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THE IMPORTANCE OF LIVE CORAL HABITAT FOR REEF FISHES AND ITS ROLE IN KEY ECOLOGICAL PROCESSES

Thesis submitted by

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This thesis included some collaborative work with Prof. Morgan Pratchett, Prof. Philip Munday, Dr. Nick Graham, Dr. Shaun Wilson, Dr. Aaron McNeil and Dr. Stefan Walker. While conducting these collaborative projects, experimental design, data collection, technical analysis and ecological interpretation were primarily conducted by me. My collaborators provided intellectual guidance, financial support, and assistance with fieldwork, technical instruction and editorial assistance. Aside from standardised formatting for the thesis, chapters three, four and six have been presented as published.

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Declaration of ethics

The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *James Cook University Policy on Experimentation Ethics, Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practise* (2001).

This project was approved by James Cook University Animal Ethics review committee. Research was conducted under animal ethics: A1682, A1594, A1272, and A1185.

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Abstract

Climate change is having major impacts in all the world's ecosystems. On coral reefs, the most conspicuous and devastating effects of climate change relate to widespread bleaching and resulting mortality of key habitat-forming corals. This, in turn, has affects on reef fishes that recruit, feed and shelter on live corals. Bleaching events often cause declines in abundance and diversity of coral associated fishes, but the proximate causes of these declines remain largely unknown. Specifically, it is unclear why coral-dwelling fishes disappear from bleached coral hosts, even though these corals continue to provide a physical habitat structure. The purpose of this research is to document the importance of live coral habitat for reef fishes, in order to understand the likely effects of coral loss caused by current and ongoing climate change.

Critical first steps to understanding the effects of coral depletion on reef fishes is to establish the range of fishes that associate with live coral habitats, and to determine which species of corals are most important as habitat. Chapter 2 combines a comprehensive literature review with independent field surveys to directly record fishes that use live coral habitats. A total of 320 different fish species, representing approximately 8% of reef fishes globally, were recorded to use live coral habitats. These fishes, from 39 different families, used a wide range (93 species) of different corals. However, reef fishes mainly used branching corals from Acroporidae and Pocilloporidae families. This study shows that many species of reef fish will be affected by extensive coral loss, especially considering that the corals most important in providing habitat are among the most susceptible corals to both biological and physical disturbances.

Coral bleaching initiates a sequence of changes in the biological and physical structure of habitat-forming corals, although the degradation of physical habitat structure can take several years. Yet well before major structural degradation transpires, coral-dwelling fishes often decline in abundance on bleached or dead corals even though they would still be expected to offer protection from predators. The aim of Chapter 3 was to test for changes in predation risk among i) healthy coral colonies, ii) bleached, but living coral colonies, iii) recently dead coral colonies, and iv) dead coral colonies that had been colonised by algae. *Psedochromis fuscus,* a common predatory reef fish, was found to avoid bleached and recently dead habitats, but targeted prey fishes on habitats with degraded pigmentation more than fishes on healthy coral habitats. This suggests that fish are visually more vulnerable to predators when associated with bleached and recently dead coral habitats. Direct measures of predation showed a decline in prey fish survivorship with declines in habitat condition from healthy through to algal covered habitats (75-58% respectively). This shows that bleached and algal covered habitats provide reduced protection for coral-dwelling fishes from predators. Moreover, the growth of algae, sponges and other invertebrates that colonise dead coral skeletons reduce access to the valuable refuge spaces and limit their ability to effectively avoid predators and explains why these habitats are often devoid of coral-dwelling fishes.

While coral-dwelling fishes typically associate with a single host colony, changes in habitat structure and increased exposure to predators following coral bleaching may provide strong motivation for fishes to vacate degraded habitats and relocate to alternative healthy habitats. Chapter 4 investigated the response of a common coral-dwelling fish (*Dascyllus aruanus*) to host coral bleaching and the loss of their coral habitat. Following host coral bleaching there was no movement of fish from corals that bleached but retained their live tissue cover. In contrast, 67% of fish vacated dead but structurally intact corals and migrated to neighbouring healthy coral colonies. Manipulative experiments revealed that selection of new habitats by relocating fishes was largely influenced by the presence of conspecifics. These results suggest that coral-dwelling fishes have the capacity to move between habitats and therefore the ability to withstand moderate levels of host coral depletion. However, with disturbances predicted to become more severe and widespread, the availability of alternative habitats becomes reduced and the distance between healthy habitats increases. This may further reduce the potential to relocate and therefore mediate habitat loss.

Many coral-dwelling fishes live in stable and hierarchically organised social groups. Therefore, it is likely that intra-specific competition will have a strong influence on the success of displaced fishes in colonising new habitats. Chapter 5 used manipulative experiments to explore intra-specific competition and colonisation of new habitats by the coral-dwelling damselfish, *D. aruanus*. Relatively few individuals (11%) were able to successfully join existing groups of conspecifics, with neither group-size nor body-size distribution predicting their success. Resident individuals similar and slightly larger in size than the intruding fish displayed the greatest levels of aggression, possibly because these individuals have the most to lose if the intruder gains entry. Competition between displaced individuals and group members will substantially reduce population resilience through relocation among coral-dwelling fishes following habitat degradation.

The recovery of fish communities following biological and physical disturbance is important in order to maintain key ecological functions. Many studies have independently investigated the effects of live coral cover and structural complexity on fish recruitment, but little is known about the combined effects these two factors. Chapter 6 involved manipulation of patch reefs to investigate the combined effect of high, medium and low live coral cover and high and low structural complexity on reef fish recruitment. In the first month following establishment of patch reefs, there were significant differences in abundance and diversity of

recruiting fishes among the six treatments, but there was no consistent difference through time. However, species composition showed significant differences among the different habitat treatments. Overall, live coral cover drove the differences, with coral-dependent species recruiting to high coral and high complexity reefs, and rubble-associated species recruiting to degraded reefs. SIMPER analysis revealed that some species of fish with no obvious dependence on live corals, still recruit preferentially to patch reefs with high coral cover. This suggests that some non-coral dependent species depend on live coral at recruitment and emphasizes that healthy live coral habitat can also be important for fishes that have no obvious dependence on live coral in their adult stage for recruitment.

This thesis elucidates the importance of live coral for reef fishes. It demonstrates that many reef fish species currently rely on live coral as a habitat. Among these coral-dependent fishes, it identifies key ecological processes that are affected once the coral habitat becomes degraded. Taken together, the findings of this thesis suggest that a degraded biological and physical structure of reef habitat may significantly affect a wide range of reef fishes, potentially undermining the success of key ecological functions. Such a scenario has far reaching implications towards the biodiversity and productivity of coral reef ecosystems, and therefore the goods and services they provide.

Table of contents

List of tables

List of figures

Chapter 1: General Introduction

Global Climate Change is emerging as the single greatest threat to the natural world (Walther et al. 2002, Hughes et al. 2003, Parmesan and Yohe 2003). In the ocean, climate change is contributing to increases in mean sea surface temperature (SST), as well as major hydrologic changes affecting hydrodynamic regimes and ocean chemistry (Roessig et al. 2004). Increased SST is also predicted to increase the frequency and intensity of tropical storms (Henderson-Sellers et al. 1998, Walsh 2004, Webster et al. 2005) leading to localised destruction of submerged marine habitats through increased wave energy and freshwater runoff (Cheal et al. 2002). Tropical coral reefs are particularly susceptible to climate change (Donner et al. 2005), owing to extreme thermal sensitivities of the major habitat-forming species, scleractinian corals (Hoegh-Guldberg 1999, Hughes et al. 2003). As SSTs rise and approach the maximum thermal tolerances for reef corals (Lough 2000, Hoegh-Guldberg 2004), naturally occurring thermal anomalies (e.g., ENSO events) will increasingly lead to severe and widespread bleaching across many species of corals (Hoegh-Guldberg 1999). The incidence and geographic extent of mass-bleaching has been increasing over the past 30 years (Hoegh-Guldberg 1999, Hughes et al. 2003), culminating in the global mass-bleaching event in 1997-1998. The 1997-1998 mass-bleaching event was the most severe and extensive bleaching event ever recorded, and effectively “destroyed” 16% of the coral reefs around the world (Wilkinson 2000). Effects of this bleaching event were most severe on reefs in the Indian Ocean where up to 99% of corals across entire reefs were killed and subsequently collapsed, resulting in structurally depauperate reef landscapes (Sheppard et al. 2002, Graham et al. 2006). These changes in biological and habitat structure also had devastating effects on the diversity and abundance of motile reef organisms, especially fishes (e.g., Sheppard et al. 2002, Garpe et al. 2006, Graham et al. 2006, Pratchett et al. 2009a).

Corals are central to the physical and biological structure of coral reef habitats, contributing to surface topography and habitat-diversity (Carpenter et al. 1981, Bruno and Bertness 2000), as well as playing a major role in the biochemical and nutrient cycles (e.g., Wild et al. 2004). Removal or destruction of corals will therefore profoundly alter the structure and dynamics of coral reef habitats, with significant impacts on highly diverse assemblages of species that associate with coral reefs (e.g., Wilson et al. 2006, Munday et al. 2007, Pratchett et al. 2008a). Climate-induced coral bleaching has been linked to significant and widespread declines in the abundance of coral reef fishes (e.g., Kokita and Nakazano 2001, Jones et al. 2004, Graham et al. 2006, Pratchett et al. 2006a, 2008a), species extirpations and extinctions (Hawkins et al. 2000, Munday 2004), and dramatic shifts in community structure (e.g., Bellwood et al. 2006). In general, coral bleaching and coral loss have the greatest impact on fishes that are directly dependent on live corals for food or shelter (reviewed by Wilson et al. 2006, Pratchett et al. 2008a). For example, many coral-dwelling fishes (e.g. damselfishes, hawkfishes and coral gobies) exhibit rapid and dramatic declines in abundance following coral bleaching (Spalding and Jarvis 2002, Munday 2004), which might be expected given that these fishes depend on their host corals to provide physical defense against predators (Beukers and Jones 1997). However, declines in the abundance of coral-dwelling fishes often precede any change in structural integrity (Bellwood et al. 2006), suggesting these fishes require not only the physical structure provided by intact coral skeletons, but also rely on live coral tissue.

Scleractinian corals provide food, recruitment cues, and possibly many other important resources for coral-dwelling fishes (Jones and Syms 1998, Donner et al. 2005, Wilson et al. 2006). Many fishes preferentially settle on live corals (e.g. Booth and Beretta

1994, Munday et al. 1997, Öhman et al. 1998, Holbrook et al. 2000, Booth and Beretta 2002, Jones et al. 2004), and may use visual and olfactory cues to find appropriate settlement habitats (Sweatman 1988, Booth 1992). The unique odour of live coral tissues processes may also assist displaced coral-dwelling fishes in finding new host corals across a reef after a bleaching event, and illustrate the potential importance of live and healthy coral hosts. The importance of live coral in structuring reef fish populations and communities is demonstrated by rapid and significant declines in the health (Kokita and Nakazono 2001, Jones and McCormick 2002, Pratchett et al. 2004, Berumen et al. 2005), recruitment (Booth and Beretta 2002, Feary et al. 2007a), abundance (Williams 1986, Sano et al. 1987, Booth and Beretta 2002, Halford et al. 2004, Jones et al. 2004, Munday 2004, Bellwood et al. 2006, Pratchett et al. 2006a, Wilson et al. 2006), and diversity (Lewis 1997, Syms and Jones 2000, Messmer et al. 2011) of fishes following declines in coral abundance. Up to 65% of fishes are negatively affected by extensive coral loss (reviewed by Pratchett et al. 2011a), but for many of these fishes it is unknown how or why they depend on live corals.

Effects of coral loss on coral reef fishes have been variously attributed to either the loss of live coral cover (e.g., Jones et al. 2004, Pratchett et al. 2006a), and/ or declines in topographic complexity (Garpe et al. 2006, Graham et al. 2006). Climate-induced coral bleaching often kills corals, but unlike most physical disturbances (e.g., cyclones) leaves the underlying skeleton completely intact (Hoegh-Guldberg 1999). However, exposed coral skeletons are then subject to a whole suite of bio-eroding organisms that undermine the structural integrity of these carbonate structures (Hutchings 1986). Over time wave energy and borers break down the coral into pieces, and transform a structurally complex coral habitat into a rubble-dominated habitat (Steneck 1988). It generally takes 2-5 years for dead coral skeletons to collapse (Sano et al. 1987), and there have been several reports of marked declines in the abundance of reef fishes corresponding with widespread collapse of reef habitats (Sano et al. 1987, Graham et al. 2006, Wilson et al. 2006).

The pervasive view in the literature investigating effects of climate change is that coral associated fishes are declining as a result of declining structural complexity in reef habitats (Graham et al. 2006). The local abundance of coral reef fishes is often correlated with availability of shelter holes (Hixon and Beets 1993) and structural complexity (Sano et al. 1987, McCormick 1994, Nanami and Nishihira 2002). These studies implicitly assume that predation increases with declines in topographic complexity, but few studies have actually measured changes in predation intensity or efficacy associated with changing habitat structure (but see Beukers and Jones 1997). Declines in the abundance of coral-dwelling fishes following host coral bleaching may be attributable to either movement of fishes to alternate habitats or colonies (Wilson et al. 2006, Pratchett et al. 2008a), or mortality, which probably results from predation (Booth and Beretta 2002) (Figure 1.1). Recovery of fish communities following disturbances is driven by the input of larvae fishes through recruitment. Therefore, the condition of the benthos is important for the replenishment of fishes and the relationship between the requirements of recruiting species and coral cover and substrate complexity (Jones et al. 2004, Feary et al. 2007a).

