resource declines on specialised species (e.g. Harcourt et al. 2002; Munday 2004; Charrette et al. 2006), the effect of ecological specialisation on genetic structure has received relatively little attention. However, ecological specialisation has the potential to reduce gene flow and population connectivity if the restricted use of resources by specialised species limits their geographical distribution (e.g. Ortego et al. 2010) and/or prevents successful dispersal between isolated populations (e.g. Koivula et al. 2002).

Comparative studies of the genetic structure of related species with contrasting levels of ecological specialisation are relatively rare. A phylogeographic study of three Hawaiian butterflyfishes with varying levels of dietary specialisation found high levels of gene flow across the Hawaiian archipelago for all three species (Craig et al. 2010). In contrast, a phylogeographic study of four species of Atlantic wrasse found that species with wide distributions and broad habitat preferences had low levels of genetic population structuring and shared a high number of haplotypes, whereas species with specialised habitat preferences had high levels of genetic structuring between populations suggesting lower levels of migration (Rocha et al. 2005). Higher genetic structure and lower genetic diversity was also found in fragmented populations of a habitat specialist gecko species compared to a sympatric generalist species (Hoehn et al. 2007). Likewise, a study of fine-scale genetic structure between a habitat specialist and generalist species of carabid beetle showed that although genetic differentiation differed significantly between populations of both species, the specialist species had greater genetic structure than the generalist species (Brouat et al. 2003). Similar findings of greater population structuring in specialist compared to generalist species have also been reported for kestrels (Alcaide et al. 2009) and snakes (DiLeo et al. 2010). While these studies have greatly advanced our understanding of the potential effects of ecological specialisation on genetic structure, it is still too early for a scientific consensus on this topic. As studies have focused predominantly on habitat specialists, a crucial knowledge gap is the effect of dietary specialisation on genetic structure.

Coral reef butterflyfishes (Genus *Chaetodon*) provide an ideal model in which to investigate questions regarding dietary specialisation, vulnerability to environment change, extinction risk and population genetic structure because members of this diverse family display a range of ecological attributes. For example, the geographic range size and abundance of species within this family vary by several orders of magnitude (Jones et al. 2002; Pratchett et al. 2008b). The dietary preferences and ecological specialisation of individual species also vary significantly and range from species such as *Chaetodon kleinii* that feed on soft corals, hard corals, reef substrates and other macro-invertebrates, to species such as *C. baronessa* that only feed on a small number of hard coral species (Pratchett 2005). Recent research has indicated that many butterflyfishes are highly susceptible to coral loss caused by a range of disturbances (Wilson et al. 2006). In particular, some species are very sensitive to the effects of climate-induced coral bleaching because they feed predominantly on hard corals (Pratchett et al. 2008b). Susceptibility differs among species, but butterflyfishes with specialised diets are most at risk from the impacts of climate change on coral reefs (Pratchett et al. 2008b). These attributes make butterflyfishes ideal candidates to explore the links between population connectivity and dietary specialisation and their influence on extinction risk more generally, while also providing specific data on the vulnerability of butterflyfishes to the impacts of climate change.

The chevron butterflyfish, *C. trifascialis,* has the most specialised diet of all butterflyfishes, feeding almost exclusively on a few species of tabular *Acropora* corals (Pratchett 2005). Tabular *Acropora* corals are highly sensitive to climate-induced bleaching and have fluctuated in abundance following bleaching episodes (Marshall and Baird 2000). Due to *C. trifascialis*' highly specialised dietary ecology and its reliance on these sensitive coral species, declines in population abundance are predicted as ocean temperatures rise. Declines of almost 100% have already been reported for *C. trifascialis* following coral loss at some locations (Moorea: Berumen and Pratchett 2006b; Seychelles: Graham et al. 2006; Great Barrier Reef: Pratchett et al. 2006); however, fluctuations in local population sizes in response to coral loss are unknown for most regions. In contrast*,* the related redfin butterflyfish, *C. lunulatus*, is also an obligate corallivore but has a generalist diet, consuming a broad range of hard corals from many different genera (Pratchett 2005). Although *C. lunulatus* is also susceptible to coral loss, populations have not declined to the same extent as those of *C. trifascialis* (Berumen and Pratchett 2006b; Pratchett et al. 2006; Wilson et al. 2006). As both species have similar life histories their differential response to coral loss has largely been attributed to their differing levels of dietary specialisation (Pratchett et al. 2008b). With coral loss and degradation of reef ecosystems predicted to increase (Hoegh-Guldberg et al. 2007), *C. trifascialis* is likely to be at high risk of local extinction. However, the potential for recovery from local declines through recolonisation by gene flow and connectivity between populations is not yet known.

Due to their bi-partite life history and dispersive larval phase, populations of coral reef fishes have been traditionally regarded as “open” systems, with high levels of gene flow across large geographic distances (Sale 1991; Caley et al. 1996; Mora and Sale 2002; Jones et al. 2009).

However, this “open” population paradigm has been challenged by recent findings of fine scale (4-30 km) genetic structure between reef fish populations (Taylor and Hellberg 2003; Hoffman et al. 2005; Gerlach et al. 2007; Bay et al. 2008) and evidence that reef fishes may be connected on much smaller spatial scales than have previously been assumed (Jones et al. 2005; Planes et al. 2009). For example, a recent study of the vagabond butterflyfish (*C. vagabundus*) in Papua New Guinea found that approximately 60% of larvae returned to the same reef where they were spawned, despite spending an average of 38 days in the pelagic environment (Almany et al. 2007). Although recent genetic studies have also shown high panmixia (e.g. Haney et al. 2007; Horne et al. 2008; Gaither et al. 2010), the extent to which populations of reef fish are open or closed is still regarded as unknown (Mora and Sale 2002). It is possible therefore, that gene flow and connectivity between *C. trifascialis* and *C. lunulatus* populations may be low, even though both species have large geographic ranges (Allen et al. 1998) and reasonably long pelagic larval durations (PLD ~40 days, Leis 1989).

To examine whether there were differences in population genetic structure between the dietary specialist *C. trifascialis* and the dietary generalist *C. lunulatus*, mitochondrial control region sequence data and 11/12 polymorphic microsatellite loci were analysed. In particular, I was interested in determining their susceptibility to historical and recent environmental changes on reefs, and predicting their recovery potential in areas where local populations have declined. Therefore the demographic history and population genetic structure of both species was compared at five locations across the Pacific Ocean. The specific aims were to (i) detect evidence of population declines at any of the sampling locations; (ii) estimate levels of gene flow between sampling locations to enable predictions of likely recovery potential; and (iii) compare recent and historical patterns in demographic history and population structure to provide an overall estimate of vulnerability for both species. Based on their reliance on tabular *Acropora* corals and reported loss of coral at Lizard Island and Moorea (Berumen and Pratchett

2006b; Pratchett et al. 2008b), it was hypothesised that *C. trifascialis* would show evidence of recent population declines. Greater population structure was also expected in *C. trifascialis* compared to *C. lunulatus* due to its specialised ecology.

5.3 METHODS

5.3.1 Sampling collection and laboratory procedures

Tissue samples were collected from up to 50 individuals of each species at five locations across the Pacific: Lizard Island, Northern Great Barrier Reef; Heron Island, Southern Great Barrier Reef; Kimbe Bay, Papua New Guinea; Noumea, New Caledonia; and Moorea, French Polynesia (Fig. 3.1). Fish were collected using hand nets and samples of fin tissue were immediately preserved in 90% EtOH following collection. Genomic DNA was extracted from ~2mm^2 of tissue samples using proteinase-K digestion and silica based purification (Elphinstone et al. 2003). Twelve polymorphic microsatellite loci were amplified for 231 individuals in *C. lunulatus* (Table 5.2, Lawton et al. 2010, Appendix 1), and 11 polymorphic microsatellite markers for 209 individuals in for *C. trifascialis* (Table 5.3, Lawton et al. 2010, Appendix 1). Each forward primer was directly labelled with one of three fluorescent labels (TET, FAM, or HEX) and microsatellite loci were amplified in 10µL multiplex PCR reactions containing 5 µL 2x QIAGEN Multiplex PCR Master Mix (3mM $MgCl_2$), 1µL primer mix (0.2µM of TET labelled primer, and 0.4µM each of FAM and HEX labelled primers), and 10-40 ng of genomic DNA. Reactions were cycled in a BioRad C1000 Thermal Cycler (Cycling parameters: hot start activation for 15 min at 95^{o}C, 40 cycles of 30 s denaturing at 94^{o}C, 90 s annealing at 58^{o}C, 60 s extension at 72^{o}C, and a final extension at 60^{o}C for 30 min). 10µL of PCR product was column purified using Sephadex G-25 resin. Alleles were identified using a capillary sequencer (Megabase, Amersham Biosciences) with a 400 base pair size standard and scored using Fragment Profiler© 1.2 (Amersham Biosciences).

The mitochondrial control region I (D-loop) was amplified using PCR in up to 30 individuals from each location for each species using the universal primers CRA (5'-TTC CAC CTC TAA CTC CCA AAG CTA G-3') and CRE (5'-CCT GAA GTA GGA ACC AGA TG-3') (Lee et al. 1995). Individuals from Papua New Guinea and Heron Island were amplified in 25µL PCR reactions containing 1 x PCR buffer, 2.5mM $MgCl_2$, 0.2µM each dNTP, 1 unit BioTaq DNA polymerase (Bioline™), 100ng DNA and 0.5µM each primer. Amplification was performed on a BioRad C1000 Thermal Cycler (Cycling parameters: 2 min at 94°C, 30 cycles of 30 s denaturing at 94°C, 45 s annealing at 49°C, 60 s extension at 72°C, and a final extension at 72°C for 10 min). PCR purification and sequencing was carried out by Macrogen Inc. Individuals from Lizard Island, New Caledonia and French Polynesia were amplified and sequenced by Messmer (2010), following the same methods. Multiple individuals were sequenced in reverse direction to test the reliability of the sequences. As the consensus of forward and reverse sequences was entirely congruent, the remaining individuals were only sequenced in forward direction. Sequences were aligned (bp) using Sequencher™ v.4.2.2 (Gene Codes Corporation, Ann Arbor, MI, USA). All sequences were trimmed to the shortest sequence length (*C. lunulatus*: 363 bp; *C. trifascialis*: 353 bp).

5.3.2 Descriptive Statistics

The number of alleles, observed and expected heterozygosities, and conformation to Hardy-Weinberg expectations for each microsatellite locus were examined using Arlequin 3.5 (Excoffier and Lischer 2010). Linkage disequilibrium was tested using GENEPOP on the web (Raymond and Rousset 1995) and the presence of null-alleles using Micro-checker 2.2.3 (Van Oosterhout et al. 2004). Significance levels were adjusted for multiple tests using a false discovery rate (FDR) correction (Benjamini and Hochberg 1995). All microsatellite loci were in Hardy-Weinberg equilibrium for both species (P>FDR corrected $\alpha = 0.0011$). There was no evidence of scoring error due to stuttering or large allele dropout in any of the loci for *C.*

lunulatus, but there was some suggestion of null alleles due to homozygote excess in Lun05 and Lun20 for the French Polynesia samples. There was no evidence of linkage disequilibrium among loci for *C. lunulatus* (P>FDR corrected $\alpha = 0.0078$). For *C. trifascialis,* there was some suggestion of null alleles due to homozygote excess in Lun03 for the Heron Island and Papua New Guinea samples, and Tri38 for the Heron Island, Papua New Guinea and French Polynesia samples. There was evidence of linkage disequilibrium (P < FDR corrected $\alpha = 0.00807$) for one pair of loci for the *C. trifascialis* Heron Island samples (Lun05 and Tri08) and three pairs of loci for the *C. trifascialis* New Caledonia samples (Tri38 and Lun03; Lun05 and Lun22; Lun03 and Lun22). However, as there was no consistent evidence for null alleles or linkage disequilibrium across all sampled locations, the entire data set was retained and examined. Nucleotide diversity (π) of the mitochondrial DNA (mtDNA) sequence data was estimated in Arlequin 3.5 (Excoffier and Lischer 2010) and haplotype diversity (h) was estimated in DnaSP 5.10.01 (Librado and Rozas 2009) for each location and each species. A maximum likelihood approach implemented in Modeltest 0.1.1 (Guindon and Gascuel 2003; Posada 2008) was used to determine the best evolutionary model and obtain gamma corrections. Aikaike information criterion (AIC) indicated that the K80+G model best described both species with a gamma correction of 0.196 for *C. lunulatus* and 0.320 for *C. trifascialis*. Because this model was not available in Arlequin 3.5 (Excoffier and Lischer 2010) a similar model (Kimura 2P) was implemented.

5.3.3 Demographic history

Recent demographic history was investigated using microsatellite allele frequencies. The occurrence of recent genetic bottlenecks in each location for each species was investigated using a test of heterozygosity excess implemented in Bottleneck 1.2.0.2 (Cornuet and Luikart 1996; Piry et al. 1999). Heterozygosity excess is expected in populations that have experienced a significant reduction in size because the number of alleles is reduced faster than heterozygosity by a rapid loss of rare alleles (Cornuet and Luikart 1996). An infinite alleles model (IAM), a stepwise mutation model (SMM), and a two phase model (TPM), which incorporates elements of the IAM and SMM model (variance=12, SMM = 95%, Piry et al. 1999), were used. Statistical significance was assessed using the Wilcoxon signed ranks test, a robust test applied to data sets with less than 20 polymorphic loci (Luikart and Cornuet 1998). Significance levels were adjusted for multiple tests using FDR as above. As an alternate approach to detect recent genetic bottlenecks the M-ratio test implemented in M_P_Val (Garza and Williamson 2001) was used. The ratio of the number of alleles to the range in allele size (the M-ratio) is expected to be lower in declining populations due to the loss of rare alleles at intermediate allele size classes. A series of equilibrium M-ratio distributions were generated for each location and species using a wide range of input parameters (θ = 1–100; proportion of non-one-step mutations (ps) = 0.01–0.99; average size of non-one-step mutations (Delta G) = 2–10) and these were compared to observed M-ratios. Results were considered significant if 5% of simulated equilibrium M-ratios were less than the observed M-ratio for each location (Garza and Williamson 2001).

Historical demography was investigated using mitochondrial sequence data. Fu's F_s statistic (Fu 1997) and the R_2 statistic (Ramos-Onsins and Rozas 2002) were calculated for each location for each species as these are the most powerful tests for detecting population growth using sequence data (Ramos-Onsins and Rozas 2002). Calculations were implemented in Arlequin 3.5 (Excoffier and Lischer 2010) and DnaSP 5.10.01 (Librado and Rozas 2009) and significance was assessed using 10,000 coalescent simulations. Significance levels were adjusted for multiple tests using FDR as above. Significant negative F_s statistics and significant low R_2 statistics can be interpreted as signatures of population expansion (Fu 1997; Ramos-Onsins and Rozas 2002). Historical demography was also investigated using mismatch distributions of pairwise nucleotide differences among individuals. Populations that have undergone expansion typically show a smooth or unimodal distribution, whereas more stable populations show a ragged or multimodal distribution (Rogers and Harpending 1992). The distributions of pairwise nucleotide differences expected under models of constant and sudden expansion were generated for each location for each species in DnaSP. The best fit model was determined using the sum of square deviations (SSD) from the observed mismatch distribution and log-likelihood ratio tests following the methodology outlined in Burnham & Anderson (2002).

5.3.4 Population Structure

Population structure was investigated using three complementary approaches for each species: an analysis of molecular variance (AMOVA) and pairwise comparisons between locations (mtDNA and microsatellite data), haplotype networks (mtDNA data), and a Bayesian model-based clustering method (microsatellite data). Genetic structuring between locations was tested with AMOVA using the F_{ST} analogues Φ_{ST} for mtDNA data and R_{ST} for microsatellite data (10,000 permutations). Pairwise genetic distances (Φ_{ST} and R_{ST}) were calculated to test for significant differences between individual pairs of locations (10,000 permutations). Analyses were implemented in Arlequin 3.5 and significance levels were adjusted for multiple tests using FDR as above. Relatedness and spatial distribution of mtDNA haplotypes was assessed using a minimum spanning haplotype network. Haplotype networks were computed for each species using a pairwise distance model in Arlequin 3.5. The minimum spanning tree was drawn for clarity of presentation.

A Bayesian clustering analysis was implemented in Structure 2.3 (Pritchard et al. 2000) to identify the number of distinct genetic clusters (*K*) represented by the microsatellite data. This programme uses a Monte Carlo Markov Chain (MCMC) approach to detect potentially existing genetic structure without imposing prior population substructure. Individuals are placed in *K* predetermined sub-groups, using allele frequencies at multiple loci, based on their likelihood of belonging to that subgroup. For each species, a series of ten independent trials were run for each value of *K* from 1 to 5, with an initial burn-in of 1,000,000 iterations and an additional 10,000,000 iterations. Correlated allele frequencies and the admixture model were assumed. Summary statistics (log likelihood and alpha) were monitored to verify convergence. Because initial simulations failed to converge and AMOVA results indicated that population structure was very low for both species, simulations were run with a LOCPRIOR model which uses sampling locations as prior information. This model can improve performance where the signal of structure is too weak to be found using the standard model (Hubisz et al. 2009). All simulations were run on the computer clusters at Cornell University's Computational Biology Service Unit (CUCBSU; http://cbsuapps.tc.cornell.edu/index.aspx). The most likely number of clusters was determined using Delta *K* (Δ*K*) following Evanno et al. (2005) by examining the second order rate of change in the posterior probability of observing the data given the number of clusters (Ln *Pr(X|K))*. The number of clusters best fitting the data is taken to be the value of *K* at which *Pr(X|K*) plateaus.

5.4 RESULTS

5.4.1 Genetic Diversity

Microsatellite loci were highly polymorphic in both species (Tables 5.1, 5.2 & 5.3). The number of detected alleles per locus across all locations ranged from 9 to 31 for *C. lunulatus*, and from 10 to 38 for *C. trifascialis*. Within locations, the number of detected alleles per locus ranged from 4 to 26 alleles with a mean of 14.6 (±0.8 S.E.) alleles in *C. lunulatus,* and from 4 to 29 alleles with a mean of 14.1 (±0.9 S.E.) in *C. trifascialis*. Expected heterozygosities were high, averaging 0.79 (±0.02 S.E.) and 0.85 (±0.02 S.E.) across all loci and locations for *C. lunulatus* and *C. trifascialis* respectively. Genetic diversity was also high for the mtDNA sequence data, with a total of 84 and 81 different haplotypes identified for *C. lunulatus* and *C. trifascialis* respectively. Nucleotide diversities ranged from 0.024 to 0.050 for *C. lunulatus* and were higher than those of *C. trifascialis,* which ranged from 0.011 to 0.016 (Table 5.1). With the exception of the *C. lunulatus* samples from French Polynesia (*h*=0.748), haplotype diversities in all other locations were similar for both species, ranging from 0.897 to 0.983 for *C. lunulatus*, and from 0.941 to 0.980 for *C. trifascialis.*

Table 5.1 Descriptive statistics for microsatellite loci and mitochondrial sequence data for *C. lunulatus* and *C. trifascialis* from five locations. HI: Heron Island; LI: Lizard Island; PNG: Papua New Guinea; NC: New Caledonia; FP: French Polynesia

	Microsatellite data				Mitochondrial data		
	N	*Na*	*Ho*	*He*	*N*	π	*h*
<u>*C. lunulatus*</u>							
HI	38	13.4 (4 - 23)	0.76 (0.37 - 0.95)	0.79 (0.37 - 0.95)	27	0.046	0.897
LI	46	15.4 (6 - 24)	0.79 (0.52 - 0.93)	0.81 (0.37 - 0.94)	27	0.045	0.937
PNG	50	15.3 (5 - 23)	0.78 (0.40 - 1.00)	0.78 (0.37 - 0.94)	29	0.050	0.983
NC	49	16.7 (5 - 26)	0.80 (0.40 - 0.94)	0.81 (0.37 - 0.95)	26	0.048	0.948
FP	48	12.3 (5 - 22)	0.73 (0.33 - 0.92)	0.77 (0.37 - 0.91)	26	0.024	0.748
<u>*C. trifascialis*</u>							
HI	40	13.6 (6 - 27)	0.82 (0.60 - 0.95)	0.84 (0.37 - 0.96)	29	0.014	0.980
LI	40	14.7 (7 - 29)	0.87 (0.55 - 0.97)	0.84 (0.37 - 0.96)	28	0.016	0.971
PNG	43	14.8 (4 - 27)	0.80 (0.50 - 0.93)	0.84 (0.37 - 0.96)	27	0.013	0.949
NC	47	14.5 (6 - 26)	0.80 (0.62 - 0.95)	0.84 (0.37 - 0.96)	25	0.015	0.948
FP	39	13.0 (6 - 26)	0.82 (0.67 - 0.97)	0.83 (0.37 - 0.95)	26	0.011	0.943

Microsatellite statistics are averages (range) over all loci for each location and species: Number of samples (*N*), number of alleles (*Na*), observed heterozygosities (*Ho*) and expected heterozygosities (*He*), nucleotide diversity (π) and haplotype diversity (*h*).

5.4.2 Demographic History

Heterozygosity excess tests showed no evidence of recent genetic bottlenecks for the dietary generalist *C. lunulatus* at any location except Heron Island, which was significant under the IAM (Table 5.4). In contrast, a highly significant heterozygosity excess was detected in the dietary specialist *C. trifascialis* at all five locations under the IAM, providing strong evidence for recent genetic bottlenecks (Table 5.4). For both species, heterozygosity excess tests were non-significant for all locations under the TPM and the SMM ($P>0.66$ for all tests). The M-ratios were high ($M>1$ for all locations) and well above 0.68, which Garza & Williamson (2001) suggest as an upper limit for M-ratios in populations which have experienced bottlenecks. All

Table 5.2 Number of samples (*N*), number of alleles (*Na*), observed heterozygosities (*Ho*) and expected heterozygosities (*He*) of 12 microsatellite loci for *C. lunulatus* from five locations.

	Lun01	Lun03	Lun05	Lun07	Lun08	Lun10	Lun20	Lun22	Lun36	Tri13	Tri38	Tri42
Heron Island												
N	38	37	38	38	38	38	38	38	38	38	37	38
Na	16	8	22	10	20	18	16	11	23	4	7	6
Ho	0.79	0.84	0.95	0.87	0.89	0.84	0.87	0.89	0.89	0.37	0.38	0.53
He	0.84	0.86	0.94	0.85	0.93	0.93	0.92	0.86	0.95	0.38	0.52	0.52
Lizard Island												
N	46	47	46	47	44	46	45	43	45	44	44	46
Na	17	9	24	14	19	22	19	12	23	6	13	7
Ho	0.85	0.87	0.85	0.83	0.84	0.87	0.84	0.88	0.93	0.52	0.55	0.63
He	0.83	0.85	0.93	0.87	0.92	0.93	0.93	0.85	0.94	0.54	0.58	0.57
Papua New Guinea												
N	50	49	50	49	50	50	50	47	50	50	50	50
Na	21	11	23	14	23	21	17	12	23	5	9	5
Ho	0.9	0.86	0.86	0.84	1	0.92	0.84	0.91	0.96	0.48	0.4	0.4
He	0.87	0.87	0.9	0.85	0.93	0.92	0.92	0.84	0.94	0.42	0.5	0.45
New Caledonia												
N	49	50	47	50	50	47	50	48	50	50	49	50
Na	19	11	23	15	23	23	21	14	26	5	12	8
Ho	0.88	0.86	0.89	0.92	0.86	0.91	0.84	0.92	0.94	0.44	0.71	0.4
He	0.88	0.87	0.94	0.9	0.93	0.93	0.93	0.86	0.95	0.43	0.65	0.44
French Polynesia												
N	48	48	48	48	48	48	48	48	48	48	47	48
Na	12	9	16	16	20	11	14	7	22	5	10	5
Ho	0.83	0.77	0.81	0.88	0.92	0.73	0.73	0.67	0.9	0.33	0.68	0.48
He	0.77	0.78	0.91	0.89	0.86	0.84	0.86	0.77	0.88	0.44	0.67	0.53

Table 5.3 Number of samples (*N*), number of alleles (*Na*), observed heterozygosities (*Ho*) and expected heterozygosities (*He*) of 11 microsatellite loci for *C. trifascialis* from five locations.