1.1 Predation

Predation on coral reefs can influence patterns of abundance and exert a considerable influence on community structure of coral reef fishes at a variety of scales (Hixon and Menge 1991, Caley and St John 1996, Hixon and Carr 1997, Almany 2004). It is expected therefore, that predation plays an important role in observed declines in abundance of small reef fishes following coral bleaching (Wilson et al. 2006, Pratchett et al. 2008a). Coral bleaching

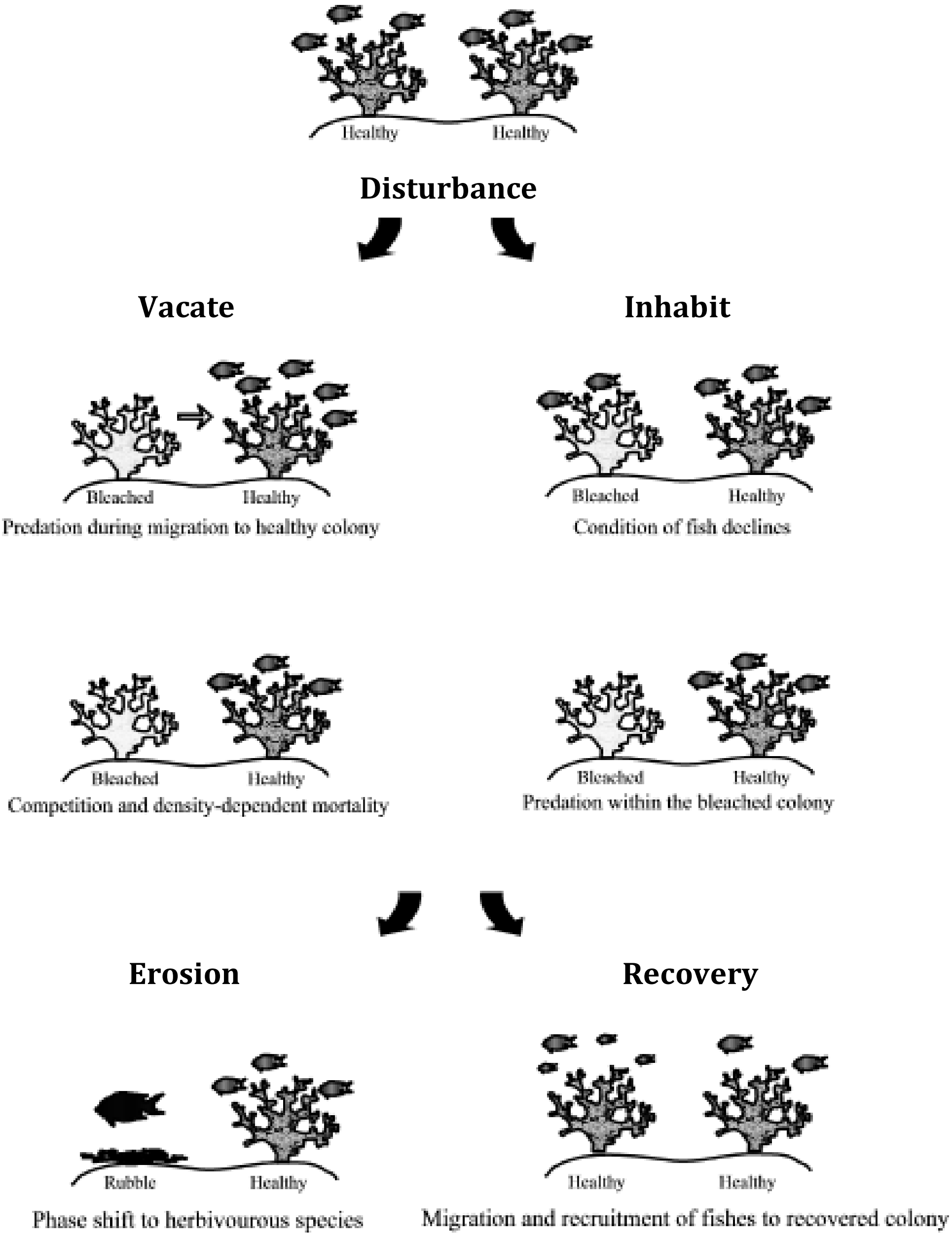

Figure 1.1: The role of predation, migration, condition and competition as proximal causes of declines in the abundance of coral-dwelling fishes following host coral bleaching. Other factors like competition and condition can also further magnify the impact. The loss of live coral cover can result in increased algal cover and erosion of complexity. Alternatively, corals that recover will facilitate the recovery of fish communities through recruitment and migration

reduces the pigmentation of the corals from a deep hue to a pale or white appearance but leaves the structural integrity of the coral intact (Hoegh-Guldberg 1999). Most coral reef fishes are brightly coloured and therefore standout against the stark white bleached corals. When host corals bleach, coral-dwelling damselfishes may be immediately subjected to increased predation risk due to increased perception of prey fishes against the white background of bleached corals. Fishes within the bleached host coral may also become stressed with the change in their surroundings leading to changes in their behaviour. Stressed fishes may make themselves more vulnerable to predation as well as a decline in their health and condition (Feary et al. 2009, McCormick et al. 2010). Once dead, colonies become over grown with algae, sponges and other invertebrates that take up valuable refuge spaces, this may further reduce the ability for fishes to shelter effectively. If bleached and dead colonies no longer provide an effective habitat, coral-dwelling fishes may vacate their host coral in search of alternative healthy habitats.

1.2 Movement

Although many reef fishes are site attached there is the potential that small-scale patchy disturbances and the removal of resources might force fishes to move to find more favourable habitats (Lewis 1997, Wilson et al. 2006). A study by Garpe et al. (2006) found that bleach-resistant corals supported twice as many coral-dwelling fishes post-bleaching as they did prior to the mass bleaching event (bleached corals had significantly less). This data suggests that coral-dwelling fishes may respond to host-coral bleaching by relocating to nearby and unaffected coral hosts. Coral-dwelling fishes are likely to vacate their host coral if it is no longer fulfilling their resource requirements. For example, fishes would be expected to move in search of a new habitat if the current habitat was physically degraded or did not provide adequate protection from predators. The potential for motile reef organisms to find other suitable habitats depends upon the scale of the disturbance and densities of con-specifics in surrounding areas. Furthermore, fishes that detect and approached a new suitable habitat must also be able to successfully join the resident community.

1.3 Competition

Observations of common coral-dwelling fishes (e.g., *Dascyllus* spp.) indicate that they occur in fairly stable social groups (Sweatman 1985, Forrester 1990, Holbrook et al. 2000). Within the social groups there is often a strict size-based dominance hierarchy (Coates 1980). Following disturbances, fishes associated with impacted habitat may vacate their degraded host colony, either driven by changes in habitat condition or the increased threat of predation and relocate to alternative healthy habitats. Migrating fishes may attempt to join existing fish communities on remaining colonies if there are no empty colonies available or they prefer to relocate to colonies containing conspecifics. This could be problematic, as some fishes are highly aggressive towards conspecifics (Zumpe 1965, Rasa 1969, Ebersole 1985, Forrester 1991, Johnson et al. 2000, Whiteman and Cote 2002).

The intense aggressive response is due to competition between individuals for the same ecological resource (e.g., shelter), namely the coral head. Competition may dictate the success of individuals to successfully relocate if suitable habitats are limited or fishes choose to join conspecific groups. Success may be driven by multiple factors: size (intruder and resident members), sex, aggressiveness and size of resident group. Alternatively the fish might be allowed to enter the group unchallenged or they may be able to force their way in based on their physical dominance. This inturn might lead to the expulsion of already existing individuals (forcible eviction) as new fish might be capable of challenging and overtaking its dominance in the rank. Competitively inferior individuals might not be successful at relocating to more favourable healthy habitats following host colony degradation forcing them to remain associated with degraded colonies or spend more time exposed to predators as they continue to search and compete for habitat.

1.4 Recruitment

A decline in live coral cover can reduce the abundance of fish recruits that rely on live coral for habitat (Lewis 1997, Booth and Beretta 2002) resulting in recruitment failure, and have the potential to influence future adult population size (Booth and Wellington 1998). Habitat degradation could contribute to a decline in settlement as live coral cover declines and through a possible suppression of settlements cues. In a study in Kimbe Bay (PNG), as many as 65% of coral reef fish species were found to associate with live coral after settlement (Jones et al. 2004). Reductions in live coral may exert a negative influence on both settlement and recruitment in a range of coral reef fishes (Lewis 1997, Booth and Beretta 2002). While most studies have looked into the affects of recruitment limitation and how this will drive population fluctuations (Doherty and Williams 1988, Caley et al. 1996, Levin 1998, Hixon et al. 2002) very few have considered habitat-recruitment limitation, in particular the change in coral cover and structural complexity. Of the studies that have looked at habitat condition on recruitment (e.g., Caley and St John 1996, Booth and Beretta 2002, Feary et al. 2007a, McCormick et al. 2010) none to my knowledge have investigated the combined effects of varying live coral cover and structural complexity. Therefore, the presence of living coral tissue and structural complexity may be a critical factor in shaping patterns of recruitment or early post settlement survivorship (Beukers and Jones 1997, Öhman et al. 1998, Holbrook et al. 2000). This also has the ability to impact species that are not restricted to settle onto live coral. For example, three species of damselfish at One Tree Island suffered a decline in recruitment following the 1998 bleaching event, even though only one of these species recruits to live coral (Booth and Beretta 2002). This suggests that the loss of coral cover could have far-reaching effects on the composition of reef fish communities as the impacts are not just restricted to species that settle into live coral.

1.5 Research aims and objectives

The purpose of this thesis was to test the importance of live coral for reef fishes to improve predictions about the effects of climate-induced coral bleaching, and associated coral loss, on coral reef fishes. There have been several recent studies documenting declines in the abundance of coral reef fishes following mass-bleaching and mortality of scleractinian corals (Booth and Beretta 2002, Spalding and Jarvis 2002, Jones et al. 2004, Pratchett et al. 2009a), but the proximal causes of these declines remain largely unknown. This thesis comprises five independent chapters, each focussed on key processes that may influence associations between reef fishes and scleractinian corals.

Chapter 2 combines a comprehensive desktop review with independent field-based surveys to quantify the proportion of coral reef fish species that are specifically dependent on live coral. Understanding of the importance of corals for coral reef fishes is currently limited to a few key families (e.g., butterflyfishes and damselfishes), whereas there may be a very large proportion of reef fish species that live, feed or shelter on live corals. This chapter will greatly increases the range of fishes known to rely on live corals, but also document the specific range of coral species that are used by different reef fishes.

Chapter 3 explores the importance of live coral (as distinct from bleached or dead coral colonies) in providing a refuge from predators. This chapter (and several of the subsequent chapters) focuses on coral-dwelling damselfishes, which are a taxonomically diverse assemblage of small-bodied fishes (e.g., *Chromis* spp., *Dascyllus* spp., *Pomacentrus* spp.) and tend to associate with individual coral colonies (Sale 1971, Feary et al. 2007b). Like many small reef fishes, coral-dwelling damselfishes are highly susceptible to predation (Beukers and Jones 1997), and shelter within live corals to evade predators. This chapter tests whether live corals provide a more effective predator refuge compared to bleached and dead coral colonies with equivalent structural complexity.

Chapter 4 explores if and when coral-dwelling fishes vacate their host colonies and what factors influence successful colonization of new microhabitats by coral-dwelling damselfishes that are displaced following bleaching and/ or mortality of host corals. Such disturbances can be spatially patchy, but it is unclear whether fishes subject to degradation of their immediate habitat are able to move and exploit alternative nearby healthy habitat patches. Three factors were considered that may influence the initiation and success of movement among habitat patches, including the condition of original host corals, the local abundance of alternative coral hosts, and the occurrence of conspecifics on alternative coral habitat.

Chapter 5 explicitly tests the extent to which size-based competitive hierarchies moderate successful colonization of available coral hosts among conspecific damselfishes. Many coral-dwelling fishes form stable social groups based on size-based hierarchies and have been observed to show aggression towards other conspecifics (Coates 1980, Forrester 1991). The strong need for displaced individuals to belong to a group means that they will attempt to join existing groups of conspecifics. For displaced individuals, it is uncertain how this aggression will influence the success of relocation. This chapter examines the success of individuals at joining established groups of conspecifics, what factors influence success and which group members elicit aggression based on intruder size.

Chapter 6 tests the importance of live coral cover and structural complexity of coral habitats during recruitment by coral reef fishes. Many reef fishes have been shown to recruit to live corals, including many species that do not associate with corals as adults (Jones et al. 2004). It is unclear, however, whether these fishes utilize live corals simply because they provide structurally complex micro-habitats. This study used experimentally constructed patch reefs consisting of six different habitat treatments; three levels of live coral cover (high, medium, low) crossed with 2 levels of structural complexity (high, low), to test the independent and combined effects of live coral cover and structural complexity on the recruitment and recovery of fish communities.

Chapter 2: Importance of live coral habitat for reef fishes[2]

2.1 Abstract

Live corals are the key habitat forming organisms on coral reefs, contributing to both the biological and physical habitat structure. Present and ongoing declines in live coral cover caused by natural and anthropogenic impacts are therefore, likely to cause declines in the abundance and diversity of coral reef fishes. Understanding the importance of corals for coral reef fishes is however, restricted to a few key families of fishes, whereas it is likely, that a vast number of reef fish species will be adversely affected by the loss of live corals. This study used data from published literature together with independent field based surveys (addressing inherent bias in current literature) from Lizard Island, Northern Great Barrier Reef, Australia to quantify the diversity of coral reef fishes that use live coral habitats. A total of 320 species of fishes from 39 families have been reported from the literature and field surveys to use live coral habitats, accounting for approximately 8% of all reef fishes. Many of those fishes that use live corals are from the families Pomacentridae (68 species) and Gobiidae (44 species) and most (66%) are either planktivores or omnivores. Collectively, reef fishes have been reported to use at least 93 species of coral, mainly from the genus *Acropora*. The corals that supported the greatest number of fish species were, *Acropora pulchra, A. hyacinthus, A formosa, Pocillopora damicornis and Porities cylindrica,* which are nearly all open branching corals. The large number of fishes that rely on coral highlights the important

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[2] A manuscript of this chapter is in preparation for the submission to the journal *Fish and Fisheries.*

consequences of habitat degradation and coral loss for biodiversity and productivity of coral reef fishes. Moreover, it is likely that we have under-estimated the number of fishes that use live coral habitats and this proportion is an absolute minimum. Further research on rare fishes and increased sampling in deeper water habitats and remote locations are likely to reveal even more fishes that use live corals. Reducing and reversing rates of coral loss on coral reefs throughout the world should therefore be an unequivocal focus of coral reef management, not only to maintain coral dominated habitats, but also to maximise biodiversity of fishes and sustainability of reef-based fisheries.

2.2 Introduction

Coral reef ecosystems are renowned for their high biodiversity and productivity (e.g., Connell 1978, Hoegh-Guldberg 1999), which is at least partly due to the diverse and complex habitat provided by scleractinian corals (Luckhurst and Luckhurst 1978, Bell and Galzin 1984, Chabanet et al. 1997). Live corals represent an important biological substrate that is critical in providing food and shelter for reef-associated organisms (Caley and St John 2006, Cole et al. 2008, Wilson et al. 2010). Live coral also helps to moderate competition and predation interactions for associated fishes by providing refuge spaces and specific niches (e.g., feeding) within the colony (Webster and Hixion 2000, Stewart and Jones 2001, Schmitt and Holbrook 2002). Even for those fishes that do not explicitly live on or in live corals, the physical structure provided by good coral growth might greatly enhance individual survivorship and species co-existence, by moderating competition and predation.

Over 25 percent of all marine fish species associate with corals reefs (Lieske and Myers 1994, Spalding et al. 2001, Allen 2008), but not all of these fishes are specifically reliant on live corals (Cinner et al. 2009). Some fishes depend on live coral for food, habitat, and/ or settlement (Sale et al. 1984, Caley and St. John 1996, Cole et al. 2008, Simpson et al. 2008) but there are many reef-associated fishes that do not appear to have any obvious dependence on live coral (Jones et al. 2004, Wilson et al. 2006, Pratchett et al. 2008a). It is clear however, that many fishes are more abundant in areas with high coral cover (Jones et al. 2004, Munday et al. 2007, Pratchett et al. 2008a) and so the real importance of live corals for fishes has probably been under-estimated. Recent reviews on coral feeding fishes indicate that approximately 5% of reef fishes rely on live coral for food (Cole et al. 2008, Rotjan and Lewis 2008). A further 5-7% of species (based on specific studies in restricted locations) are estimated to live exclusively within live coral habitats, taking the proportion of fishes reliant on live corals to approximately 12% (Munday et al. 2007). Habitat dependence varies between species and often emulates behavioural decisions with regards to predation pressure, reproduction and foraging requirements. Consequently, the exact relationship between fish and coral, and the species of fish that associate with live coral habitats are poorly understood and can vary greatly between species, life stages and changes in spatial scale (Wilson et al. 2010).

Reef fishes generally use live coral habitats for one of two different reasons. Firstly, the complex architecture of corals, especially branching species, provides an effective refuge for small-bodied fishes to evade predators (Holbrook and Schmitt 2002). Secondly, live coral provides a food source for many fishes that are specialised to feed on coral tissue (Cole et al. 2008). Additionally, fishes may associate with corals because they provide good access to prey resources (e.g., juvenile butterflyfishes, Cole et al. 2008), while simultaneously providing effective shelter. Furthermore, coral cover may moderate competition and predation even for those species not intimately associated with live coral. For larger fish, predators aggregate in areas of live coral if they contain high densities of small prey fishes (Stewart and Jones 2001). Most literature on the relationship between fishes and live coral as habitat relates to small-bodied planktivorous reef fishes (e.g., damselfish) that are commonly found associating with branching coral colonies (Sale 1972, Booth and Beretta 2002, Feary et al. 2007a,b, Bonin et al. 2009, McCormick et al. 2010).

Significant and widespread declines in the abundance of fishes following extensive coral loss (Sano et al. 1987, Jones et al. 2004, Graham et al. 2006, Cheal et al. 2008) is evidence of the strong reliance on live corals by many reef fishes. Coral loss, and associated habitat degradation, represents a major threat to biodiversity, accounting for 37% of all marine extinctions and several local extinctions of coral reef fishes (Dulvy et al. 2003, Garpe et al. 2006, Graham et al. 2006, Pratchett et al. 2008a). Coral loss is caused by a range of different disturbances (e.g., coral bleaching, disease, outbreaks of *Acanthaster planci*, tropical storms) that reduce live coral cover and/or topographic complexity (Hughes et al. 2003, Wilkinson 2004). In a meta-analysis of 17 independent studies, Wilson et al. (2006) showed that 62% of reef fishes declined in abundance following declines in coral cover of greater than 10%. This is most evident for small-bodied coral-dwelling and coral-feeding reef fishes, which exhibit generally rapid and pronounced declines in abundance following extensive coral loss. For larger fishes, there is often a lag in their response (Pratchett et al. 2004, Graham et al. 2007), whereby the greatest declines in abundance and diversity of reef fishes tend to occur 4-5 years after acute disturbances (e.g., coral bleaching) that cause coral loss (Jones et al. 2004, Garpe et al. 2006, Graham et al. 2006). This lag is attributed to either declines in topographic complexity that occurs several years after extensive coral mortality (Wilson et al. 2006, Pratchett et al. 2008a), and/or the extended period required for recruitment failure to become manifest in fishes that are unaffected by coral loss as adults.

Fishes that are most at risk from the loss of live coral habitat are those species with a specific and direct reliance on corals (e.g., for food, habitat or recruitment: Pratchett et al. 2006a, 2009a, Wilson et al. 2006). However, the extent to which these fishes are impacted by coral loss also depends on their ecological versatility. Generalist fishes that are able to utilise a wide range of different coral types, and potentially alter their patterns of coral use are much more likely to be able to withstand temporary reductions in coral abundance. For specialists fishes (e.g., coral gobies that inhabit only a single species of coral) however, declines in coral availability may have a disproportionate impact on local densities (Pratchett et al. 2008a, 2011a), because coral-dependent fishes often use corals (especially *Acropora*) that are extremely vulnerable to cyclones, extreme temperatures, and outbreaks of coral eating crown-of-thorns starfishes (Marshall and Baird 2000, Loya et al. 2001, Madin and Connolly 2006).

With projected increases in the frequency and severity of disturbances (e.g., climate induced coral bleaching) that cause extensive coral loss (e.g., Hoegh-Guldberg et al. 2007), it is important to understand which fishes depend on live coral, the species of coral, and the strength of their associations. This will assist in understanding the importance of live coral, differences in vulnerability of fishes to declines in live coral habitat, and the potentially confounding influence of declines in habitat complexity when there is extensive coral loss. The purpose of this study was to document the full range of reef fishes that utilise live coral habitat. Data on habitat association was collated from 110 published papers and 4 monographs dating back 41 years (Appendix 2.1). To qualify for inclusion, I looked for evidence of association with live coral habitat based on visual observation (surveys), collection and experimental outcomes. Where possible, the species of coral with which fishes associated with was noted, as well as the specific life stage (as juveniles, adults, or both) at which fishes use corals.

There is an inherent bias associated with data collected from published literature whereby most studies focus on common fish species rather than comprehensively studying all fishes associated with specific corals. To partly re-dress this issue (and assess the extent of bias) underwater visual surveys were conducted to record all fishes associated with specific coral habitats. Fishes that were immediately above coral habitats (e.g., planktivorous damselfishes) were slowly approached to see if and where they retreated to coral habitats. Non-coral-dwelling fishes were observed to flee across the reef in the water column while coral-dwelling fishes would retreat into the colony directly below. Fish surveys were conducted in 2009 on five exposed, five sheltered and five lagoonal reefs around Lizard Island, Great Barrier Reef (GBR) (14°41'S, 145°27'E). At each reef, five visual belt transects (1 m x 10 m) were conducted surveying a total of 537 individual coral colonies and covering a total of 750 m^2 and. Surveys were conducted in November to capture fish species that had recently recruited to the reef (majority of recruitment is observed over this summer period in the southern hemisphere). Each fish was identified to species (Randell et al. 1997, Allen et al. 2003) ascribed to species-specific life-history categories (juvenile versus adult) and the species or coral with which it was associated with was recorded. The information collected from these surveys (see Reference 100, Appendix 2.1) was added to the data collected from published literature. This combined data set will help us identify what species of fish associate with live coral, what species of coral they associate with, and at what stage of their life.

2.3 Fishes associated with live coral

2.3.1 Community range

Based on published literature and field surveys, a total of 320 species of fishes (from 39 families) have been recorded to associate with live coral habitat (Table 2.1), representing 8% (320 out of 4000 species) of all coral reef fishes. Previous estimates based on geographically restricted analyses of reef fish assemblages (in Kimbe Bay, PNG and Australia's Great Barrier Reef), suggested that 9 to 11% (59 – 104 spp.) of local reef fishes were dependent on corals for food or habitat (Jones et al. 2004, Munday et al. 2007, Pratchett et al. 2008a). This study greatly increases the absolute number of fishes considered to use live corals, whereas lower estimates of the proportion of fishes that use live corals may suggest that there are fewer fishes reliant on live corals at peripheral reef locations, compared to the Indo-Pacific archipelago where previous studies (Jones et al. 2004, Munday et al. 2007) were conducted. However, it is most likely that the overall proportion of fishes reliant on live corals has been underestimated due to a paucity of studies on fish coral interactions in many locations and we must emphasize that this estimate is an absolute minimum. It is expected that many more species that have not been captured in our surveys or literature, express dependence on live coral habitat. For example, many species of the same genus show similar ecological niches, and therefore it is likely that if a few species of a particular genus are known to associate with live coral, then it is possible that other species within the genus may also. Furthermore, data on many cryptobenthic species is extremely lacking (but see Bellwood et al. 2006), but it is likely that many of these species are intimately linked with live corals Of the 320 species of fish recorded to associate with live coral cover, 92% are from the Indo-Pacific bioregion (Table 2.1). This equates to approximately 7.7% of fishes in the region. The Indo-Pacific (Pacific Ocean, Indian Ocean and Red Sea) comprises approximately 75% of the world’s coral reefs (Bruno and Seilg 2007) and contains the centre of global marine diversity for many prominent taxa including fish, crustaceans and corals (Roberts et al. 2002). Field surveys conducted around Lizard Island suggest that just over 6.7% (98/1460 LIRS Lizard Island Life Database) of fish species recorded on the GBR associated with live coral habitat. In the Caribbean, meanwhile, only 13 species of fish was found to associate with live coral for habitat (Table 2.1). While reef fish diversity in this region is significantly lower (500-700spp., Lieske and Myers 2001) this still represents at least 2% of fishes. The percentage of fish associating with live coral habitat is possibly much lower than observed in the

Table 2.1: List of all documented fish species that have and association with live coral for habitat, coral species used and geographical distribution.

R = Response to coral loss. ↑ = increase, ↓ = decrease, ↕ = increase and decrease, - = no data. Data from Pratchett et al. (2008).

J = juvenile, A = Adult. See Appendix 2.1 for references.