	Tri13	Tri38	Tri42	Tri22	Lun05	Tri46	Lun03	Tri10	Lun22	Tri14	Tri08
Heron Island											
N	40	40	40	40	40	40	40	40	40	40	40
Na	14	27	6	9	13	7	22	18	12	8	14
Ho	0.95	0.83	0.6	0.83	0.85	0.75	0.75	0.85	0.95	0.88	0.8
He	0.87	0.96	0.56	0.82	0.89	0.72	0.93	0.93	0.88	0.82	0.87
Lizard Island											
N	40	39	40	40	40	40	39	38	39	39	39
Na	12	29	8	8	14	7	23	19	17	11	14
Ho	0.93	0.92	0.55	0.8	0.93	0.68	0.95	0.95	0.97	0.9	0.97
He	0.87	0.96	0.55	0.82	0.9	0.67	0.93	0.94	0.89	0.78	0.91
Papua New Guinea											
N	43	42	42	43	43	43	43	43	43	43	43
Na	12	26	4	12	13	8	27	19	15	12	15
Ho	0.93	0.86	0.5	0.86	0.91	0.7	0.67	0.88	0.86	0.77	0.86
He	0.87	0.96	0.51	0.85	0.9	0.68	0.93	0.94	0.89	0.81	0.89
New Caledonia											
N	47	46	47	45	45	45	47	46	47	45	44
Na	14	25	7	10	14	6	26	21	14	9	13
Ho	0.85	0.76	0.64	0.8	0.87	0.62	0.89	0.87	0.83	0.69	0.95
He	0.86	0.96	0.6	0.84	0.92	0.64	0.94	0.93	0.92	0.76	0.91
French Polynesia											
N	39	38	39	39	39	39	39	39	39	39	39
Na	14	26	7	7	12	6	23	15	14	7	12
Ho	0.82	0.95	0.67	0.69	0.9	0.72	0.9	0.82	0.97	0.69	0.87
He	0.87	0.95	0.61	0.82	0.91	0.71	0.94	0.84	0.88	0.75	0.89

Table 5.4 Analysis of recent genetic bottlenecks in *C. lunulatus* and *C. trifascialis* from five locations using an infinite alleles model (IAM). Significant values at FDR corrected α = 0.022 are shown in bold. Location abbreviations follow Table 5.1.

	HI	LI	PNG	NC	FP
C. lunulatus	**0.02**	0.06	0.15	0.15	0.08
C. trifascialis	**<0.001**	**<0.01**	**<0.001**	**<0.001**	**<0.01**

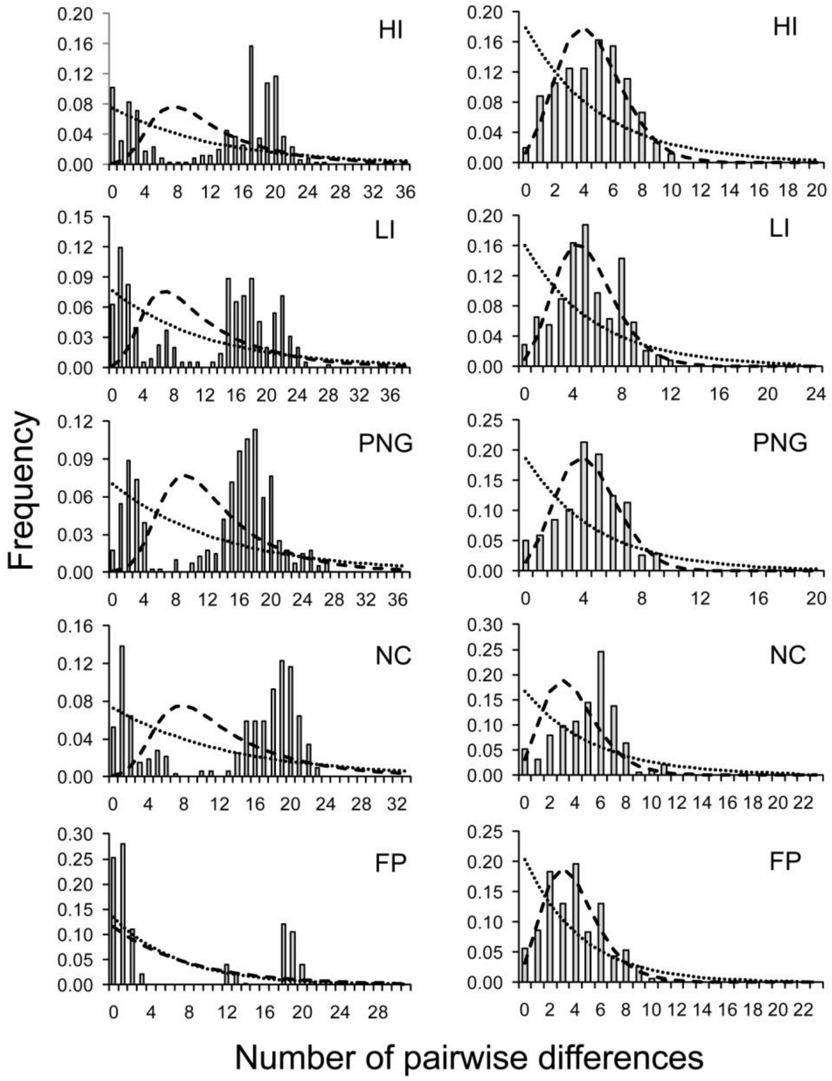

Figure 5.1 Mismatch distributions for *C. lunulatus* (left column) and *C. trifascialis* (right column) from five locations. Filled bars indicate the observed frequency of pairwise distributions, dashed lines indicate the expected distribution under a model of exponential expansion and dotted lines indicated the expected distribution under a constant population model. Location abbreviations follow Table 5.1.

M-ratios were non-significant, regardless of input parameters, providing no evidence for recent genetic bottlenecks.

Neutrality indices and mismatch distribution analyses revealed contrasting demographic histories for *C. lunulatus* and *C. trifascialis.* F_s statistics were negative and highly significant in all locations for the dietary specialist *C. trifascialis* and for *C. lunulatus* samples from Papua New Guinea*.* The Heron Island and French Polynesia samples of *C. trifascialis* also had low and significant R_2 statistics (Table 5.5), indicating historical expansion. All locations had unimodal mismatch distributions for *C. trifascialis* (Fig. 5.1), providing further evidence of historical population expansion, and log-likelihood analyses were significant for all locations except New Caledonia, indicating that a sudden expansion model provided the best fit to the observed mismatch distributions (Table 5.6). In contrast, mismatch distributions for the dietary generalist *C. lunulatus* were characterised by bimodal peaks in all locations, indicative of more stable populations (Fig. 5.1) and log-likelihood analyses of mismatch distributions were non-significant for all locations (Table 5.6), supporting a constant population model.

Table 5.5 Neutrality test results for *C. lunulatus* and *C. trifascialis* from five locations. Significant values at FDR corrected $\alpha = 0.022$ are shown in bold. Location abbreviations follow Table 5.1.

	Fu's F	*P*	Roza's R_2	*P*
C. lunulatus				
HI	-2.65	0.16	0.12	0.53
LI	-3.80	0.09	0.08	0.25
PNG	**-8.69**	**<0.01**	0.10	0.31
NC	-3.95	0.07	0.12	0.51
FP	0.57	0.63	0.09	0.13
C. trifascialis				
HI	**-19.62**	**<0.0001**	**0.06**	**<0.01**
LI	**-13.93**	**<0.0001**	0.08	0.09
PNG	**-9.02**	**<0.001**	0.09	0.15
NC	**-9.87**	**<0.0001**	0.08	0.05
FP	**-12.95**	**<0.0001**	**0.05**	**<0.0001**

Table 5.6 Mismatch distribution analysis of *C. lunulatus* and *C. trifascialis* from five locations. Data are mean number of pairwise differences (mismatch), sums of squared deviation from observed values under constant population (SSD con) and exponential expansion (SSD exp) models, log-likelihood ratio of population model fits (Log-likelihood) and *P* values. Significant values at FDR corrected $\alpha = 0.022$ are shown in bold. Location abbreviations follow Table 5.1.

	Mismatch	SSD con	SSD exp	Log-likelihood	*P*
C. lunulatus					
HI	12.36	0.046	0.063	4.78	0.09
LI	12.03	0.025	0.033	4.75	0.09
PNG	13.26	0.036	0.048	4.79	0.09
NC	12.69	0.046	0.061	4.05	0.13
FP	6.45	0.078	0.075	0.49	0.78
C. trifascialis					
HI	4.60	0.057	0.008	18.08	**<0.001**
LI	5.22	0.062	0.014	16.41	**<0.001**
PNG	4.37	0.073	0.011	17.00	**<0.001**
NC	4.99	0.080	0.059	3.15	**0.21**
FP	3.90	0.052	0.010	17.22	**<0.001**

5.4.3 Population Structure

AMOVA analyses for both species revealed that almost all of the genetic variation in both microsatellite and mtDNA data was within locations (Microsatellite data: 97.2% for *C. lunulatus* and 99.7% for *C. trifascialis*, mtDNA data: 83.4% for *C. lunulatus* and 93.2% for *C. trifascialis*). Very little variation was attributed among locations (Table 5.7). Although the microsatellite data of the dietary generalist *C. lunulatus* produced a low overall R_{ST} value, this was still highly significant ($P < 0.0001$). In contrast, the overall R_{ST} value for the dietary specialist *C trifascialis* was order of magnitude lower compared to *C. lunulatus* and non-significant ($R_{ST} = 0.003$, $P = 0.37$). Overall Φ_{ST} values were larger when using the mtDNA data (*C. lunulatus:* $\Phi_{ST} = 0.166$, *C. trifascialis:* $\Phi_{ST} = 0.068$) and highly significant for both species ($P < 0.0001$, Table 5.7).

Table 5.7 Analysis of molecular variance (AMOVA) results for *C. lunulatus* and *C. trifascialis* from five locations using microsatellite (R_{ST}) and mitochondrial (Φ_{ST}) data.

Source of variation	d.f.	SS	Variance components	% of variation	R_{ST} / Φ_{ST}	P
C. lunulatus						
Microsatellite data						
Among locations	4	19910	39	2.9	0.0278	<0.0001
Within locations	461	627339	1361	97.2		
Total	465	647249	1400			
Mitochondrial data						
Among locations	4	757	5.9	16.6	0.1661	<0.0001
Within locations	130	3860	29.7	83.4		
Total	134	4617	35.6			
C. trifascialis						
Microsatellite data						
Among locations	4	12230	7	0.3	0.0027	0.371
Within locations	413	1032546	2500	99.7		
Total	417	1044776	2507			
Mitochondrial data						
Among locations	4	39	0.2	6.8	0.0680	<0.0001
Within locations	130	430	3.3	93.2		
Total	134	469	3.5			

Pairwise comparisons based on the microsatellite data indicated that the Papua New Guinea and French Polynesia samples were significantly different from all other locations for *C. lunulatus*, but there were no significant differences between Lizard Island, Heron Island and New Caledonia (Table 5.8). Pairwise comparisons of *C. trifascialis* indicated that there were no significant differences between any locations (Table 5.8). Using the mtDNA data, pairwise comparisons showed that the French Polynesia samples were significantly different from all other locations for both species (Table 5.8). *C. trifascialis* samples from Lizard Island were also significantly different from those collected at Heron Island.

Table 5.8 Pairwise comparison values (above diagonal) and significance levels (below diagonal) between *C. lunulatus* and *C. trifascialis* from five locations using microsatellite (R_{ST}) and mitochondrial (Φ_{ST}) data. Significant values at FDR corrected $\alpha = 0.017$ are shown in bold. Location abbreviations follow Table 5.1.

	HI	LI	PNG	NC	FP
C. lunulatus					
R_{ST}					
HI	-	0.011	0.016	0.011	0.077
LI	NS	-	0.027	-0.007	0.044
PNG	**0.012**	**<0.001**	-	0.015	0.054
NC	NS	NS	**0.013**	-	0.040
FP	**<0.001**	**<0.001**	**<0.001**	**<0.001**	-
Φ_{ST}					
HI	-	-0.015	-0.011	-0.030	0.397
LI	NS	-	0.016	-0.017	0.404
PNG	NS	NS	-	-0.028	0.370
NC	NS	NS	NS	-	0.429
FP	**<0.001**	**<0.001**	**<0.001**	**<0.001**	-
C. trifascialis					
R_{ST}					
HI	-	-0.004	-0.009	-0.002	0.024
LI	NS	-	-0.009	-0.008	0.012
PNG	NS	NS	-	-0.005	0.025
NC	NS	NS	NS	-	0.009
FP	NS	NS	NS	NS	-
Φ_{ST}					
HI	-	0.059	0.035	0.056	0.228
LI	**<0.05**	-	0.007	0.029	0.065
PNG	NS	NS	-	-0.006	0.096
NC	NS	NS	NS	-	0.104
FP	**<0.001**	**<0.05**	**<0.01**	**<0.01**	-

The haplotype network based on mtDNA data for the dietary specialist *C. trifascialis* was characterised by multiple starlike patterns where haplotypes were separated by only a few base pair changes (Fig. 5.2). Fourteen haplotypes were shared by individuals of at least two locations and the greatest number of base pair changes separating any two haplotypes was six. In contrast, 19 nodes of the *C. lunulatus* haplotype network were separated by at least five base pair changes (maximum base changes was 16) and only six haplotypes were shared between locations (Fig. 5.2). With the exception of a single cluster of haplotypes in the *C. lunulatus* network that comprised 21 individuals from French Polynesia and one individual from Papua New Guinea, there was little haplotype partitioning by geographic location for either species, and all locations shared at least one haplotype with each other.

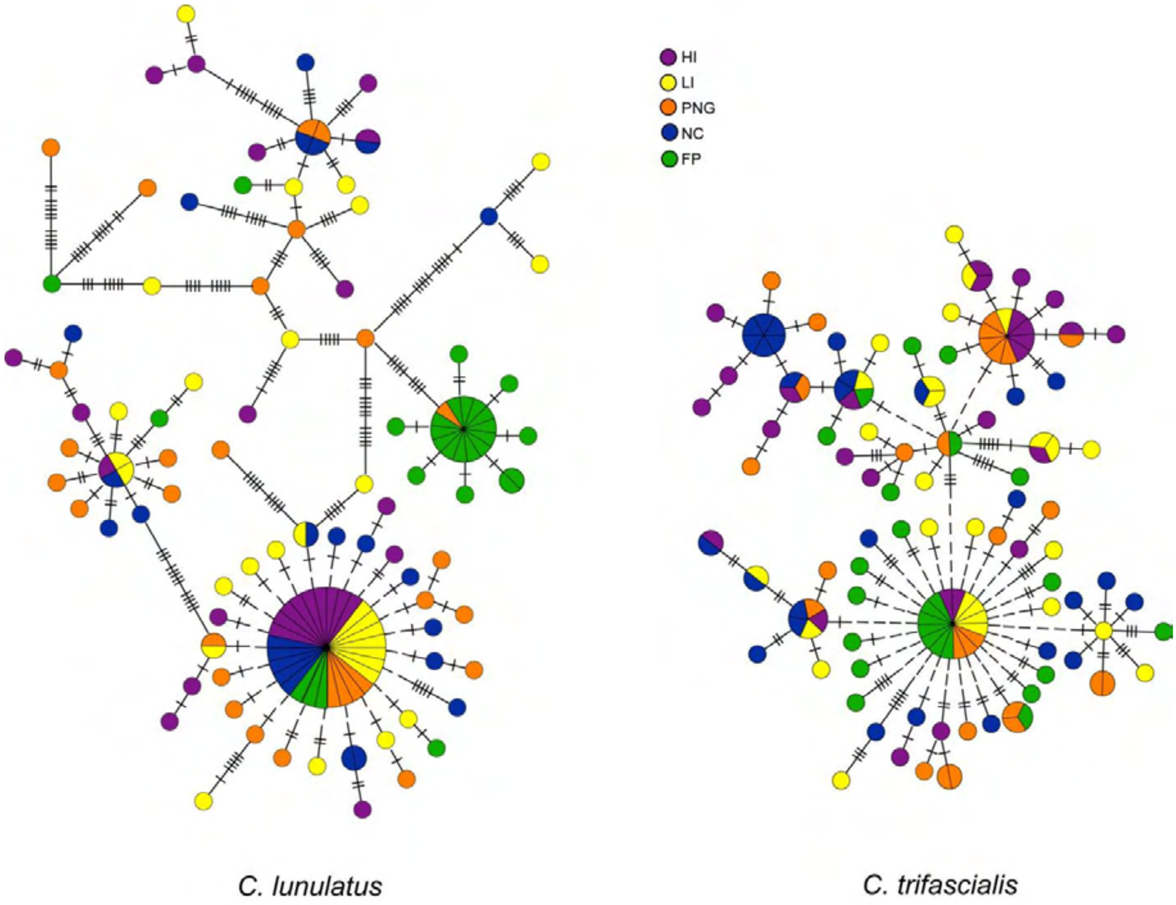

Figure 5.2 Haplotype minimum spanning tree based on the mitochondrial control region of *C. lunulatus* (left) and *C. trifascialis* (right) from five locations. Colours indicate geographical source of haplotypes. Circle sizes are proportional to the number of individuals that share each haplotype and are colour coded by location. Location abbreviations follow Table 5.1.

Results of the Bayesian clustering analysis of the microsatellite data returned the highest posterior likelihood probability for K=2 in both species. Delta K (ΔK) was also highest for K=2 in both species (Fig 5.3), indicating that the most likely number of distinct genetic clusters is two. For both species, individuals from French Polynesia comprised one distinct cluster, and individuals from the other four locations grouped together to form the second cluster.

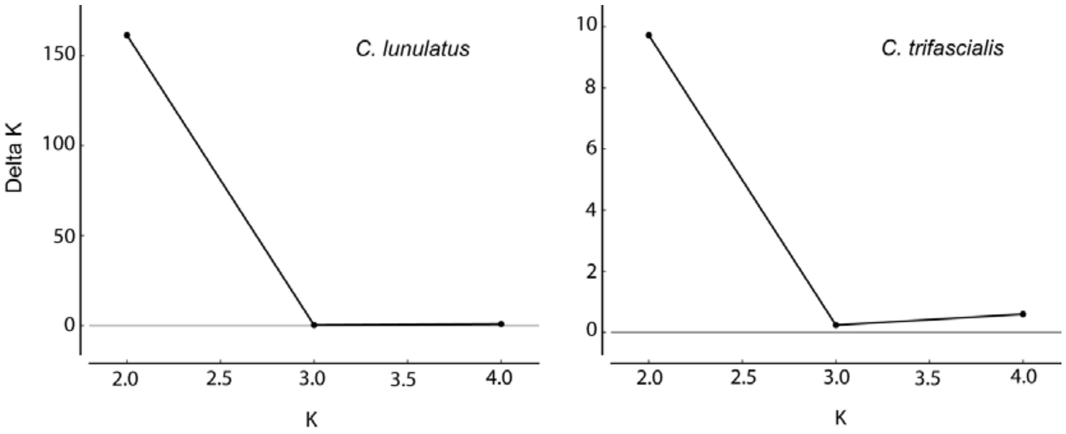

Figure 5.3 Delta *K* values for combined outputs of Structure analyses for *K*=1 to 5 inferred genetic clusters in five populations of *C. lunulatus* and (left) and *C. trifascialis* (right).

5.5 DISCUSSION

This study revealed marked differences in the population genetic structure of two species with contrasting levels of dietary specialisation. Analyses using mtDNA and microsatellite data show that *C. trifascialis* and *C. lunulatus* exhibit very different demographic histories and patterns of genetic structure despite similar life histories and comparable levels of genetic diversity. Although the dietary specialist *C. trifascialis* has experienced genetic bottlenecks, there is strong evidence for high gene flow between locations. In contrast to expectations, the dietary generalist *C. lunulatus* had higher levels of population structure than *C. trifascialis*. Due to its extremely specialised diet, *C. trifascialis* is highly vulnerable to declining abundance of the tabular *Acropora* corals it preferentially feeds on (Pratchett et al. 2008b). However, the high gene flow detected here suggests there is potential for *C. trifascialis* populations to recover from local declines through colonisation from healthy source populations.

As expected, heterozygosity excess tests for genetic bottlenecks revealed *C. trifascialis* has experienced recent population declines at all five locations. This genetic evidence confirms significant known declines reported at Lizard Island (Pratchett et al. 2008b) and Moorea (Berumen and Pratchett 2006b). Declines in branching coral cover from roughly 66% in 1996 to

7% in 2002 have been documented in Kimbe Bay, Papua New Guinea (Jones et al. 2004), while substantial fluctuations in total coral cover (ranging from <1% to >80%) have been recorded at Heron Island between 1966 and 1996 (Connell et al. 1997). The finding of genetic bottlenecks at the remaining three locations therefore, provides strong evidence for the hypothesis that *C. trifascialis* has suffered recent and consistent population declines throughout its geographic range following coral loss. One caveat to this assertion is that genetic bottlenecks were detected under an infinite alleles model (IAM), but not under a step-wise mutation model (SMM) or a two phase model (TPM) - generally considered to be the most appropriate model for microsatellite loci (Ellegren 2000). Although the IAM can occasionally detect genetic bottlenecks erroneously (Luikart and Cornuet 1998), the detection of bottlenecks under the IAM at locations where *C. trifascialis* populations are known to have declined severely suggests that the significant results obtained for the other three locations are indeed reflective of real genetic bottlenecks. Similar findings have been reported for kangaroo rats, with genetic bottlenecks detected under an IAM but not under a SMM in populations known to have experienced recent demographic reductions (Busch et al. 2007). Most studies documenting the response of specialised species to changes in resource availability have focused on fluctuating habitat availability (e.g. Kotze and O'Hara 2003; Munday 2004). The finding of genetic bottlenecks in *C. trifascialis* suggests that fluctuating food availability can also negatively impact specialised species, although further comparative studies are needed to determine whether this finding applies to other specialist species. In contrast to *C. trifascialis*, heterozygosity excess was not detected in four of the five locations examined for the generalist C*. lunulatus.* This differential response could be the result of its generalised dietary preferences, which may enable the use of alternative food sources in periods of resource decline, thereby preventing any reductions in population size. If however, resource depletion is particularly severe, then it is likely that both dietary specialists and generalists will be equally affected (e.g. Pratchett et al. 2006). We found no evidence of genetic bottlenecks at any location for either species based on M-ratio tests. In contrast to recent bottlenecks detected by tests of heterozygosity excess, the M-ratio test is most effective at detecting older, more severe declines (Williamson-Natesan 2005). Consequently, these tests are predicted to provide evidence of population decline and recovery over different time scales (Garza and Williamson 2001). The finding of significant bottlenecks under heterozygosity excess tests but not M-ratio tests for *C. trifascialis* suggests that genetic bottlenecks have only occurred in very recent times, while the non-significant results under both tests for *C. lunulatus* suggests that populations have been relatively stable in recent times.

Contrasting demographic histories for both species were also evident under analyses based on mtDNA data, which provides information over more historical timeframes compared to microsatellite data (Avise 2000). The significant neutrality tests and mismatch distributions for *C. trifascialis* are consistent with a hypothesis of historical genetic bottlenecks and demographic expansion, whereas the non-significant results for *C. lunulatus* support a conclusion of long-term demographic stability. The demographic histories of both species are likely to have been strongly impacted by the geological history of Pacific coral reefs. Pleistocene sea level changes driven by repeated glaciation cycles have been implicated as a major factor contributing to the evolutionary history of reef fishes (Benzie 1999; Fauvelot et al. 2003). Declining sea levels are likely to have lead to a reduction in available reef habitat and the disappearance of lagoons enclosed by volcanic islands (Fauvelot et al. 2003). Reef fishes are hypothesised to have experienced periods of range expansion and contraction, leading to cycles of genetic isolation, secondary contact and subsequent introgression (Palumbi 1994; Benzie 1999). Genetic signatures of climate induced bottlenecks and demographic expansion have been detected in many reef fishes (e.g. Bay et al. 2004; Klanten et al. 2007; Bay et al. 2008), including butterflyfish populations in French Polynesia (Fauvelot et al. 2003), and similar processes are likely to be a key contributor to the demographic patterns in mtDNA reported here. The different demographic histories of the two species may further reflect an increased susceptibility of *C. trifascialis* to environmental variations compared to *C. lunulatus* as a result of its highly specialised diet. Specialised species are likely to have been more vulnerable than generalist species to fluctuations in habitat or food availability during periods of sea level change and as a consequence, ecological specialisation has been proposed as a primary driver of different demographic histories in several reef fishes. For example, climate-induced bottlenecks were detected in three species of Hawaiian butterflyfishes (Craig et al. 2010). The species with the most specialised diet suffered the largest bottlenecks, the cause for these bottlenecks was proposed to be reduced habitat and food availability following rapid sea level rises (Craig et al. 2010). Similarly, lagoon specialist reef fishes in French Polynesia were found to have experienced stronger genetic bottlenecks than species inhabiting the outer reef slope during periods of sea level decline when lagoonal habitats are likely to have disappeared (Fauvelot et al. 2003). This study therefore adds further support to the hypothesis that ecological specialisation can impact population genetic structure by affecting both historical and recent demographic patterns, although further replication is needed as this study only compares the demographic history of two species.

Local extinctions and population declines can be countered by high gene flow and connectivity through dispersal between populations (Hanski 1999; Jones et al. 2009). Analyses using microsatellite data detected very little genetic structure between locations for *C. trifascialis,* revealing high levels of gene flow. This limited genetic structuring across such large geographic scales (sampling locations were situated >1000km apart) suggests a substantial capacity for local populations to recover from declines through the dispersal of larvae from other unaffected populations. A greater level of population structuring was detected using the mtDNA data, however, the shallow phylogeny and absence of any geographic groupings in the haplotype network for *C. trifascialis* supports relatively high gene flow between locations over the more historical time scales encompassed by mtDNA data. This finding of large scale gene flow is also indirectly supported by molecular phylogenies of the Chaetodontidae, which indicate that although there is clear evidence for allopatric speciation between Pacific Ocean and Indian Ocean populations in many other butterflyfish species (e.g. *C. lunulatus* and *C. trifasciatus*), Pacific Ocean and Indian Ocean populations of *C. trifascialis* are still considered to comprise a single species (Bellwood et al. 2010). Limited or no genetic structure between populations located thousands of kilometres apart has been found in a number of other marine fishes in studies using both microsatellite markers and mtDNA (e.g. Purcell et al. 2006; Haney et al. 2007; Klanten et al. 2007; Horne et al. 2008; White et al. 2009; Gaither et al. 2010). This study provides a further example of reef fish populations with high gene flow across large spatial scales.