Taxa	J	A	Habitat association	Distribution	Reference	R
Acanthuridae (n=15)						
Acanthurus auranticavus	-	X	*Acropora hyacinthus*	West Indian	55	-
Acanthurus blochii	-	X	*Acropora hyacinthus*	Indo - Pacific	55	↕
Acanthurus dussumieri	X	-	*Pocillopora damicornis*	Indo - Pacific	99	↕
Acanthurus nigricans	-	-	*Acropora pulchra*	East Indian	50	↓
Acanthurus nigrofuscus	-	X	*Acropora hyacinthus, A. pulchra*	Indo - Pacific	50, 55	↕
Acanthurus triostegus	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Ctenochaetus striatus	X	-	*Acropora pulchra, Porites rus*	Indo - Pacific	50, 59	↕
Ctenochaetus strigosus	X	-	*Porites compressa*	Indo - Pacific	23	↕
Naso brachycentron	-	-	*Acropora pulchra*	Indo - Pacific	50	↑
Naso lituratus	-	-	*Acropora pulchra*	Pacific	50	↕
Naso sp.	-	X	*Acropora hyacinthus*		55	-
Paracanthurus hepatus	X	X	*Pocillopora eydouxi*	Indo - Pacific	64, 79, 90	-
Zebrasoma flavescens	X	-	*Porites compressa*	NW & Central Pacific	23, 84, 109	↑
Zebrasoma scopas	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Zebrasoma veliferum	-	-	*Acropora formosa, A. pulchra, A. yongei, Echinopora mammiformis, Porities cylindrica*	Pacific	50, 100	↕
Aulostomidae (n=1)						
Aulostomus chinensis	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Apogonidae (n=24)						
Apogon angustatus	X	X	*Porites spp.*	Indo - Pacific	60	-
Apogon bandanensis	-	X	*Porites cylindrica*	East Indo - West Pacific	34	-
Apogon compressus	-	X	*Acropora spp., Porities cylindrica, P. nigrescens*	Asian Pacific	34, 79, 90	-
Apogon cyanosoma	X	X	*Acropora formosa, Echinopora mammiformis, Heliopora coerulea, Porities cylindrica, Seristopora hystrix*	Asian Pacific	90, 108	↕

Taxa	J	A	Habitat association	Distribution	Reference	R
Apogon doederleini	X	-	*Acropora formosa, Pocillopora damicornis, Porites cylindrica, Seriatopora hystrix*	West Pacific	106, 108	-
Apogon fragilis	X	X	*Porites cylindrica*	Indo - West Pacific	34, 106	-
Apogon gracilis	X	-	*Seriatopora hystrix*	Indo - Pacific	108	-
Apogon guamensis	-	X	*Acropora spp.*	Indo - West Pacific	79	-
Apogon leptacanthus	-	X	*Porites cylindrica,*	Indo - West Pacific	34, 79, 90	-
Apogon notatus	-	X	Live coral	Asian Pacific	90	-
Apogon thermalis	X	X	*Echinopora mammiformis, Seriatopora hystrix*	Indo - Asian Pacific	100	-
Archamia fucata	-	X	*Porites cylindrica*	Indo - West Pacific	34, 79, 89, 90	-
Archamia macroptera	-	X	Live coral	West Pacific	89	-
Archamia zosterophora	-	X	*Acropora spp., Porities cylindrica*	West Pacific	34, 35, 79	-
Cheilodipterus artus	-	X	*Porites cylindrica*	Indo - Pacific	34, 90	-
Cheilodipterus quinquelineatus	X	X	*Acropora formosa, A. yongei, Pocillopora damicornis, Seriatopora hystrix, Porites cylindrica*	Indo - Pacific	34, 89, 100, 108	↓
Fowleria marmorata	X	-	*Pocillopora damicornis, Seriatopora hystrix*	Indo - Pacific	108	-
Ostorhinchus capricornis	-	X	Live coral	West Pacific	3, 89	-
Ostorhinchus compressus	-	X	Live coral	Indo - West Pacific	89	-
Pseudamia gelatinosa	-	X	Live coral	Indo - Pacific	90	-
Rhabdamia gracilis	-	X	Live coral	Indo - West Pacific	90	-
Siphamia fistulosa	X	-	*Pocillopora damicornis*	West Pacific	79	-
Sphaeramia nematoptera	-	X	*Porites cylindrica, P. nigrescens*	West Pacific	34, 79, 89, 90	-
Zoramia leptacantha	-	X	*Porites cylindrica*	Indo - Pacific	35, 89	-
Balistidae (n=5)						
Balistapus undulatus	-	X	*Acropora hyacinthus, A. pulchra*	Indo - Pacific	6, 50, 55	↕

Taxa	J	A	Habitat association	Distribution	Reference	R
Melichthys niger	-	X	*Porites lobata*	Circumtropical	105	↓
Melichthys vidua	-	X	*Acropora pulchra*	Indo - Pacific	6, 50	-
Odonus niger	-	-	*Acropora pulchra*	Indo - Pacific	50	↑
Rhinecanthus aculeatus	-	-	*Acropra pulchra*	Indo - Pacific	50	-
Blenniidae (n=9)						
Atrosalarias fuscus holomelas	X	X	*Heliopora coerulea, Porities cyclindrica*	Indo - Pacific	89, 90, 100, 110	↕
Cirripectes sp.	-	X	*Echinopora mammiformis, Pocillopora eydouxi, Porities cylindrica*	GBR	100	-
Cirripectes stigmaticus	-	X	*Acropora spp., Pocillopora spp.*	Indo - West Pacific	79, 110	-
Ecsenius bicolor	-	X	*Heliopora coerulea*	Indo - Central Pacific	100	-
Ecsenius stictus	-	X	*Porites spp.*	GBR	110	-
Exallias brevis	-	X	*Acropora spp., Millepora spp., Pocillopora eydouxi, Seriatopora spp., Porites spp.*	Indo - Pacific	4, 79, 89, 100	-
Meiacanthus grammistes	-	X	*Echinopora mammiformis*	Asian Pacific	100	-
Plagiotremus tapeinosoma	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Petroscirtes mitratus	-	X	*Pocillopora eydouxi*	Indo - West Pacific	100	-
Caesionidae (n=1)						
Pterocaesio marri	-	X	*Acropora spp.*	Indo - Pacific	38	↓
Callionymidae (n=1)						
Synchiropus splendidus	-	X	Live coral	Asian Pacific	90	-
Caracanthidae (n=2)						
Caracanthus maculatus	-	X	*Acropora spp., Pocillopora eydouxi, Stylophora mordax*	Central Pacific	4, 64, 79, 89, 90	-
Caracanthus unipinna	-	X	*Acropora corymbosa, A. humilis, A. millepora, A. spathulata, Pocilloporidae, Poritidae, Stylophora mordax*	Indo - Pacific	42, 64, 79, 80, 86, 89,	-

Taxa	J	A	Habitat association	Distribution	Reference	R
					90, 100, 104	
Centriscidae (n=1)						
Aeoliscus strigatus	-	X	Live coral	Indo - Asian Pacific	64, 90	-
Chaetodontidae (n=23)						
Chaetodon aureofasciatus	X	-	*Acropora corymbosa, A. divaricata, A. formosa, A. hyacinthus, A. millepora, A. nasuta, A. spathulata, A. yongei, Pocillopora spp.,Stylophora pistillata*	Indo - Pacific	87, 100, 104	↓
Chaetodon auriga	X	X	*Acropora formosa, A. millepora, A. pulchra, Montipora spp., Porites cylindrica*	Indo - Pacific	50, 87, 100, 106	↓
Chaetodon baronessa	X	X	*Acropora divaricata, A. formosa, A. hyacinthus, A. millepora, A. muricata, A. spathulata*	East Indo - West Pacific	87, 100	↓
Chaetodon citrinellus	X	-	*Acropora hyacinthus, A. millepora, A. muricata, A. pulchra*	Indo - Pacific	50, 87	↓
Chaetodon ephippium	X	-	*Porites cylindrica*	Indo - Pacific	106	↑
Chaetodon kleini	-	X	*Acropora formosa*	Indo - West Pacific	100	↓
Chaetodon lineolatus	X	-	*Acropora formosa, Seristopora hystrix*	Indo - Pacific	100	↓
Chaetodon lunula	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Chaetodon lunulatus	X	X	*Acropora formosa, A. muricata, A. pulchra, A. spathulata, Montipora spp., Pocillopora spp., Porities cylindrica, Seristopora hystrix*	Pacific	50, 87, 100	↓
Chaetodon melannotus	X	-	*Acropora muricata, Montipora spp., Porites spp.*	Indo - West Pacific	87	↓
Chaetodon octofasciatus	-	X	*Acropora spp., Porites spp.*	Indo - Asian Pacific	97	-
Chaetodon ornatissimus	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Chaetodon pelewensis	-	-	*Acropora pulchra*	Pacific	50	↓
Chaetodon plebeius	X	X	*Acropora formosa, A. loripes, A. millepora, A. muricata, A. spathulata, Pocillopora damicornis, Porities cylindrica, Seristopora hystrix*	East Indo - West Pacific	87, 99, 100, 112	↓
Chaetodon rainfordi	X	-	*Acropora formosa, A. hyacinthus, A. millepora, A. nasuta, A. yongei, Pocillorpra damicornis, Porites spp.*	West Pacific	31, 87, 100	↓

Taxa	J	A	Habitat association	Distribution	Reference	R
Chaetodon reticulatus	-	-	*Acropora pulchra*	Pacific	50	↓
Chaetodon trifascialis	X	X	*Acropora divaricata, A. hyacinthus, A. formosa, A. muricata, A. pulchra*	Indo - Pacific	50, 87, 100, 112	↓
Chaetodon ulietensis	-	X	*Acropora pulchra, Porities cylindrica*	East indo - Pacific	50, 100	↓
Chaetodon unimaculatus	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Chaetodon vagabundus	X	-	*Acropora millepora, A. muricata, A. pulchra*	Indo - Pacific	87	↕
Forcipiger longirostris	-	-	*Acropora pulchra*	Indo - Pacific	50	↑
Heniochus acuminatus	-	X	*Acropora formosa*	Indo - Pacific	100	-
Heniochus chrysostomus	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Cirrhitidae (n=7)						
Cirrhitus pinnulatus	X	-	*Acropora pulchra, Pocillopora meandrina, Porites compressus*	Indo - Pacific	44, 50	-
Neocirrhites armatus	-	X	*Acropora spp., Pocillopora elegans, P. eydouxi, P. verrucosa, Stylophora modax*	West Pacific	63, 89, 90	-
Paracirrhites arcatus	X	X	*Acropora pulchra, Pocillopora meandrina, Porites compressa, Stylophora spp.*	Indo - Pacific	22, 44, 47, 50, 52, 64	↕
Paracirrhites forsteri	-	X	*Acropora spp., Stylophora spp., Pocillopora eydouxi, P. meandrina*	Indo - Pacific	4, 64, 89, 100	↓
Paracirrhites hemistictus	-	X	*Millepora spp.*	East indo - Pacific	22, 89	-
Paracirrhites nisus	-	X	*Pocillopora spp.*	Indo - Pacific	4, 89	-
Paracirrhites xanthus	-	X	*Pocillopora spp.*	Central Pacific	4, 89	-
Diodontidae (n=1)						
Diodon hystrix	-	-	*Acropora pulchra*	Circumtropical	50	↓
Fistulariidae (n=1)						
Fistularia commersonii	-	-	*Acropora pulchra*	Indo -Pacific	50	-
Gobiesocidae (n=1*)*						
Diademichthys lineatus	-	X	Live coral	West Indian	89, 90	-

Taxa	J	A	Habitat association	Distribution	Reference	R
Gobiidae (n=44)						
Amblygobius phaelena	-	X	*Pocillopora damicornis*	Indo - Pacific	99	-
Asteropteryx semipunctatus	X	-	*Acropora formosa, Pocillopora damicornis, Seriatopora hystrix*	Indo - Pacific	108	↓
Bryaninops amplus	-	X	*Gorgonian spp.*	Indo - Pacific	90	-
Bryaninops erythrops	-	X	*Millepora spp., Porites cylindrica, P. lutea*	Indo - Pacific	4, 79, 90	-
Bryaninops natans	-	X	*Acropora spp.*	Indo - West Pacific	4, 41, 89, 90	-
Bryaninops ridens	-	X	*Millepora spp.*	Indo - Pacific	41	-
Bryaninops tigris	-	X	*Antipathes sp.*	Indo - Pacific	4, 90	-
Bryaninops yongei	-	X	*Cirripathes sp, Antipatharian spp.*	Indo - Pacific	41, 90	-
Coryphopterus glaucofraenum	-	X	*Acropora cervicornis, A. prolifera, Porites porites*	West Atlantic	96	-
Elacatinus dilepis	X	X	Live coral	Western atlantic	39	-
Elacatinus evelynae	-	-	Live coral	Western atlantic	39	-
Eviota bifasciata	X	X	*Acropora cerealis, A. kimbeensis, A. nasuta, A. speciosa*	Asian Pacific	101	-
Eviota distigma	-	X	*Acropora divaricata, Stylophora pistillata*	Indo - Pacific	41, 104	-
Eviota gymnocephalus	-	X	*Seriatopora hystrix*	West Pacific	104	-
Eviota nigriventris	X	X	*Acropora cerealis, A. kimbeensis, A. nasuta, A. speciosa*	West Pacific	101	-
Eviota queenslandica	-	X	*Acropora spp., Montipora spp.*	East Indo - West Pacific	7	↑
Eviota sebreei	-	X	Live coral	Indo - West Pacific	41	-
Eviota sp.	-	X	*Acropora corymbosa, A. humilis, Porites lutea, Seriatopora hystrix*	GBR	81, 104	-
Gobiodon acicularis	X	X	*Echinopora horrida, E. mammiformis, Hydnophora rigida, Porites spp.*	West Central Pacific	4, 76	-
Gobiodon albofasciatus	-	X	*Pocillopora spp., Stylophora spp.*	West Pacific	79	-
Gobiodon axillaris	X	X	*Acropora cerealis, A. digitifera, A. gemmifera, A. loripes, A. millepora, A. nasuta, A. secale, A. tenuis, A. valida*	Central Pacific	72, 74, 75, 86, 89	↓
Gobiodon brochus	X	X	*Acropora elseyi, A. loripes, A. nasuta, A. tennuis*	West Central Pacific	73, 74, 75, 89	-
Gobiodon ceramensis	-	X	*Acropora appressa, A. corymbosa, A. humilis, A. tizardi, Stylophora pistillata*	Asian Pacific	4, 86, 104	-
Gobiodon citrinus	X	X	*Acropora formosa, A. nobilis, A. spathulata*	Indo - West	4, 41, 64,	↓