In contrast to the dietary specialist *C. trifascialis,* significant genetic differentiation among locations was detected in both the microsatellite and mtDNA data for the dietary generalist *C. lunulatus.* The finding of differing levels of population structure in *C. trifascialis* and *C. lunulatus* further highlights the variation in spatial scales that reef fish populations may be connected over and provides another example of contrasting population structure in closely related marine fishes with similar life-histories (e.g. Galarza et al. 2009; Gaither et al. 2010). These findings were contrary to expectations based on studies of other specialised species (e.g. Brouat et al. 2003; Rocha et al. 2005; DiLeo et al. 2010). One explanation for this discrepancy may be that these studies were all conducted on habitat specialist species. In each of these studies, areas of unsuitable habitat acting as barriers to dispersal were proposed as the mechanism resulting in greater population structuring in specialised species. In this study, *C. trifascialis* is specialised compared to *C. lunulatus* only in terms of its dietary preferences (Pratchett 2005, 2007a). Studies at varying geographic scales across several locations have shown that both species are broadly distributed across the same habitats (Findley and Findley

2001; Berumen and Pratchett 2006b). Furthermore, coral food sources for both species, including tabular *Acropora* corals, are also widely distributed (Veron 2000). Thus, unsuitable habitats will probably be similar for both species and dispersal barriers are more likely to be created by currents and other large scale oceanic processes (Barber et al. 2002) which would be expected to affect each species equally. Although some dietary specialists may also be restricted in their habitat use by the distribution of food resources (e.g. Ortego et al. 2010), the results of this study suggest the specialised diet of *C. trifascialis* does not restrict dispersal. Further studies comparing gene flow in dietary specialists and generalists are needed to determine whether this is a species specific result, or whether dietary specialisation in itself does not restrict dispersal in the same way that habitat specialisation appears to.

5.5.1 Conclusions

The findings of this study have important implications for the vulnerability of the specialised coral-feeder *C. trifascialis* to predicted coral loss in the future (e.g. Hoegh-Guldberg et al. 2007). The historical genetic bottlenecks and recent population declines detected here indicate this species will be highly vulnerable to any future loss of the *Acropora* corals it preferentially consumes. However, the finding of high gene flow between locations over both recent and historical timeframes suggests there is potential for *C. trifascialis* populations to recover from local declines. There is however, evidence that perturbations to shallow coastal environments are increasing in both geographical scale and severity (e.g. coral bleaching, Hoegh-Guldberg 1999), and simultaneous disturbances across very large scales will greatly increase likelihood of species extinctions, even for those species with higher resilience due to large-scale gene flow. A comparative analysis of the related but generalised coral-feeder *C. lunulatus* revealed a more stable demographic history compared to *C. trifascialis*. As this study only considered two species, it cannot show a causative connection between ecological specialization and genetic structure. However, results suggest that the greater vulnerability of specialised species to environmental change may lead to significant reductions in population size. Furthermore, the lower level of population structure detected in *C. trifascialis* compared to *C. lunulatus* suggests that dietary specialisation may not affect gene flow in the same way that habitat specialisation appears to, possibly because it does not directly restrict dispersal. These results highlight the need for a fresh approach in evaluating vulnerability in specialised species that includes assessment of adaptive capacity and recovery potential as well as sensitivity to environmental change.

Chapter 6: General discussion

Coral-feeding butterflyfishes are among the most vulnerable of all reef fishes to ongoing coral loss due to their dependence on scleractinian corals for food (Pratchett 2005; Cole et al. 2008; Lawton et al. In press-b). Comparative analyses on proportional declines in the abundance of reef fishes following extensive coral loss (e.g., due to coral bleaching or outbreaks of crown-of-thorns starfishes) have suggested that butterflyfishes feeding exclusively on hard corals (obligate corallivores) with highly specialised diets are more likely to go locally extinct than any other group of fishes (Pratchett et al. 2008b). As the frequency, intensity and magnitude of disturbance events on coral reefs increase (Donner et al. 2005; Hoegh-Guldberg et al. 2007), these fishes may be at considerable risk of global extinction (Pratchett et al. 2008b). However, this study has shown that, despite the strong reliance of coral-feeding butterflyfishes on hard corals for food (Chapters 2 and 3), the availability of coral prey has limited influence on geographical variation in the abundance of coral-feeding butterflyfishes (Chapter 4). Furthermore, high levels of gene flow detected among locations across the Pacific Ocean for two species of butterflyfishes suggest that there is high potential for populations to recover from local declines through colonisation from healthy source populations (Chapter 5).

6.1 Resilience of butterflyfishes to coral loss

The resilience of coral-feeding butterflyfishes to any future coral loss on reefs will be determined in the short term by their ability to feed on alternative coral resources if preferred coral prey becomes scare. Chapters 2 and 3 showed that the dietary composition of coral-feeding butterflyfishes varied in accordance with changes in resource availability at both local (Chapter 2) and regional (Chapter 3) scales. Variation was highest for species with the most generalised diets (e.g. *C. citrinellus, C. lunulatus*). However, even the most specialised species, *C. trifascialis*, increased feeding on alterative coral taxa at sites in French Polynesia where the availability of preferred *Acropora* corals was extremely low (Chapter 3). These findings suggest that coral-feeding butterflyfishes are able to feed on non-preferred coral resources when necessary and, consequently, should be able to persist through periods of moderate coral loss. The key question arising from these findings is what are the longer–term consequences (in terms of individual fitness) for butterflyfishes that are forced to rely on sub-optimal coral prey? Research has demonstrated that increased use of non-preferred coral prey by butterflyfishes can have significant negative impacts on growth (Berumen and Pratchett 2008) and condition (Pratchett et al. 2004; Berumen et al. 2005). If feeding on non-preferred coral prey is prolonged, reproductive output and survival may also be impacted.

While short-term use of non-preferred coral prey may be an important strategy to withstand temporary disturbances, fundamental shifts in coral communities due to recurrent or prolonged disturbances (e.g. Berumen and Pratchett 2006b; Pratchett et al. 2011) may ultimately lead to declines in the abundance of specialist coral-feeding butterflyfishes. Such a situation is most likely occurring for the *Acropora* specialist *C. trifascialis* in Moorea, French Polynesia. Following a decline in total coral cover on Tiahura reef, Moorea, from 37.4% in 1979 to 14.5% in 1982, the abundance of *C. trifascialis* decreased from an average of 0.95 individuals to zero individuals per 200m^2 (Bouchon-Navaro et al. 1985). By 2003, total coral cover at Tiahura reef had increased back to 37.6%, however, the *C. trifascialis* population had not recovered and average abundance was still only 0.10 individuals per 200m^2 (Berumen and Pratchett 2006b). Surveys conducted at Tiahura reef in 2010 indicated that abundance of *C. trifascialis* has remained relatively low, with an average of just 0.23 individuals per 200m^2 (R.J. Lawton and M.L. Berumen, unpublished data). During this same time the coral community at Tiahura has shifted from one dominated by *Acropora* corals in 1979 to one dominated by *Pocillopora* and *Porites* corals (Berumen and Pratchett 2006b; Pratchett et al. 2011) and *Acropora* corals remain scare on this reef today (<3% total cover in 2010, R.J. Lawton, unpublished data, Pratchett et al. 2011). Feeding observations indicate that although *C. trifascialis* still feeds very selectively on the few *Acropora* corals that are available, 33% of all bites are taken on non-preferred coral taxa (Chapter 3; Lawton et al. In press-b). The failure of *C. trifascialis* populations to recover to former levels most likely reflects an accumulation of sub-lethal effects due to prolonged feeding on non-preferred coral prey which has led to a decline or complete loss of reproductive output and reduced survival. It is likely that the population of *C. trifascialis* in Moorea is only sustained through high connectivity with other locations (Chapter 5; Lawton et al. 2011) and the export of larvae from other healthy populations.

Many studies have indicated that specialist species are disproportionately affected by changes in resource availability compared to generalist counterparts (e.g. Harcourt et al. 2002; Kotze and O'Hara 2003; Swihart et al. 2003; Charrette et al. 2006; Aitken and Martin 2008). In agreement with these findings, Chapter 4 demonstrated that resource availability had the strongest influence on the abundance of the most specialised species. But despite the strong links found in previous studies between total coral cover and butterflyfish abundance (Bell and Galzin 1984; Bouchon-Navaro et al. 1985; Cadoret et al. 1999; Bozec et al. 2005; Pratchett and Berumen 2008; Emslie et al. 2010), the availability of coral dietary resources had only a weak influence on geographical variation in abundance of individual coral-feeding butterflyfishes in the current study (Chapter 4). These results may reflect a threshold effect, whereby the abundance of coral-feeding butterflyfishes is only significantly affected if coral cover declines below a certain level. This critical threshold level is likely to vary among reefs and locations as the response of butterflyfishes to coral loss will be moderated by a range of factors. The initial density of butterflyfishes on a reef will have a large influence on their response as coral loss. Intuitively, declines in coral cover will greatly reduce the local carrying capacity of a reef. However, if other factors (e.g. territoriality) are acting to maintain local densities of butterflyfishes well below the maximum carrying capacity, coral loss may have no discernable effects on butterflyfish abundance.

The species composition of the butterflyfish community will also be an important determinant of response to coral loss. Empirical evidence indicates that obligate corallivores consistently suffer greater declines in abundance than facultative corallivores following coral loss, and within the obligate corallivore guild, species with specialised diets are more vulnerable than those with generalised diets (Berumen and Pratchett 2006b; Pratchett et al. 2006; Wilson et al. 2006; Graham 2007). This evidence suggests that butterflyfish communities with high numbers of obligate specialists will be most vulnerable to coral loss. Similarly, the particular coral species or genera that decline in abundance are also important. Coral loss on reefs is typically not uniform across all coral taxa (e.g. Pratchett et al. 2004; Pratchett et al. 2011), with some taxa such as *Acropora* being more susceptible to particular disturbance events than other taxa (e.g. coral bleaching: Marshall and Baird 2000; crown-of-thorns starfish predation: Pratchett 2007b). Declines in the abundance of preferred coral prey, such as *Acropora hyacinthus*, will have a greater effect on butterflyfish communities than declines in the abundance of non-preferred coral prey.

Aside from versatility in dietary composition (which influences susceptibility to disturbances), butterflyfishes may increases species level resilience by recovering rapidly in the aftermath of major disturbances (Hughes et al. 2005). Chapter 5 indicated that butterflyfish populations are highly connected across large geographic scales, suggesting that if local populations decline, recruitment is likely to be maintained and there is a high potential for recovery. Support for this prediction is provided by the high levels of gene flow detected across large geographic scales for *C. lunulatus* and *C. trifascialis* (Chapter 5). Furthermore, genetic evidence indicates that *C. trifascialis* has undergone considerable population declines in both recent and historical times across multiple locations (Chapter 5), yet populations of *C. trifascialis* still exist in all these locations today and at some sites are highly abundant (Chapter 4). In combination, these results indicate that butterflyfish populations have a high capacity to recover from local declines, and will therefore be fairly resilient to disturbance events occurring on a local scale.

This study provides important insights into the ecology of the dietary specialist *C. trifascialis* and its likely vulnerability to disturbance events on reefs. Previous studies have shown that C. trifascialis has a highly specialised diet, feeding almost exclusively on tabular *Acropora* corals in a number of locations (e.g. Reese 1981; Irons 1989; Pratchett 2005). This study confirmed that *C. trifascialis* is a fundamental dietary specialist, with low levels of dietary versatility and a very narrow dietary niche across large geographic scales (Chapters 2 and 3; Lawton et al. In press-a; Lawton et al. In press-b). Based on this highly specialised diet, is has been predicted that *C. trifascialis* will be highly vulnerable to coral loss (Pratchett et al. 2008b). However, this study demonstrated that the availability of corals resources had only a limited influence on geographic variation in the local abundance of this species (Chapter 4) and there is strong evidence that *C. trifascialis* populations have a high recovery potential (Chapter 5; Lawton et al. 2011). These findings indicate that the vulnerability of *C. trifascialis* to coral loss on reefs is likely to be much lower than would be predicted based on its highly specialised diet and high dependence on *Acropora* corals. There is however, significant concern associated with increasing severity and scale of coral reef disturbances. In 1998, for example, temperature induced coral bleaching occurred throughout much of the Indian Ocean and Caribbean, causing very widespread coral loss (Goreau et al. 2000; Graham et al. 2008). If these ocean-scale disturbances continue to occur, then it is possible that even very widespread and well connected species of reef fishes will be threatened with extinction.

6.2 Future research directions

For coral-feeding butterflyfishes, the strength and basis of dietary selectivity are fundamental in assessing the likely effects of declines in live coral cover, and/or shifts in the community structure of coral assemblages (e.g., due to sustained and ongoing climate change) on species persistence. Chapters 2 and 3 showed that some coral taxa, in particular *Acropora* corals, are highly preferred food sources for butterflyfishes. However, the drivers of these differential feeding preferences are not well understood. Recent research has demonstrated that juvenile butterflyfishes grow fastest on exclusive diets of their preferred coral prey (Berumen and Pratchett 2008) and physiological condition of butterflyfishes is lower in habitats with low availability of preferred coral prey (Berumen et al. 2005), suggesting that corals may differ in nutritional quality. Analysis of the C:N ratio of coral tissue has indicated that there are indeed differences in nutritional quality between some coral taxa, with *Acropora* corals having a lower C:N ratio, and therefore a higher nutritional quality, compared to *Pocillopora* corals (Graham 2007). However, as *Pocillopora* corals are also preferentially fed on by some butterflyfishes (Chapters 2 and 3, Pratchett 2005) nutritional differences are unlikely to be sole driver of prey preferences. Coral-feeding butterflyfishes are expected to preferentially feed on coral resources that maximise their growth and reproductive output (Tricas 1989). In addition to nutritional quality, the net energy intake gained from each unit of foraging effort (e.g. per bite) will strongly influence these factors (Tricas 1989). Coral colony morphology (Tricas 1989), the presence of defensive nematocysts (Gochfeld 2004) and the functional jaw morphology of individual butterflyfish species (Motta 1988) can all influence the amount of coral tissue removed by each bite, and thus the net energy intake per bite. Cole et al. (2011, Appendix 1) found that the amount of coral tissue removed per bite by four butterflyfish species was not significantly different when feeding on *Acropora hyacinthus* compared to *Pocillopora damicornis*. However, both of these corals are preferred prey and selectively fed on by all four butterflyfish species (Pratchett 2007a). Future research is needed to determine whether food intake (e.g. the amount coral tissue removed per bite) varies between preferred and non-preferred coral prey across a range of butterflyfish species, to test whether there are important functional limitations to feeding on certain corals.

Chapter 3 indicated that resource availability has only a limited influence on the local abundance of coral-feeding butterflyfishes. However, it is possible that the resource categories used in this chapter were too poorly resolved to effectively assess variation in the abundance of key dietary components for some species. Repetition of this study using a finer taxonomic resolution is necessary to determine whether the weak effect of resource availability on local abundance patterns is a true finding or a result of resource categorisations. As Chapter 3 considered the local abundance of adult butterflyfishes only, further research is necessary to determine the influence of coral resource availability on settlement and recruitment patterns of juvenile butterflyfishes. Hard corals are known to be an important settlement habitat for many butterflyfishes and micro-habitat choice experiments have shown that juveniles of some species exhibit strong selection for specific coral taxa (Pratchett et al. 2008a). Consequently, the availability of coral resources as settlement habitat is likely to be a strong determinant of local abundance for juvenile butterflyfishes and should be a focus of future research efforts to determine the vulnerability of coral-feeding butterflyfishes to coral loss.

Comparing variation in resource use across sites with differing resource availability (Chapters 2 and 3) can provide an indication of ecological versatility (Hughes 2000), and therefore allow predictions of how species are likely to respond to disturbance events leading to changes in resource availability. However, resource use can be influenced by a range of factors, such as competition or predation, in addition to resource availability (McLoughlin et al. 2010). Disturbance events on coral reefs typically result in a decline in total resource availability (e.g. hard coral cover) as well as changes in the availability of specific resources (e.g. Pratchett et al.

2004; Pratchett et al. 2011). For coral-feeding butterflyfishes, these changes may result in increased competition for limited coral resources and it is possible that subordinate species or individuals may be prevented from feeding on coral resources by dominant competitors (Berumen et al. 2005). The importance of considering ecological processes when assessing patterns of resource use has recently been emphasized, particularly within the context of predicting the response of organisms to environmental change (McLoughlin et al. 2010). But, as yet, studies of resource selectivity in butterflyfishes have only considered patterns of resource use in isolation. Comparison of resource selection functions at multiple locations with varying resource availability and varying densities of butterflyfishes will provide insight into the interactive effects of factors such as a density and competition on resource selection and will enable predictions of how the butterflyfish community as a whole is likely to respond to disturbance events.

Chapter 5 revealed that there is high gene flow across large geographic scales for *C. lunulatus* and *C. trifascialis*, indicating that there are high levels of genetic connectivity between populations. However, a study of the related vagabond butterflyfish, *C. vagabundus*, in Kimbe Bay, Papua New Guinea, has revealed that natal homing is fairly common, with approximately 60% of settled juveniles returning to the same reef where they were spawned (Almany et al. 2007). This finding suggests that despite the high gene flow detected in the current study (Chapter 5), demographic connectivity may be relatively low for some butterflyfish populations. Further research is needed to determine the connectivity of butterflyfish populations at intermediate spatial scales (e.g. along the Great Barrier Reef) to reconcile these contrasting results. Contrary to expectations based on genetic studies of habitat specialists (e.g. Brouat et al. 2003; Rocha et al. 2005; DiLeo et al. 2010), population genetic structure was lower in the dietary specialist *C. trifascialis* compared to the dietary generalist *C. lunulatus*, suggesting that dietary specialisation may not affect genetic structure in the same way that habitat specialisation appears to (Chapter 5). As this study only compared the genetic structure of two butterflyfish species, further research comparing the genetic structure of a range of related butterflyfish species with varying levels of dietary specialisation is necessary to determine the generality of this finding.

6.3 Concluding remarks

This study has shown that coral-feeding butterflyfishes with specialised diets are extremely vulnerable to coral loss as they appear to be largely inflexible in their dietary requirements. However, the availability of their preferred coral resources had only a minor influence on geographic variation in local abundance patterns and specialist species were generally common on surveyed reefs. These findings indicate that macro-ecological theories predicting that specialist species are locally rare (Brown 1984; Brown et al. 1995) are not universally true and specialist species often have other characteristics which confer high ecological resilience. Supporting this, genetic evidence indicated that butterflyfish populations have substantial potential to recover from local declines. These results highlight the need to be wary of assigning species high vulnerability status based solely on their level of ecological specialisation.

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Effects of climate change on reef-building corals and associated fishes

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ABSTRACT

Coral reef ecosystems are extremely vulnerable to global climate change owing to extreme environmental sensitivities and consequent bleaching of reef-building scleractinian corals. Severe coral bleaching often kills scleractinian coral, leading to longer-term changes in the biological and physical structure of coral reef habitats. The loss of corals, and corresponding changes in habitat structure, also has a significant effect on coral reef fishes. Coral loss has the greatest and most immediate effect on fishes that depend on live corals for food or shelter. Highly specialized fishes that live or feed on only a very restricted suite of coral species may thus face extinction due to ongoing bleaching and coral depletion. Many coral-reef fishes that do not depend directly on live coral are nonetheless dependent on the topographic complexity provided by healthy coral growth. Sustained and ongoing climate change thus poses a significant threat to coral reef ecosystems and urgent action is required to minimize future effects of climate change and maximize resilience of coral reef ecosystems.

INTRODUCTION

Corals reefs are ecologically, economically and socially important ecosystems, renowned for their high biodiversity and productivity (e.g., Connell 1978; Hoegh-Guldberg 1999). However, coral reefs are being rapidly degraded throughout the world, contributing greatly to declines in biodiversity and productivity among coastal ecosystems (Worm *et al.* 2006). In the latest review on the status of the world's coral reefs, Wilkinson (2008) estimated that 19% of coral reefs have been essentially lost (whereby coral cover has declined by >90% and there is limited prospect of recovery), and a further 35% of reefs face a similar fate by 2050. The cause(s) of coral reef degradation vary greatly among geographic locations (e.g., Pandolfi *et al.* 2003). However, it is the areas closest to urban centres and large human populations that tend to exhibit the most pronounced degradation of coastal environments (Jackson *et al.* 2001; Pandolfi *et al.* 2003; Wilkinson 2008). A disproportionate number of coral reefs have been lost in east Africa, south-east Asia, and the central and southern Caribbean (Wilkinson 2004), caused by chronic pollution, eutrophication, sedimentation, overfishing and/ or destructive fishing practices. The long-term effects of anthropogenic disturbances are also being compounded by the increasingly large-scale impacts of global climate change (Hughes *et al.* 2003; Hoegh-Guldberg *et al.* 2007).

Climate change is widely regarded as the single greatest threat to the future of coral reef ecosystems, though the effects of climate change compound upon chronic long-term degradation of coral reef ecosystems (Hughes *et al.* 2003; West and Salm 2003; Hoegh-Guldberg *et al.* 2007; Wachenfeld *et al.* 2007). The long-term and cumulative effects of anthropogenic disturbances and increased fragmentation of coral reef habitats have greatly eroded reef resilience, making coral reef habitats much more susceptible to climate change (Hughes *et al.* 2003). Coral reefs that are isolated from direct anthropogenic disturbances and coastal processes are not immune from the effects of global climate change, but it is likely that they will recover more rapidly in the aftermath of climatic disturbances (e.g., Sheppard *et al.* 2002).

Changes in atmospheric conditions due to anthropogenic climate change have direct effects on marine ecosystems, resulting in i) significant warming of shallow and surface waters (e.g., Gille 2002), and ii) increasing concentrations of CO_2 in ocean waters (Roessig *et al.* 2004). Water has a higher heat capacity than air, which means that increases in water temperatures lag behind that of atmospheric temperatures (Lough 2007). Even so, the average temperature at the surface of the ocean has increased 0.6^{o}C over the last century, compared to 0.8 ^{o}C for land-surface air temperature (Folland *et al.* 2002). Increasing temperatures are critically important because they bring baseline ocean temperatures much closer to the maximum thermal tolerances for reef organisms. Scleractinian corals especially, function very close to their upper thermal limit, such that bleaching may occur when sea temperatures exceed normal local limits by as little as 1.0°C (Jokiel and Coles 1990). A significant component of anthropogenically produced CO_2 (approximately one third, thus far) is also dissolved in the world's oceans (Roessig *et al.* 2004). Additional CO_2 dissolved in the ocean reacts with seawater to form weak carbonic acid, causing pH to decline and reducing the availability of dissolved carbonate ions required by many marine calcifying organisms (e.g. corals, other invertebrates, and coralline algae) to build their shells or skeletons (Orr *et al.* 2005).

Other climate related changes that will effect coral reef ecosystems include increasing severity of tropical cyclones (Madin and Connolly 2006), sea level rise

(Short and Neckles 1999), and changes to ocean circulation and current patterns (Munday *et al.* 2008, 2009). Tropical cyclones are expected to become more intense in a warmer world (Webster *et al.* 2005), causing greater damage to key habitat-forming species, such as corals and seagrasses (Madin and Connolly 2006). Sea level rise will lead to a redistribution of intertidal and shallow coastal habitats (Short and Neckles 1999). Changes to ocean circulation and current patterns will alter dispersal of marine larvae (Munday *et al.* 2008, 2009), and combined with reductions in vertical water mixing, will limit the supply of nutrients and subsequent productivity of aquatic ecosystems. Climate relates changes in environmental and habitat conditions will directly affect many coral reef organisms, resulting in changes in population dynamics, distribution and abundance (Munday *et al.* 2008), or for those species that are unable to adapt to changing conditions, climate change may lead to local or global extinction (e.g., Munday 2004). The most critical effects however (especially, in the shorter term), will result from changes in the biological and physical structure of coral reef habitats, formed by scleractinian (“hard”) corals (Pratchett *et al.* 2008).

EFFECTS OF CLIMATE CHANGE ON CORALS

Coral reefs are considered to be among the most vulnerable ecoystems to global climate change (Walther *et al.* 2002), owing to sensitivities of habitat-forming corals to both increasing temperatures and ocean acidification (Hoegh-Guldberg *et al.* 2007). Ocean warming has already caused large-scale and severe episodes of coral bleaching throughout the world. In 1998, coral bleaching occurred in >50 countries throughout the world, killing up to 90% coral colonies. Australia was largely spared during the 1998 global mass-bleaching; bleaching was conspicuous and widespread, but bleached corals mostly recovered (Wilkinson 2004) and overall mortality rates were generally low (Maynard *et al.* 2008; Anthony and Marshall 2009). However, large-scale bleaching has been observed in Australia and appears to be increasing in frequency and severity (Figure 1). On the Great Barrier Reef (GBR) major instances of coral bleaching have been recorded at fairly regular intervals extending back to 1980, when conspicuous bleaching of common corals (mostly, *Acropora* and *Montipora*) was first noted at several isolated reefs between Townsville and Cairns (Oliver 1985). The most extensive and most severe bleaching episode to affect the GBR occurred in 2002 (Berkelmans *et al.* 2004; Maynard *et al.* 2008), corresponding with the highest sea surface temperatures (often $>33^{O}C$) recorded on the GBR. During this event, bleaching was recorded at 54% of reefs surveyed across the length and breadth of the GBR (Berkelmans *et al.* 2004).