Taxa	J	A	Habitat association	Distribution	Reference	R
				Pacific	76, 89, 90, 100	
Gobiodon histrio	X	X	*Acropora digitifera, A. gemmifera, A. humulis, A. loripes, A. millepora, A. nasuta, A. secale, A. spathulata, A. tenuis, A. valida*	Indo - Pacific	25, 72, 73, 74, 75, 86, 100, 104	↓
Gobiodon micropus	X	X	*Acropora loripes, A. nasuta, A. tenuis*	Indo - Pacific	75, 86, 90	-
Gobiodon oculolineatus	X	X	*Acropora cerealis, A. humilis, A. loripes, A. millepora, A. tenuis*	NW Pacific	76, 100	-
Gobiodon okinawae	X	X	*Acropora cerealis, A. divaricata, A. loripes, A. millipora, A. nasuta, A. tenuis, A. yongei, Echinopora mammiformis*	East Indo - Asian Pacific	4, 64, 75, 89, 99, 100, 101	↓
Gobiodon quinquestrigatus	X	X	*Acropora aspera, A. cerealis, A. corymbosa, A. digitifera, A. divaricata, A. gemmifera, A. humilis, A. kimbeensis, A. loripes, A. millepora, A. nasuta, A. secale, A. selago, A. speciosa, A. syrangodes, A. tenuis, A. tizardi, A. valida*	Pacific	4, 27, 64, 72, 74, 75, 100, 101, 104	-
Gobiodon reticulatus	-	X	Live coral	West Indian	41	-
Gobiodon rivulatus	X	X	*Acropora cerealis, A. digitifera, A. gemmifera, A. humilis, A. loripes, A. microclados, A. millepora, A. nasuta, A. secale, A. tenuis, A. valida, Pocillopora spp., Stylophora spp.*	Indo - West Pacific	41, 42, 72, 75	↓
Gobiodon sp.	-	X	*Acropora caroliniana*	PNG	78	↓
Gobiodon species B	X	X	*Acropora caroliniana*	PNG	78	-
Gobiodon species C	X	X	*Acropora elseyi*	PNG	76	-
Gobiodon species D	X	X	*Acropora divaricata*	West Central Pacific	76	-
Gobiodon spilophthalmus	-	X	*Stylophora pistillata*	Indo - Asian Pacific	100	-
Istigobius sp.	-	X	*Acropora spp., Montipora spp.*	Indo - West Pacific	7	-
Paragobiodon echinocephalus	X	X	*Acropora humilis, A. tenuis, Pocillopora damicornis, Seriatopora hystrix, Stylopora pistillata*	Indo - Pacific	41, 56, 64, 89, 100, 104, 108	-
Paragobiodon lacunicolus	-	X	*Pocillopora damicornis*	Indo - Pacific	56, 64, 89	-

Taxa	J	A	Habitat association	Distribution	Reference	R
Paragobiodon melanosomus	X	X	*Seriatopora caliendrum, S. hystrix, Stylophora pistallata*	Indo - West Pacific	56, 101	-
Paragobiodon modestus	-	X	*Pocillopora damicornis*	Indo - Pacific	56, 89	-
Paragobiodon xanthosoma	X	X	*Seristopora hystrix*	Indo - Pacific	27, 28, 56, 57, 64, 89, 90, 100, 101, 113, 114	-
Pleurosicya micheli	-	X	*Porities cylindrica*	Indo - Pacific	41, 89, 90	-
Pleurosicya prognatha	-	X	Live coral	West Indian	41	-
						-
Haemulidae (n=4)						-
Diagramma pictum	-	-	*Acropora hyacinthus*	Indo - West Pacific	55	-
Haemulon flavolineatum	X	-	*Acropora cervicornis, A. prolifera, Porites porites*	West Atlantic	70, 96	↑
Plectorhinchus chrysotaenia	-	X	*Acropora hyacinthus*	West Pacific	55	-
Plectorhinchus lineatus	-	X	*Acropora hyacinthus*	West Pacific	55	-
Holocentridae (n=8)						
Myripristis murdjan	-	-	*Acropora pulchra*		50	↓
Myripristis violacea	-	X	*Acropora spp., Porites rus*	Indo - Pacific	79	↑
Neoniphon argenteus	-	X	*Acropora pulchra, A. spp.*	Indo - Pacific	50, 79	-
Neoniphon sammara	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Sargocentron melanospilos	-	X	*Acropora formosa, A. hyacinthus, Porities cylindrica*	Indo - West Pacific	100	-
Sargocentron microstoma	-	X	*Acropora pulchra, A. spp., Pocillopora eydouxi*	Indo - Pacific	50, 79	-
Sargocentron seychellense	-	X	Live coral	West Indian	64	-
Sargocentron spiniferum	-	X	*Acropora hyacinthus*	Indo - Pacific	55	-
Kyphosidae (n=1)						
Kyphosus vaigensis	-	X	*Acropora hyacinthus, A. pulchra*	Indo - Pacific	50, 55	-

Taxa	J	A	Habitat association	Distribution	Reference	R
Labridae (n=32)						
Cheilinus undulatus	X	-	*Acropora spp.*	Indo - Pacific	79	↓
Cheilinus chlorourus	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Cheilinus trilobatus	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Cheilio inermis	-	-	*Acropora pulchra*	Indo - Pacific	50	↑
Choerodon fasciatus	-	X	*Porities cylindrica*	West Pacific	100	↓
Coris aygula	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Coris variegata	X	-	*Pocillopora damicornis*	West Indian	108	↕
Diproctacanthus xanthurus	X	X	Live coral	West Central Pacific	90	-
Epibulus Insidiator	-	X	*Acropora hyacinthus, A. pulchra*	Indo - Pacific	50, 55	↓
Gomphosus caeruleus	X	-	Live coral	Indian	36	↕
Gomphosus varius	X	X	*Acropora hyacinthus, A. pulchra, Heliopora coerulea, Pocillopora meandrina, Porities cylindrica*	Indo - Pacific	44, 50, 55, 100	↕
Halichoeres chrysus	-	X	Live coral	East Indo - Asian Pacific	90	-
Halichoeres hortulanus	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Halichoeres melanurus	X	X	*Acropora corymbosa, A. hyacinthus, A. loripes, A. millepora, Echinopora mammiformis, Pocillopora damicornis, P. eydouxi, Porites spp., Stylophora pistillata*	West Pacific	55, 97, 100, 104	↕
Halichoeres ornatissimus	-	-	*Acropora pulchra*	Pacific	50	-
Halichoeres trimaculatus	-	-	*Acropora pulchra*	Indo - Pacific	50	↑
Hemigymnus fasciatus	X	-	Live coral	Indo - Pacific	64	↕
Hemigymnus melapterus	X	X	*Acropora hyacinthus, Porities cylindrica*	Indo - Pacific	55, 64	↓
Labrichthys unilineatus	X	X	*Acropora millepora, A. nasuta, A. secale, Echinopora mammiformis, Pocillopora damicornis, P. meandrina, Porities cylindrica, Stylophora pistillata*	Indo - West Pacific	36	↓
Labroides bicolor	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Labroides dimidiatus	X	X	*Acropora formosa, A. nasuta, A. pulchra, Pocillopora meandrina, Porities cylindrica*	Indo - Pacific	50, 100	↕
Labropsis micronesica	-	X	*Acropora spp.*	Central Pacific	79	-
Oxycheilinus digramma	-	X	*Acropra hyacinthus*	Indo - Pacific	55	-
Pseudocheilinus hexataenia	X	X	*Acropora pulchra, A. spp., Pocillopora spp.*	Indo - Pacific	36, 50	↓

Taxa	J	A	Habitat association	Distribution	Reference	R
Stethojulis bandanensis	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Thalassoma amblycephalum	X	-	Live coral	Indo - Pacific	36, 82	↕
Thalassoma duperrey	X	-	*Porites pukoensis*	East Central Pacific	24	-
Thalassoma hardwicke	X	X	*Acropora pulchra, Pocillopora damicornis, P. verrucosa, Porites lobata, P. rus*	Indo - Pacific	37, 50, 61, 63, 112	↕
Thalassoma lunare	X	-	Live coral	Indo - Pacific	112	↕
Thalassoma lutescens	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Thalassoma quinquevittatum	-	X	*Pocillopora verrucosa, Porites lobata, P. rus*	Indo - Pacific	37	↑
Thalassoma sp.	X	-	*Pocillopora meandrina, P. verrucosa*	Indo - Pacific	58	-
Lethrinidae (n=5)						
Gnathodentex aureolineatus	-	-	*Acropora pluchra*	Indo - Pacific	50	↓
Lethrinus atkinsoni	-	X	*Acropora hyacinthus*	Pacific	55	-
Lethrinus laticaudis	-	X	*Acropora hyacinthus*	West Pacific	55	-
Lethrinus sp.	-	X	*Pocillopora damicornis*	GBR	99	-
Monotaxis grandoculis	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Lutjanidae (n=9)						
Lutjanus apodus	-	-	Live coral	West Atlantic	64	↓
Lutjanus bohar	-	X	*Acropora hyacinthus*	Indo - Pacific	55	↕
Lutjanus carponotatus	-	X	*Acropora hyacinthus*	Indo - West Pacific	44	↓
Lutjanus fulviflamma	-	X	*Acropora hyacinthus*	Indo - Pacific	55	↑
Lutjanus fulvus	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Lutjanus gibbus	-	X	*Acropora hyacinthus*	Indo - Pacific	55	↕
Lutjanus kasmira	X	-	*Pocillopora damicornis*	Indo - Pacific	99	↕
Lutjanus quinquelineatus	X	X	*Acropora formosa, Porities cylindrica*	Indo - West Pacific	100	-
Lutjanus russelli	-	X	*Acropora hyacinthus*	Indo - West Pacific	55	-

Taxa	J	A	Habitat association	Distribution	Reference	R
Monacanthidae (n=3)						
Cantherhines dumerilii	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Cantherhines pullus	-	-	Live coral	West Atlantic	64	-
Oxymonacanthus longirostris	X	X	*Acropora formosa, A. humilis, A. loripes, A. nasuta*	Indo - West Pacific	90, 100	↓
Mullidae (n=7)						
Mulloidichthys flavolineatus	-	-	*Acropora pulchra, Pocillopora damicornis*	Indo - Pacific	50, 99	↑
Mulloidichthys vanicolensis	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Parupeneus barberinus	-	X	*Acropora hyacinthus*	Indo - Pacific	55	↕
Parupeneus cyclostomus	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Parupeneus insularis	-	-	*Acropora pulchra*	Eastern Central Pacific	50	-
Parupeneus multifasciatus	-	-	*Acropora pulchra*	Pacific	50	↑
Parupeneus pleurostigma	-	-	*Acropora pulchra*	Indo - Pacific	50	↑
Nemipteridae (n=1)						
Scolopsis bilineatus	-	X	*Acropora formosa, A. hyacinthus*	Indo - West Pacific	55, 100	-
Ostraciidae (n=2)						
Ostracion cubicus	X	-	*Acropora formosa*	Indo - Pacific	50, 64, 100	↓
Ostracion meleagris	-	-	*Acropora pulchra*	Indo - East Pacific		-
Pempheridae (n=1)						
Parapriacanthus ransonneti	-	-	*Acropora spp.*	Indo - West Pacific	4	-
Pinguipedidae (n=2)						
Parapercis cylindrica	-	-	*Pocillopora damicornis*	West Pacific	99	↓
Parapercis millepunctata	-	-	*Acropora pulchra*	Indo - Pacific	50	↑

Taxa	J	A	Habitat association	Distribution	Reference	R
Pomacanthidae (n=4)						
Centropyge aurantonotus	-	-	Live coral	West Atlantic	50, 64	-
Centropyge flavissima	-	-	*Acropora pulchra*	Indo - Pacific		-
Pomacanthus semicirculatus	-	X	*Acropora hyacinthus*	Indo - West Pacific	55	↕
Pomacanthus sexstriatus	X	X	*Acropora formosa, A. hyacinthus, A. tenuis*	Indo - Pacific	55, 100	-
Pomacentridae (n=68)						
Abudefduf abdominalis	X	-	Live coral	East Central Pacific	24	-
Abudefduf bengalensis	X	-	*Acropora formosa*	West Pacific	100	-
Abudefduf septemfasciatus	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Abudefduf sexfasciatus	-	X	*Acropora formosa, A. pulchra, Porities cylindrica*	Indo - Pacific	50, 100	↓
Abudefduf vaigiensis	X	-	Live coral	Indo - Pacific	24	↑
Acanthochromis polyacanthus	-	X	*Acropora formosa, A. hyacinthus, Echinopora mammiformis, Porities cylindrica*	West Pacific	100	↕
Amblyglyphidodon curacao	X	X	*Acropora aculeus, A. florida, A. formosa, A. hyacinthus, A. intermedia, A. jacquelineae, A. muricata, A. nasuta, A. paniculata, A. plumosa, A. robusta, A. secale, A. selago, A. solitaryensis, A. valenciennesi, A. valida, Echinopora mammiformis, Isopora brueggemani, I. palifera, Porities cylindrica*	West Pacific	2, 12, 97, 100, 111	↕
Amblyglyphidodon leucogaster	X	X	*Acropora aculeus, A. hyacinthus, A. intermedia, A. jacquelineae, A. muricata, A. paniculata, A. plumosa, A. secale, A. subglabra, A. valenciennesi, Isopora brueggemani*	Indo - West Pacific	12, 85, 111	↕
Amblypomacentrus breviceps	X	-	*Pocillopora damicornis*	West Central Pacific	99	-
Cheiloprion labiatus	-	-	*Acropora formosa*	Indo - West Pacific	4, 100	↓
Chromis atripectoralis	X	X	*Acropora divaricata, A. formosa, A. millepora, A. valida, Echinopora lamellosa, Pocillopora eydouxi, Stylophora pistillata*	Indo - Pacific	64, 88, 89, 90, 100, 111	↕
Chromis caerulea	X	-	*Pocillopora damicornis*	Indo - Pacific	99	-
Chromis dimidiata	X	X	Live coral	Indian	36, 83	↕
Chromis nitida	X	-	*Pocillopora damicornis*	West Pacific	108	-