Given projected increases in sea surface temperatures, if corals are unable to acclimatize or adapt, coral bleaching events will become more frequent and more severe with time (Hoegh-Guldberg 1999, Donner *et al.* 2005). By 2050, most coral reefs are expected to be subject to annual thermal anomalies equivalent to those experienced in 1998 (Hoegh-Guldberg 1999), suggesting that mass bleaching will occur at intervals much less than the time required for corals (populations and communities) to recover from successive major bleaching events (Donner *et al.* 2005). Given strong taxonomic differences in susceptibility to bleaching (e.g., Baird and Marshall 2002), recurrent mass-bleaching will cause marked changes in the taxonomic composition of coral assemblages (e.g., Riegl and Purkis 2009). However, the future state of coral communities will depend not only upon the differential bleaching susceptibilities of coral taxa (e.g., Baird and Marshall 2002), but also upon their capacity for recovery between successive bleaching events (Hughes *et al.* 2003). Effects of increasing temperature will be further exacerbated by ocean acidification, which may reduce coral growth and population resilience (Hoegh-Guldberg *et al.* 2007).

The pH of oceans has already declined dropped by 0.1 pH unit, associated with increasing concentrations of H^+ and HCO_3^{2-}(bicarbonate) ions and corresponding declines carbonate ion (CO_3^-) concentrations. Declines of carbonate ions decrease the saturation state of calcium carbonate, particularly evident in more soluble calcite polymorphs such as aragonite and magnesium calcite (Kleypas and Langdon 2006). Reef building corals and crustose coralline algae construct skeltons from aragonite and magnesium calcite respectively, are therefore particularly sensitive to changes in saturation states of calcium carbonate. Coral calcification rates are positively related to aragonite saturation state (Gattuso *et al.* 1998) and field data show that the growth rates of massive corals have declined by 15 – 20% over the past two decades (De'ath *et al.* 2009; Cooper *et al.* 2008). These declining growth rates of massive corals have not yet been irrefutably linked with changes in ocean carbonate chemistry, but may be the result of changes in ocean chemistry, water quality and/ or temperature effects (e.g., Anthony *et al.* 2008).

EFFECTS OF CORAL LOSS ON FISHES

Coral loss and associated changes in biological and physical structure of coral reef habitats have an important influence on the abundance and diversity of coral reef fishes (Wilson *et al.* 2006; Pratchett *et al.* 2008). Declines in coral cover generally lead to declines in the abundance of reef fishes, especially among fishes that rely on live coral for food, shelter and/ or recruitment (Kokita and Nakazono 2001; Munday 2004; Pratchett *et al.* 2004). Extensive coral loss may also result in declines in habitat and topographical complexity (Sheppard *et al.* 2002; Graham *et al.* 2007), which are critical for sustaining high diversity of reef fishes and other reef-associated organisms

(Wilson *et al.* 2006; Pratchett *et al.* 2009). In the aftermath of extensive coral bleaching, the skeletons of dead corals are highly susceptible to biological and physical erosion (Hutchings 1986; Glynn 1997). Over time, coral skeletons of erect branching corals (e.g., *Acropora* and *Pocillopora*) break down into coral rubble (Sheppard *et al*. 2002, Graham *et al*. 2006), whereas more robust skeletons of massive corals (e.g., *Porites*) may become dislodged or gradually eroded in situ (Sheppard *et al.* 2002), potentially causing major declines in topographic relief. When coral loss is combined with structural collapse of reef habitats, up to 65% of reef fishes may experience declines in abundance (e.g. Jones *et al.* 2004; Graham *et al.* 2007). For fishes that are directly reliant on corals, sustained and ongoing declines in live coral cover may ultimately lead to local or global extinction. This is particularly so, for highly specialist fishes that rely on only a limited suite of coral species (Munday 2004).

Corals as food

Scleractinian corals are an important source of food for at least 133 species (and 11 different families) of coral reef fishes (Cole *et al.* 2008; Brooker *et al.* 2010, Berumen and Rotjan 2010). The majority (69 species) of coral-feeding fishes are butterflyfishes (family Chaetodontidae), and more than half (69 out of 125 species) of all butterflyfishes feed at least in part on scleractinian corals (Allen *et al.* 1998; Cole *et al.* 2008; Froese and Pauly 2010). Coral feeding is an unusual feeding habit for most families of reef fishes. Aside from butterflyfishes, <5% of species (and often much less) within each of the major families of coral reef fishes are known to feed on corals; Only 10 species of wrasses (family Labridae), 8 species of damselfishes (family Pomacentridae) and 8 species of parrotfishes (family Scaridae) are reported to feed on live corals (Cole *et al.* 2008). On the GBR, there are 27 species of fishes known to feed on coral, nearly all (70%) of which are butterflyfishes (Figure 2).

Of those fishes that do feed on hard corals, only 31% (41 of 133 spp) are considered to be obligate coral feeders, meaning that they feed almost entirely (>80%) on live corals and their abundance is strongly linked to local coral abundance (Cole *et al.* 2008; Pratchett *et al.* 2008). Most importantly, these fishes exhibit rapid and dramatic declines in abundance following extensive coral depletion, such as that caused by mass coral bleaching, outbreaks of coral-eating crown-of-thorns starfish (*Acanthaster planci*), or severe tropical storms (Kokito and Nakazono 2001, Sano 2004, Jones *et al*. 2004, Wilson *et al*. 2006, Pratchett *et al*. 2006, 2008). Moreover, obligate corallivores tend to have a highly specialized predator–prey relationship, and only consume a limited number of the available corals. This is considered evidence of the close co-evolution between the coral community and these fishes (Reese 1977), but also greatly increases their sensitivity to coral depletion.

Butterflyfishes exhibit particularly high levels of dietary specialization (Reese 1977, Hourigan *et al*. 1988, Tricas 1989, Cox 1994, Berumen *et al.* 2005, Pratchett 2005, 2007, Niedermüller *et al*. 2009). *Chaetodon trifascialis* is among the most specialized of all reef fishes and feeds almost exclusively on tabular *Acropora* throughout its geographical range (Reese 1981; Irons 1989; Alwany *et al.* 2003; Berumen and Pratchett 2006). Most coral-feeding fishes preferentially consume species from the genera *Acropora* and *Pocillopora* (Berumen *et al*. 2005; Pratchett 2005, 2007; Cole *et al.* 2008, Niedermüller *et al.* 2009), which are also those corals that are most vulnerable to bleaching (Marshall and Baird 2000). Accordingly, many butterflyfishes (especially, *C. trifascialis*) have disappeared on reefs subject to severe coral bleaching. For less specialized coral feeders, which can switch feeding or generally feed on corals that are more resistant to disturbances, the effects of coral loss may be less severe or much more delayed (Pratchett *et al.* 2004). *Chaetodon lunulatus*, for example, consumes a much greater range of different corals (including massive *Porites*) compared to *C. trifascialis*. Following extensive coral bleaching in the central GBR in 2001-02, densities of *C. lunulatus* did not change for at least 2 years, but subsequently declined (Pratchett *et al*. 2006), possibly due to compromised fitness of individuals forced to feed on non-preferred corals.

Corals as shelter

Scleractinian corals are important contributors to both biological and physical habitat structure, such that any declines in the abundance or diversity of corals often have noticeable effects on local diversity and abundance of coral reef fishes (Jones *et al.* 2004; Graham *et al.* 2006; Pratchett *et al.* 2008). Live coral habitat is important for many reef fishes during their vulnerable juvenile stage (Feary *et al.* 2007) as well as for many small-bodied adult reef fishes that live among the branches of live corals (Sale 1971; Munday and Jones 1998). On the Great Barrier Reef, 55 species of coral reef fishes live exclusively among the branches of live corals, mostly from the families Apogonidae, Cirrhitidae, Gobiidae, Pomacentridae and Scorpaenidae (Figure 2). Coral-dwelling fishes utilise complex branching corals with a strong preference to species from the family Pocilloporidae and the genus *Acropora* (Family Acroporidae). Accordingly, severe coral bleaching greatly reduces the availability of suitable coral hosts and leads to marked declines in abundance of coral-dwelling fishes (Jones *et al.* 2004; Munday 2004; Wilson *et al.* 2006).

Many coral-dwelling fishes vacate their coral hosts as soon as they become bleached, and few coral dwelling fishes will recruit to bleached coral hosts (e.g., Feary *et al.* 2007). This suggests that live corals are more important for these small coral-dwelling fishes than just the physical structure they provide (Booth and Beretta 2002). Most coral reef fishes are brightly coloured and stand out against the stark white bleached corals resulting in higher rates of predation as their visual camouflage is reduced to reef predators (Coker *et al.* 2009). It is also possible that live healthy coral helps to provide a chemical camouflage for these small fishes, where the odours of live coral help to mask the fish odours from predators.

While coral-dwelling fishes may sometimes persist on bleached corals, these fishes eventually move off in search of alternative healthy habitats if their host coral dies. Within one week of dying, algae and invertebrates (e.g., sponges, ascidians) will colonise the coral skeleton. At this stage, algae will start to take up the small gaps between the branches and reduce the available refuge spaces that fish can seek shelter within (Coker *et al.* 2009), such that fishes must move or face even higher risk of predation. The loss of live coral habitats mean that healthy habitats will become a limited resource for these fishes and the migration of fishes to new habitats will create increased competition among coral-dwelling fishes. Fishes displaced by host coral mortality will have to join existing social groups of resident fishes on these colonies or if unsuccessful, associate with less favourable habitats. Many coral-dwelling fishes have a tight social group and a strict size-based hierarchy (Forrester 1991; Wong *et al.* 2007), which will greatly limit opportunities to join established fish assemblages on relatively unaffected coral hosts. Fishes may also have to travel considerable distances to find suitable habitats (especially after extensive and widespread bleaching episodes), during which time they will be highly vulnerable to predation.

Many coral-reef fishes that do not feed on or live within live coral are nonetheless dependent on live coral, and may be negatively affected by significant coral loss (e.g., Jones *et al.* 2004). These include fishes that rely on corals to provide settlement cues and/ or moderate key biological interactions, such as competition and predation. More research is still required to quantify the full range of fishes that rely on the biological or physical structure provided by corals, and might therefore be affected by comprehensive or severe coral loss. Thus far, effects of coral bleaching or coral loss on fishes of the GBR have been restricted to highly specialized coral-dependent species, including butterflyfishes, damselfishes and gobies (Munday *et al.* 1997; Booth and Beretta 2002; Pratchett *et al.* 2006). With increased frequency or severity of bleaching episodes it is likely that these fishes may become locally extinct (Munday 2004), but also, a much greater range of different fishes are likely to be affected (e.g., Jones *et al.* 2004).

THE FUTURE FOR CORAL REEF STRUCTURE AND BIODIVERSITY

Resilience of corals

Sustained and ongoing increases in sea-surface temperatures, combined with declines in ocean pH, are expected to increasingly impact coral reefs in the future (Hoegh-Guldberg 1999; Hoegh-Guldberg *et al.* 2007). The future cover and species composition of scleractinian corals and the ecosystem they support critically depend on not only their current resistance to environmental stress but also their ability to adjust to current rates of ocean warming and acidification in the future. Evidence for past adaptation in physiological and life history characteristics are apparent from correlations between bleaching thresholds and local environmental conditions of geographically isolated coral populations (Hughes *et al.* 2003; Barshis *et al.* 2010).

Coral communities can adapt to climate change through shifts in community composition, whereby coral assemblages become increasingly dominated by more tolerant species. (e.g., Hughes *et al.* 2003). Shifts in community species composition following bleaching have been widely documented (e.g., Loya *et al.* 2001). Recovery of reefs may occur through the regrowth of more resilient survivors (Loya *et al.* 2001) or through recruitment and recovery of fast growing, but often more sensitive species (Pratchett *et al.* 2008). Little is known about the effects of climate change on the re-colonisation potential of faster growing branching corals but coral bleaching can greatly affect growth rates of corals several years following bleaching event (e.g., Jones and Berkelmans 2010). Therefore, while climate change is expected to change the community composition of reef corals, it is not yet clear how impacts on growth and recruitment will affect the fitness of corals, ecological interactions within and among species, and hence their future species composition.

Natural selection through local adaptation is expected to increase the frequency of more tolerant individuals (genotypes) within populations. While increases in thermal tolerance of some coral populations have been observed following major bleaching events (e.g. Maynard *et al*. 2008), no study to date has directly linked differences in allelic frequencies to thermal tolerance among individual corals (Maynard *et al*. 2008). Bongaerts *et al.* (2010) found significant genetic structure of *Seriatopora hysterix* and their dinoflagellate symbionts within reefs but not among similar habitats on separate reefs. This result is consistent with ecological selection, a hypothesis that would be supported by physiological or molecular data to link coral-symbiont eco-types with fitness and stress tolerance. In the Caribbean, D’Croz and Mate (2004) found divergence in genetic structure and physiological tolerance between *P. damicornis* populations in cooler and warmer areas. Similarly, Edmunds (1994) found that rates of natural bleaching differed among genotypes in *M. annularis*. To maximise potential for adaptation (at community and population levels) it is important to maximise the abundance and diversity of corals, upon which selection can then operate. Herein, the resilience of reef corals to climate change will benefit greatly from effective local management, minimising anthropogenic disturbances that threaten corals (Hughes *et al.* 2003). Maintaining high gene flow or connectivity will also promote resilience and recovery from recurrent bleaching.

Resilience of fishes

Future increases in the frequency and/ or severity of coral bleaching events are inevitable, and as such, the persistence of coral-dependant fishes will depend (at least, in part) upon their own population and community resilience. A primary determinant of resilience will be the ecological versatility of coral-dependant fishes and their ability to use alternative resources if the abundance of preferred corals declines. While switching to alternative food sources or habitat types may enable some coral-dependent fishes to persist through periods of coral loss, increased use of non-preferred coral resources can have significant sub-lethal effects, such as declines in inidivual condition (Pratchett *et al.* 2006). Physiological condition is a major determinant of individual fitness in fishes and sub-lethal effects on body condition can have flow on effects to growth, reproductive success and survivorship (Jones and McCormick 2002; Munday *et al.* 2008). If use of non-preferred coral resources is continuous or prolonged, then sub-lethal effects may accumulate over time, gradually reducing survivorship and ultimately decreasing resilience.

Over longer time periods, the resilience of coral-dependent fishes will depend on population connectivity and especially, the proportion of new recruits originating from local or external sources. Populations which suffer severe declines in abundance will be slow to recover if recruitment is predominantly from local sources (i.e. high levels of self-recruitment). If however, significant levels of recruitment come from outside sources then recovery may occur via the long distance dispersal of recruits from unaffected populations (Hughes *et al*. 2005; Jones *et al.* 2009). Recent studies on population connectivity among coral reef fishes provide strong evidence for ecologically significant levels of self-recruitment (Jones *et al.* 2009). These results suggest that for most fishes, declines in the local production of new larvae will greatly affect population viability. Climate change is expected to affect the connectivity of reef fish populations through changes in adult and larval biology and performance, and changes to larval supply and recruitment dynamics (reviewed by Munday *et al.* 2009). The net effect of these changes is likely to be an overall reduction in population connectivity (Munday *et al.* 2009), leading to increased reliance on local recruitment. In combination, these factors are likely to decrease the resilience of coral dependent fishes to the impacts of climate change.

As habitat perturbations become more frequent and more severe, it appears likely that highly specialised obligate coral feeders will be lost (Munday 2004). However, changes in the biological or physical structure of reef habitats may also benefit some fishes, such that there is no nett decline in diversity or abundance of coral reef fishes (Bellwood *et al*. 2006; Berumen and Pratchett 2006). In general, fish communities in degraded post-bleaching habitats are characterised by dietary and habitat generalists (e.g., omnivores and detritivores), which replace coral-dependent specialists (Bellwood *et al*. 2006; Graham *et al*. 2006). These post-bleaching fish assemblages may be fairly resilient to future disturbances but are nonetheless undesirable because the loss of entire functional groups (e.g., corallivores and herbivores) may have ramifications for recovery, productivity and ecosystem function (Bellwood *et al*. 2006).

CONCLUSIONS

Global climate change is being caused by anthropogenic forcing of the climate system (Houghton *et al.* 2001), and not only are atmospheric concentrations of greenhouse gases rising, but the rate is accelerating (e.g. Canadell *et al.* 2007). Increases in atmospheric temperatures are expected to continue throughout next century, and are expected to accelerate over the next two decades (Houghton *et al.* 2001). As a consequence, even if climatic impacts are not yet apparent (or have had minor influence compared to other more direct anthropogenic disturbances) the effects of global climate change on ecosystems, communities and species will become increasingly important in the coming decades. Australia's Great Barrier Reef and other important reef ecosystems (Ningaloo and many offshore coral reef systems) have so far been spared from devastating effects of climate change that have already been witnessed on reefs in the Indian Ocean and Caribbean. However, sustained and ongoing climate change will cause increasing changes in abundance and community composition of corals and fishes on Australian coral reefs. It is important therefore, to act now to maximize resilience of reef organisms and ecosystems.

Urgent action is required to minimise global greenhouse gas emissions and thereby reduce longer-term climatic impacts on coral reef ecosystems. However, drastic reductions in emission, even if they are implemented immediately, will not guarantee the persistence of ecosystems, communities or species. Reductions in global greenhouse gas emissions will prevent extreme changes in environmental conditions and reduce rates of change to which species must adapt in order to survive. In the short-term, management must be focussed on minimising all other sources of anthropogenic interference coastal ecosystems that exacerbate vulnerability to climate change (Hughes *et al.* 2003).

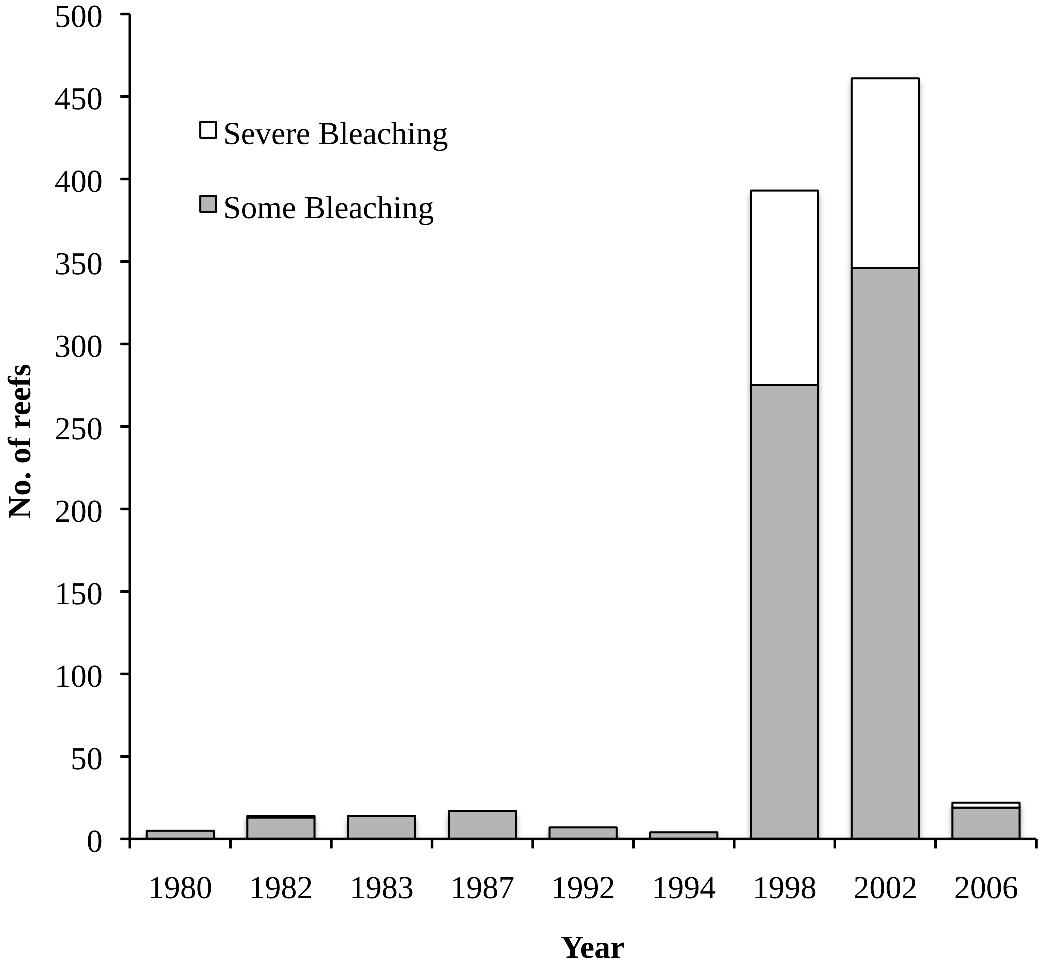

Figure 1. Recorded instances of mass coral bleaching on the Great Barrier Reef, since 1979. Seasonal “paling” of some coral colonies occurs in nearly all years, but specific instances of mass-bleaching, whereby multiple colonies and species are simultaneously affected has occurred 9 times (at intervals of 1-6 years). Data presented shows the number of reefs reported to have conspicuous evidence of bleaching, and the number of reefs with severe (>60%) bleaching. Variation in the number of reefs is partly due to limited spatial scale of surveys conducted in early years, but still there were a much higher proportion of severely bleached reefs in 1998 and 2002. For a complete account of data sources see Pratchett *et al.* 2011.

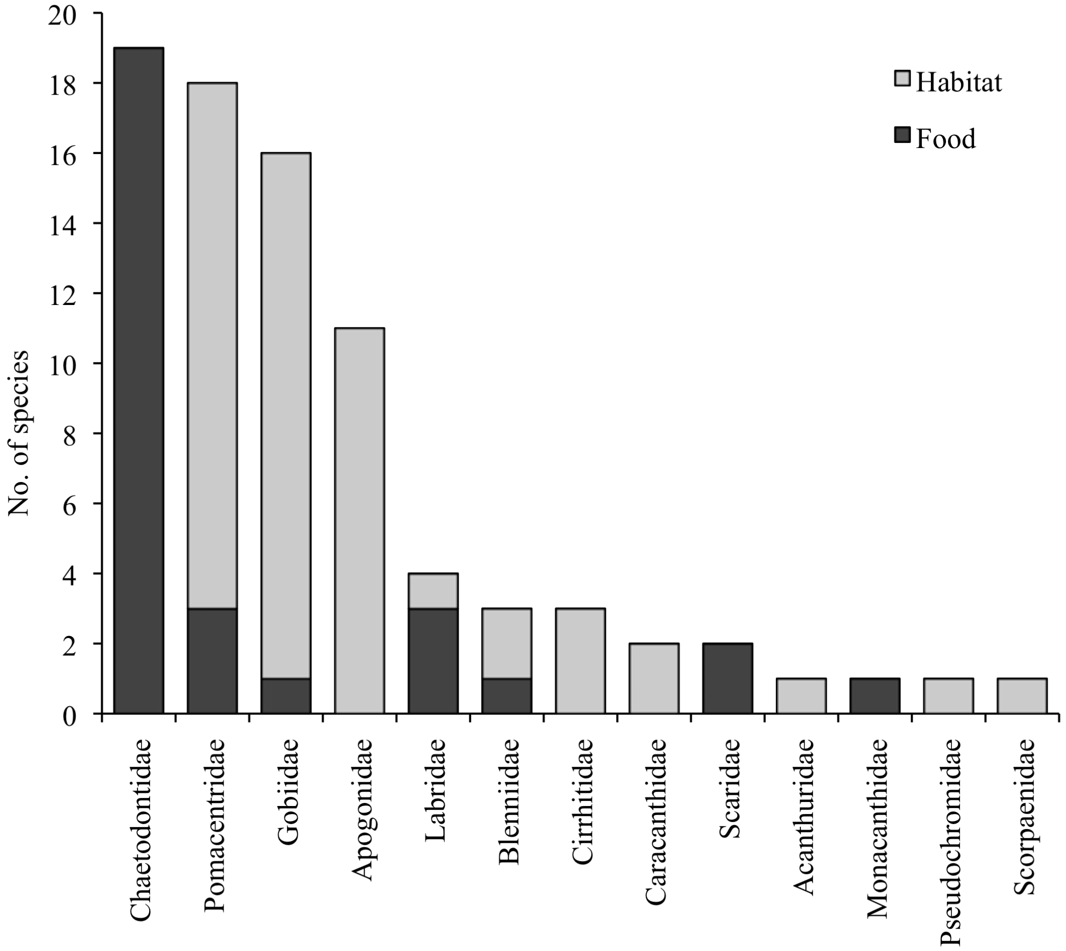

Figure 2 Coral-dependent fishes on the Great Barrier Reef, Australia; Number of species of fishes (by family) that rely on coral for either food or habitat.

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