Taxa	J	A	Habitat association	Distribution	Reference	R
Chromis ovalis	X	-	Live coral	East Pacific	24	-
Chromis retrofasciata	X	-	*Acropora aculeus, A. hyacinthus, A. intermedia, A. jacquelineae, A. kimbeensis, A. longycyanthus, A. paniculata, A. selago, A. subglabra, A. valida*	West Pacific	12	-
Chromis ternatensis	X	X	*Acropora aculeus, A. hyacinthus, A. intermedia, A. jacquelineae, A. kimbeensis, A. longycyanthus, A. muricata, A. paniculata, A. plumosa, A. secale, A. subglabra, A. valenciennesi, A. valida, Isopora palifera*	Indo - Pacific	4, 12, 36, 89, 90, 111	↕
Chromis vanderbilti	-	X	Live coral	Pacific	24	-
Chromis viridis	X	X	*Acropora cerealis, A. divaricata, A. formosa, A. humilis, A. millepora, A. nasuta, A. pulchra, A. spathulata, Echinopora mammiformis, Pocillopora damicornis, P. eydouxi, P. meandrina, Porities cylindrica, P. rus, Seriatopora hystrix*	Indo - Pacific	50, 16, 28, 58, 62, 71, 89 ,90, 100	↓
Chrysiptera brownriggii	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Chrysiptera cyanea	-	X	*Montipora aequituberculata*	Indo - West Pacific	81	↓
Chrysiptera flavipinnis	X	-	*Acropora cerealis*	West Pacific	28	↓
Chrysiptera parasema	X	X	*Acropora aculeus, A. caroliniana , A. echinata, A. granulosa, A. intermedia, A. jacquelineae, A. kimbeensis, A. longycyathus, A. millepora, A. muricata, A. paniculata, A. selago, A. subglabra, A. valida, Pocillopora verrucosa, Porites cylindrica, Seriatopora spp.*	West Pacific	12, 13, 29, 82, 97	-
Chrysiptera springeri	-	X	Live coral	West Pacific	64	-
Dascyllus albisella	X	X	*Montipora verrucosa, Pocillopora meandrina, Porites compressa*	East Central Pacific	24	-
Dascyllus aruanus	X	X	*A. aculeus, A. aspera, A. cerealis, A. corymbosa, A. cuneata, A. divaricata, A. formosa, A. humilis, A. longicyathus, A. loripes, A. nasuta, A. pulchra, A. spathulata, A. surculosa, A. tizardi, Echinopora mammiformis, Heliopora spp., Millipora tenella, Montipora digitata, Pocillopora damicornis, P. eydouxi, P. meandrina, P. verrucosa, P. cylindrica, P. lobate, Seriatopora caliendrum, S. hystrix, Stylophora pistillata*	Indo - West Pacific	50, 95	↕
Dascyllus flavicaudus	X	X	*Acropora pulchra, A. spp., Montipora verrucosa, Pocillopora eydouxi, P. meandrina*	East Central Pacific	46, 47, 50, 93, 94	-
Dascyllus marginatus	X	X	*Acropora hemprichi, A. humilis, A.seandens, Pocillopora danai, P. verrucosa, Porites spp. Seriatopora spinosa, Stylophora pistillata*	West Indian	1 ,9, 30, 33, 53, 64, 95	-

Taxa	J	A	Habitat association	Distribution	Reference	R
Dascyllus melanurus	X	X	*Acropora aculeus, A. caroliniana, A. digitifera, A. echinata, A. formosa, A. granulosa, A. humilis, A. kimbensis, A. longicyathus, A. paniculata, A. selago, A. secale, A. solitaryensis, A. subglabra, A. valida, Echinopora spp., Millipora tenella, P. damicornis, Pocillopora verrucosa, Porites cylindrica, Seriatopora hystrix*	West Pacific	13, 13, 29, 65, 97	↓
Dascyllus reticulatus	X	X	*Acropora divaricata, A. loripes, A. nasuta, A. secale, A. spathulata, Echinopora mammiformis, Pocillopora damicornis, P. eydouxi, Seristopora hystrix*	Pacific	64, 68, 88, 89, 90, 98, 99, 100, 111, 112	↕
Dascyllus trimaculatus	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Dischistodus perspicillatus	X	-	*Pocillopora damicornis, Porites cylindrica*	Indo - West Pacific	99, 106	-
Hemiglyphidodon plagiometopon	X	-	*Porites cylindrica*	West Pacific	106	-
Microspathodon chrysurus	X	X	*Acropora palmata, Millipora spp.*	West Atlantic	40, 49, 67, 103	-
Neoglyphidodon melas	X	-	*Acropora formosa, A. humilis, A. millepora, A. nasuta, A. spathulata, A. tenuis, A. valida, Pocillopora damicornis*	Indo - West Pacific	64, 79, 100, 111, 112	↓
Neopomacentrus azysron	X	-	*Acropora caroliniana, A. hyacinthus, A.kimbeensis, A.muricata, A. nasuta, A. paniculata, A. plumosa , A. selago, A. solitaryensis, A.valenciennesi, A. valida, Isopora spp., Porites cylindrica*	Indo - West Pacific	12, 38, 106	↕
Neopomacentrus bankieri	-	-	*Acropora spp., Montipora spp.*	West Pacific	7	↕
Neopomacentrus cyanomos	X	-	*Pocillopora damicornis, Porites cylindrica*	Indo - West Pacific	99, 106	-
Plectroglyphidodon dickii	-	X	*Acropora spp., Pocillopora eydouxi*	Indo - Pacific	20, 64, 89, 111	↕
Plectroglyphidodon flaviventris	-	X	*Pocillopora eydouxi*	East Central Pacific	89	-
Plectroglyphidodon johnstonianus	-	X	*Acropora spp., Pocillopra eydouxi, Stylophora spp.*	Indo - Pacific	4, 64, 89, 90	-
Plectroglyphidodon phoenixensis	-	-	*Acropora spp., Pocillopora spp.*	Indo - Pacific	79	-
Pomacentrus agassizi	-	-	*Acropora spp.*	West Indian	64	-

Taxa	J	A	Habitat association	Distribution	Reference	R
Pomacentrus alexanderae	-	-	Live coral	West Pacific	82	-
Pomacentrus amboinensis	X	X	*Acropora cerealis, A. divaricata, A. nasuta, Echinopora mammiformis, Pocillopora damicornis, Portites cylindrica, Seristopora hystrix*	West Pacific	28, 43, 45, 51, 69, 88, 99, 100, 106	↓
Pomacentrus aurifrons	X	X	*Acropora aculeus, A. caroliniana, A. kimbeensis, A. nasuta, A. paniculata, A. plumosa, A. secale, A. selago, A. solitaryensis, A.subglabra, A. valenciennesi, A. valida, Isopora brueggemani*	West Central Pacific	12, 88	-
Pomacentrus bankanensis	-	X	*Acropora formosa, Porities cylindrica*	West Pacific	38, 100	↕
Pomacentrus brachialis	-	-	*Acroporaidae*	West Pacific	92	↕
Pomacentrus callainus	-	X	Live coral	East Central Pacific	89	-
Pomacentrus chrysurus	-	-	*Acropora spp.*	West Pacific	38	↕
Pomacentrus lepidogenys	X	X	*Acropora gemmifera, A. tenuis, Pocillopora damicornis, Stylophora pistillata*	Indo - West Pacific	38, 100, 111	↓
Pomacentrus moluccensis	X	X	*Acropora aspera, A. caroliniana, A. cerealis, A. digitifera, A. divaricata, A. formosa, A. gemmifera, A. hyacinthus, A. humilis, A. intermedia, A. longycyanthus, A. loripes, A. microclados, A. millepora, A. nasuta, A. palifera, A. paniculata, A. secale, A.selago, A. solitaryensis, A. spathulata, A. tenuis, A. valida, A. yongei, Echinopora lamellosa, E. mammiformis, Heliopora coerulea, Pocillopora damicornis, P. eydouxi, P. meandrina, Porities cylindrica, P. rus, Seriatopora hystrix, S. pistillata*	West Pacific	11, 12, 14, 17, 28, 32, 83, 88, 100, 111, 112	↓
Pomacentrus nagasakiensis	X	-	*Pocillopora damicornis, Porities cylindrica*	Indo - West Pacific	69, 100, 106, 111	↓
Pomacentrus nigromanus	X	-	*Acropora aculeus, A. caroliniana, A. jacquelineae, A. kimbeensis, A. longicyanthus, A. nasuta, A. paniculata, A. plumosa, A.secale, A.selago, A. subglabra, A. valenciennesi, A. valida, Isopora palifera, Pocillopora spp., Porites spp., Seriatopora spp.*	West Central Pacific	97	-
Pomacentrus pavo	X	X	*Acropora pulchra, Porites australiensis, P. cylindrica, P. lobata*	Indo - Pacific	50, 58, 90, 106	↑
Pomacentrus sulfureus	X	-	*Live coral*	West Indian	10	↑
Pomacentrus wardi	X	-	*Acropora nasuta, Pocillipora damicornis, Porities cylindrica, Seriotopora*	West Pacific	16, 100	↕

Taxa	J	A	Habitat association	Distribution	Reference	R
			hystrix, Stylophora pistillata			
Stegastes adustus	-	-	*Acropora cervicornis, A. palmata, Montestrea spp.*	West Central Atlantic	48, 103, 107	↓
Stegastes apicalis	-	X	*Acropora hyacinthus, Porities cylindrica*	West Pacific	100	↕
Stegastes diencaeus	X	-	*Millipora spp., Montastrea annularis, Siderastrea siderea*	West Atlantic	17	-
Stegastes fasciolatus	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Stegastes fuscus	-	-	*Acropora palmata*	West Atlantic	67	-
Stegastes leucostictus	X	X	*Acropora cervicornis, A. palmata, A. prolifera, Agaricia spp., Diploria spp., Millipora spp., Montastrea annularis, Porites asteroids, P. porites, Siderastrea siderea*	West Atlantic	5, 18, 26, 48, 67, 96	-
Stegastes nigricans	X	X	*Acropora pulchra, A. spp., Porites rus, P. cylindrica*	Indo - Pacific	50, 61, 79, 100	↓
Stegastes partitus	X	-	*Acropora cervicornis A. palmata, Diploria spp., Montastrea annularis, Porites porites, P. furcata, Siderastrea spp.*	West Atlantic	17, 67, 103	↑
Stegastes planifrons	X	X	*Acropora cervicornis A. palmata, Agaricia tenuifolia, Diploria spp., Montastrea annularis, Millepora complanata, Porities furcata, P. porites, Siderastrea siderea*	West Atlantic	15, 17, 26, 40, 47, 48, 66, 67, 102, 103, 107	↑
Stegastes punctatus	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Stegastes variabilis	X	-	*Acropora palmata, Millipora spp., Montastrea annularis, Porites porites, Siderastrea siderea*	West Atlantic	17, 66	-
Pseudochromidae (n=3)						
Pseudochromis fuscus	-	X	*Echinopora mammiformis, Porities cylindrica, Seristopora hystrix, Stylophora pistillata*	Indo - Pacific	77, 100, 106	-
Ogilbyina novaehollandiae	X	-	*Pocillopora damicornis*	West Central Pacific	108	-
Pseudochromis olivaceus	-	-	*Stylophora spp., Pocillopora spp.*	West Indian	8	-

Taxa	J	A	Habitat association	Distribution	Reference	R
Scaridae (n=11)						
Chlorurus perspicillatus	X	-	Live coral	East Central Pacific	24, 50	-
Chlorurus sordidus	-	-	*Acropora pulchra*	Indo - Pacific	24	-
Scarus atrilunula	-	X	Live coral	West Indian	49	↑
Scarus dubius	X	-	Live coral	East Central Pacific	24	-
Scarus niger	-	X	Live coral	Indo - Pacific	49	↕
Scarus oviceps	-	-	*Acropora pulchra*	Indo - Pacific	50	↓
Scarus psittacus	X	-	*Acropora pulchra*	Indo - Pacific	24, 50	↓
Scarus rivulatus	-	-	*Acropora hyacinthus*	West Pacific	55	↑
Scarus tricolor	-	X	*Live coral*	Indo - Pacific	49	↑
Sparisoma aurofrenatum	X	-	*Montestrea annularis*	West Atlantic	21	↑
Scorpaenidae (n=2)						
Sebastapistes cyanostigma	-	-	*Pocillopora spp.*	Indo - Pacific	4, 64, 79	-
Sebastapistes strongia	-	-	*Agaricira sp.*	Indo - Pacific	64	-
Scorpaena coniorta	X	-	*Pocillopora meandrina*	East Central Pacific	44	-
Serranidae (n=5)						
Cephalopholis argus	-	-	*Acropora pulchra*	Indo - Pacific	50	↕
Cephalopholis boenak	X	X	*Acropora hyacinthus, Porities cylindrica*	Indo - West Pacific	55, 106	-
Cephalopholis cyanostigma	X	-	*Acropora hyacinthus, Porities cylindrica*	West Pacific	100	↑
Epinephelus merra	-	X	*Acropora pulchra, A. spp.*	Indo - Pacific	50, 79	↕
Plectropomus leopardus	-	X	*Acropora hyacinthus*	West Pacific	55	↕
Siganidae (n=5)						
Siganus corallinus	X	X	*Acropora formosa, A. hyacinthus, Echinopora mammiformis, Porities cylindrica*	Indo - West Pacific	55, 100	↓
Siganus doliatus	X	X	*Acropora formosa, A. hyacinthus*	West Pacific	55, 100	↕
Siganus lineatus	X	X	*Acropora hyacinthus*	Indo -West	55	↓

Taxa	J	A	Habitat association	Distribution	Reference	R
				Pacific		
Siganus spinus	-	-	*Acropora pulchra*	Indo -West Pacific	50	↓
Siganus vulpinus	-	-	*Acropora spp.*	West Pacific	79	↓
Syngnathidae (n=3*)*						
Bulbonaricus brauni	-	-	*Galaxea musicalis*	East Indian	79	-
Corythoichthys flavofasciatus	-	X	*Acropora formosa, A. pulchra, Echinopora mammiformis, Heliopora coerulea*	Indo - Pacific	50, 100	-
Hippocampus bargibanti	-	-	*Muricella plectana, M. paraplectana*	West Central Pacific	90	-
Synodontidae (n=2)						
Saurida gracilis	-	-	*Pocillopora damicornis*	Indo - Pacific	98	-
Synodus variegatus	-	-	*Pocillopora damicornis*	Indo - Pacific	98	-
Tetraodontidae (n=4)						
Arothron meleagris	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Arothron stellatus	-	X	*Acropora hyacinthus*	Indo - Pacific	55	-
Canthigaster bennetti	-	-	*Pocillopora damicornis*	Indo - Pacific	99	↓
Canthigaster solandri	-	-	*Acropora pulchra*	Indo - Pacific	50	-
Tripterygiidae (n=1)						
Helcogramma striatum	-	X	Live coral	West Pacific	89	-
Zanclidae (n=1)						
Zanclus cornutus	-	-	*Acropora formosa, A. pulchra, Porities cylindrica*	Indo - Pacific	50, 100	↕

Indo- Pacific due to the limited number and diversity of published fish records (Table 2.1) as well as on going reef degradation (Gardner et al. 2003, Alvarez-Filip et al. 2009). However, coral communities in the Caribbean have always been much more depauperate compared to the Indo-Pacific (Aronson and Precht 2006), and lack many of the key habitat-forming corals that are used by reef fishes (discussed below). For other geographical regions there is a significant lack of information on coral association to make any sort of comparison. This lack of information is due to the insufficient number of studies conducted in many geographic regions and emphasises how little we know about remote reefs and their associated fish communities.

The majority of fishes (59%) recorded to use live coral habitats were from just five families: Pomacentridae, Gobiidae, Labridae, Apogonidae and Chaetodontidae (Figure 2.1). Fishes within each of these families are generally small bodied (<150mm) and live or shelter within the branches of live coral colonies throughout their lives while some of these species also depend on live coral for food (Cole et al. 2008). Coral-dwelling gobies (Gobiidae), for example, are among the most specialized coral-dwelling fishes (Munday et al. 1997) spending their entire lives within tight branching colonies of a single coral colony from the genus *Acropora*, *Seriatopora* or *Stylophora* (Munday and Jones 1998, Munday et al. 1999) and feed directly on coral tissue, mucous or fat bodies. Many species of coral-dwelling gobies are also found within a very restricted range of coral species (Munday et al. 1997, 1999, Dirnwöber and Herler 2007). In contrast, there are several larger bodied (>300mm) reef fishes (e.g., Haemulidae, Holocentridae, Lethrinidae, Serranidae) that occasionally shelter beneath large table corals (Kerry and Bellwood 2012). These fishes are unequivocally using live coral habitats, but it is questionable whether removal of these habitats would have any direct effect on their distribution and abundance, although the loss of smaller prey species which are closely associated with live coral is predicted to influence individual fitness of these larger species.

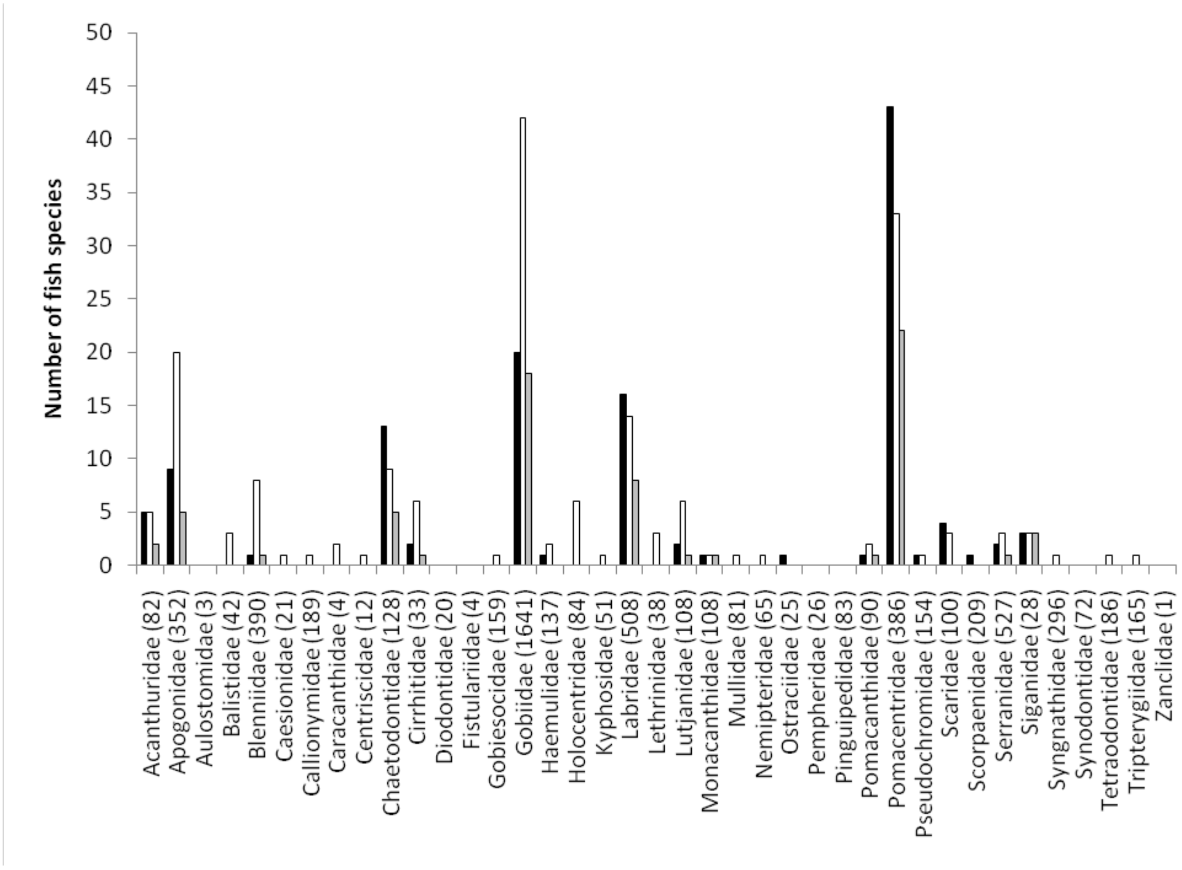

Figure 2.1: Number of fish species in each family associating with live coral habitat as juveniles and adults. ■ = Juveniles, □ = Adult and ▨ = both. Parenthese = number of species in each family (fishbase).

2.3.2 Community structure

The strength of habitat associations between fishes and live coral habitat varies depending on the way in which these fishes actually utilise live coral hosts. Reliance on live corals is intuitively, much greater among those fishes that have a permanent association with specific coral hosts (Munday et al. 1997, Holbrook et al. 2000) as opposed to those species that derive only marginal benefit from living in habitats with rich coral growth (Jones et al. 2004, Wilson et al. 2006). Of the 320 species considered in this study, it is estimated that at least 125 species (39%) are obligately dependent upon live corals, living exclusively within live corals as juveniles, adults, or both. Accordingly, it is these species that experience the greatest declines in abundance following the loss of live coral cover (Table 2.1, Pratchett et al. 2008a).

Fishes that associate with live coral habitats include all major feeding guilds: coralivores, detritivores, herbivores, invertivores, piscivores, planktivores and omnivores (Figure 2.2). Fishes belonging to different trophic groups show variance in their utilization of live coral, from coralivores that feed on live coral tissue to herbivores that feed on algae that grows on dead coral skeletons. It is fairly intuitive that coral-feeding fishes would be strongly associated with live corals, but these species only make up a small percentage (6.3%) of all coral dependent fishes. Most of the species that associate with live corals are planktivores (31.9%) and omnivores (31.6%) (Figure 2.2). For these fishes, live corals probably contribute very little to prey availability, but appear fundamental as a predator refuge. Coral-dwelling damselfishes and cardinalfishes feed in the water column immediately above specific branching corals, and retreat to within the branches when threatened (Forrester 1990, Allen 1991). Similarly, small omnivorous fishes are likely to forage within the vicinity of live corals mainly so they can seek shelter within these corals when predators approach, but it is also possible that prey concentrations are increased in close proximity to live corals (Wen et al. *In review*).

Herbivorous fishes play an important role on coral reefs by controlling macroalgae (Bellwood et al. 2004) that might otherwise inhibit coral recruitment (Hughes et al. 2007). Given their reliance on macroalgae for food, it might be expected that herbivorous fishes are most abundant with high macroalgae cover, and therefore, low coral cover (Pratchett et al. 2008a). There is however, increasing evidence that some functionally important herbivores are reliant on the physical structure provided by corals (Hoey et al. 2011), leading to positive reinforcement of macroalgae dominance following phase shifts in benthic assemblages.

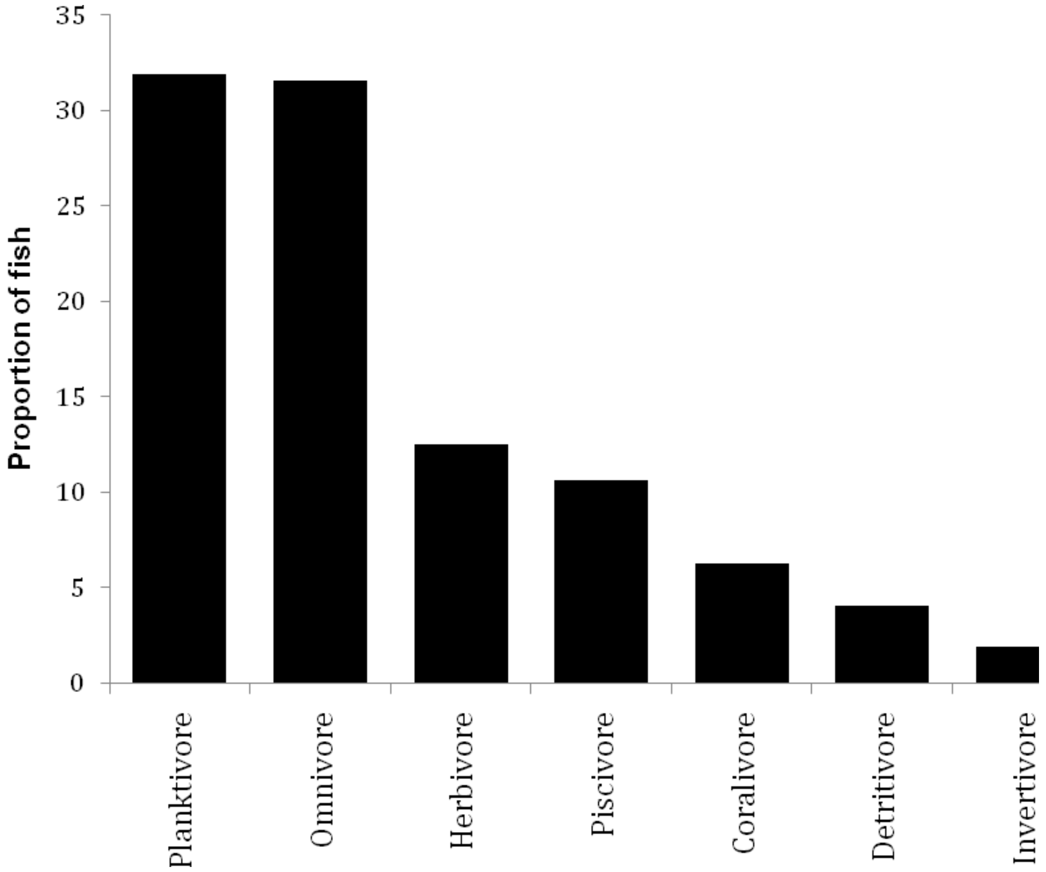

Figure 2.2: Proportion of fish associating with live coral habitat from different trophic groups.

This review identified 40 species of herbivorous fishes that associate with live coral cover (Figure 2.2). This includes grazers of algal turfs and macroalgae, scrapers, excavators and farmers, emphasizing the diversity of functional roles supported by live coral. It is important to understand the dependence of functionally important fishes on live coral habitat to help understand how disturbances and coral composition influence their distribution and abundance.

Live coral cover has strong implications for the abundance of reef associated predators due to smaller prey fishes that depend on live coral cover and structural complexity (Graham et al. 2007, Wilson et al. 2007). Piscivores provide an important link in the reef through the transfer of energy to higher trophic levels, and provision of food and livelihood through fisheries (Hixon 1991, Sadvoy 2005). In this study, 11% (34/320) of fishes were classified as piscivores (Figure 2.2) ranging from small (e.g., Cirrhitidae, Pseudochromidae) to larger bodied species (e.g., Lutjanidae, Serranidae) (Table 2.1).

Smaller predators (e.g., *Paracirrhites forester*, *Pseudochromis fuscus*) rely on live coral (Munday et al. 2003), sheltering within the branches for protection while larger mobile individuals (e.g., *Cephalopholis boenak, Plectropomus leopardus*) shelter under larger coral structures and depend on the physical structure provided by the coral (Kerry and Bellwood 2012, Table 2.1). Live coral habitat and topographic complexity provided by coral is essential for the existence of prey fishes, hunting and concealment (Helfman 1981, Samoilys 1997, Munday and Jones 1998, Kerry and Bellwood 2012).

2.4 Coral species used by fishes

Not all corals are effective in providing habitat for reef fishes, mainly due to marked differences in the overall morphology (e.g., branching versus massive), though the selection of coral habitats by reef fishes can extend well beyond gross morphological types (Feary et al. 2007b, Munday et al. 2007, Pratchett et al. 2008a). Information compiled for this study show reef fishes associate with up to 96 species of corals, from 11 Families (Figure 2.3). Of the coral species used by fishes, 52 were from the genus *Acropora*, and 12 from *Porities*. Most fishes are only using a fraction of scleractinian coral species (approx 12% globally) for habitat and may use multiple species of coral habitat if the fish is geographically widespread and different coral habitats are present in different areas (Lawton et al. 2012). Even on a small scale, coral species can vary in its abundance and presence. For example, at Lizard Island, the majority of *Dascyllus aruanus* within the lagoon associate with *Seriatopora*

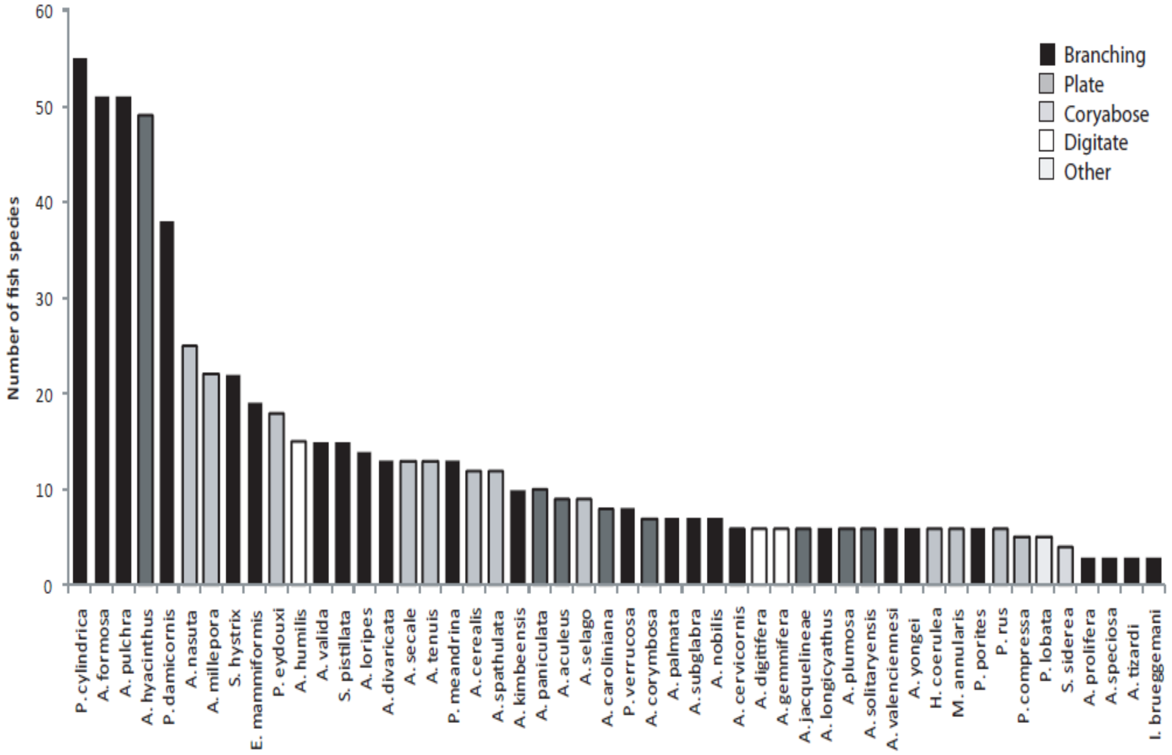

Figure 2.3: Number of fish species using each of the top 40 used coral species (total 93) and associated morphologies.

hystrix while outside the lagoon they associate mostly with *Pocilopora damicornis* due to differences in relative abundance of these coral species (D. Coker, unpublished data).

Coral species that support the greatest diversity of fishes are *Porities cylindrica* (55 species), *Acropora pulchra* (51 species), *A. hyacinthus* (49 species), *A. formosa* (39 species) and *Pocillopora damicornis* (38 species) (Figure 2.3). These corals are relatively common and frequently dominant coral assemblages within certain habitats (Veron 2000). Furthermore, these species form large branching thickets (except *A. hyacinthus*) providing plenty of refuges for fishes of varying sizes. This size allows colonies to support a high diversity of fishes within single thickets (Johnson et al. 2011). While it is clear that some coral species support a greater diversity of fishes than others, we need to keep in mind that data can be skewed towards coral species that have been extensively surveyed or particularly common in well-studied locations (e.g., *A. pulchra,* Johnson et al. 2011, *P. cylindrical,* this survey).

Fishes associate with certain species of coral, presumably because of its physical structure, availability and possible tissue properties that we are unaware of. Therefore, colony branch depth and space will influence whether the coral provides a suitable refuge space for fish or not. Many species of coral-dwelling fish associate with morphological characteristics that are branching and corymbose (Figure 2.3), whereby they provide significant protection for inhabiting fishes against high rates of predation (Beukers and Jones 1997, Holbrook et al. 2000). Colonies need to limit the entry of potential predators while associated fishes need to be able to quickly enter a colony and move with ease through the spaces between the branches. Although the morphology of plate corals doesn’t permit the movement of fishes among the branches, they still provide shelter for many larger-bodied fishes (e.g., Haemulidae, Holocentridae, Lethrinidae, Serranide), which take shelter under the structure (Table 2.1, Figure 2.3).

2.4.1 Habitat specialists

The selectivity of fishes for different coral types varies greatly, ranging from habitat generalists that utilise a very wide range of different corals (species and morphotypes) to extreme specialists that may only associate with a single coral species (Kuwamura et al. 1994, Munday et al. 1997, Bonin 2012). In general, highly specialised species are viewed to have a much stronger reliance on live corals, and are more vulnerable to any changes in coral availability (Munday 2004, Pratchett et al. 2012). In turn, specialist species often have a significant competitive advantage over generalist counterparts and exhibit higher growth and physiological condition, and ultimately greater survivorship when associated with their favoured habitats (Caley and Munday 2003).

Our review revealed 139 species of fishes that have been recorded to associate with only a single species of coral (Figure 2.4a). While this suggests many coral-dwelling fishes are extremely selective in their use of different corals, a large number of fishes (113 species) had only a single record from which habitat selectivity can be deduced (Table 2.1), either because these fishes are rare, poorly studied, or only sometimes associated with live corals. For these fishes (including, *Apogon gracilis, Eviota gymnocephalus, Chromis nitida*), further research is required to confirm that they; i) are obligately dependent on live corals, rather than only rarely using live coral for habitat, and ii) are consistently found using the same coral species in different habitats and locations. Some fishes are however, true habitat specialists and despite extensive surveys and multiple published records have only ever been recorded from a single coral species (*Gobiodon* sp. A – *Acropora tenuis, Gobiodon* sp. B – *A. carolineanus, Gobiodon* sp. C – *A. elseyi* Table 2.1). Accordingly, there is strong evidence showing that these highly specialised gobies are extremely vulnerable to acute disturbance that reduce the availability of their specific host corals (Munday et al 1997, Munday 2004, Feary et al. 2007b).

Munday (2004) quantified population declines among sympatric coral-dwelling gobies following extensive coral depletion in Kimbe Bay, Papua New Guinea. He showed that proportional declines in the abundance of these fishes were negatively correlated with their degree of habitat specialisation, whereby the fish (*Gobiodon* sp. A) that used only a single coral species, exhibited the greatest decline in abundance (Munday 2004). Similar links between coral specialisation and vulnerability to disturbances have also been recorded for other groups of fishes (Pratchett et al., 2012), which is attributed to differences in the

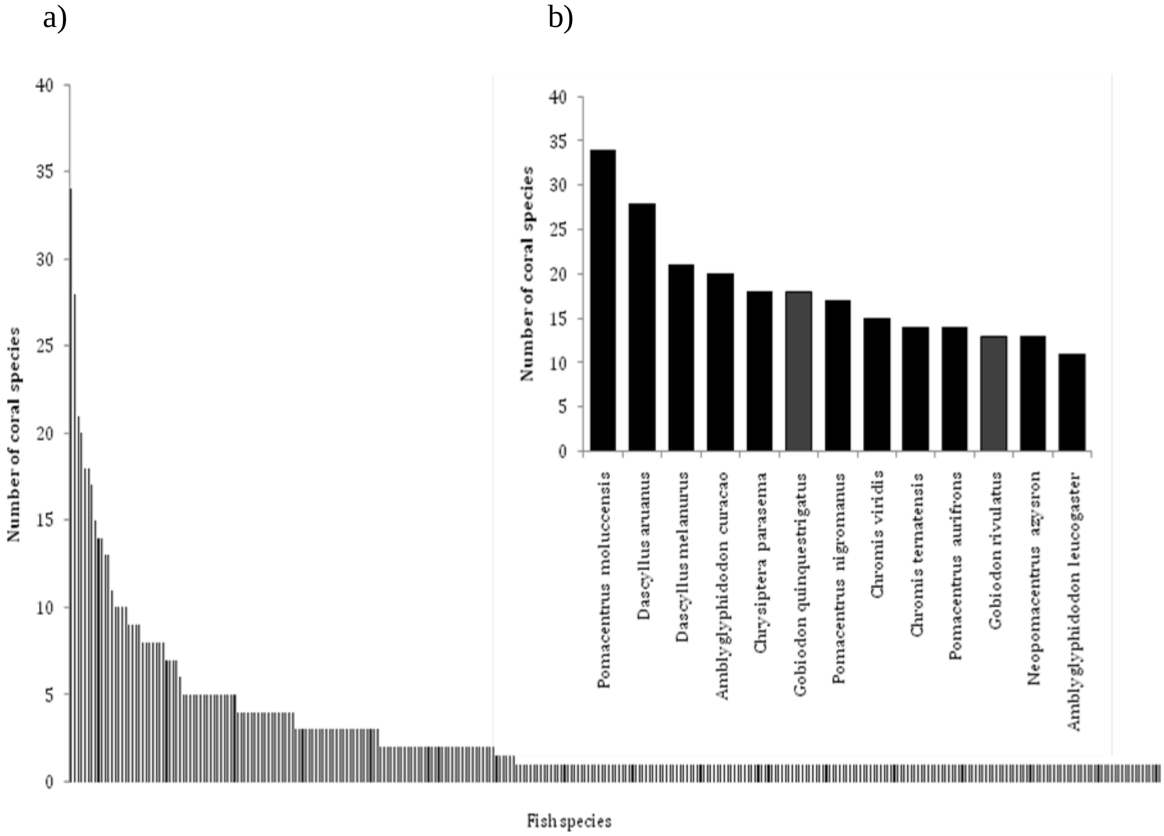

Figure 2.4: a) Number of coral species that each fish species is found to associate with, b) Top 13 fish species that associate with the highest number of coral species.

susceptibility or capacity of fishes to switch habitats following disturbances and make use of coral habitats that remain (Futuyma and Moreno 1988). For fishes that are constrained to using only a very narrow range of corals, the probability of finding suitable habitats in the aftermath of an acute disturbance will be much lower compared to fishes that will exploit almost any coral type. However, it is also possible that specialist species may escape any effects from major disturbances if they utilise habitats that are generally not susceptible to disturbance.

2.4.2 Habitat generalists

Many fishes use a wide range of different coral species, providing that they provide adequate physical shelter (Munday et al. 1997, Wilson et al. 2008a, 2010, Bonin 2012). The four most versatile species of fish that associated with the greatest range of different coral species in my review were all damselfishes (Family Pomacentridae). These species; *Amblygylphidondon curaco, Dascyllus aruanus, D. melanusrus* and *Pomacentrus moluccensis* were found to associate with over 20 coral species, and a maximum of 34 different corals for *P. moluccensis* (Figure 2.4b). This versatility allows fish species to occupy a diversity of reef habitats, often leading to increased overall abundance. Pratchett and Berumen (2008), for example, showed that highly specialised butterflyfishes were much more restricted in their distribution among reef habitats, compared to generalist species.

Despite their versatility in coral use, generalist fishes are still mostly restricted to using complex branching corals (Table 2.1). *Pomacentrus moluccensis*, for example, uses a wide range of different *Acropora* corals (24 species), but does not generally use massive, mound-shaped corals that often dominate in some coral reef habitats. Unfortunately, it is exactly these corals (*Acropora* spp.) that are most susceptible to a range of different disturbances, including climate-induced coral bleaching, severe tropical storms, and also outbreaks of coral-eating crown-of-thorns starfishes (Marshall and Baird 2000, Loya et al. 2001, Madin and Connolly 2006, Pratchett et al. 2011b). It is often expected therefore, that increased frequency and severity of acute disturbances will lead to fundamental shifts in community structure of coral assemblages, whereby robust, mound-shaped corals replace erect fragile branching species (e.g., Riegl 1999). If so, there are likely to be major reductions in the topographic complexity of reef habitats, and all coral-dependent species (regardless of their degree of habitat-specialisation) are likely to be much less abundant (Munday 2004, Bellwood et al. 2006, Pratchett et al. 2006a, Wilson et al. 2008b).

2.5 Ontogenetic patterns of coral use

The role of corals as habitat for fishes is most apparent for those species that inhabit specific coral hosts throughout their lives. However, there are a large number of fishes that recruit to live corals, and often have very specific habitat requirements as juveniles, but do not use corals as adults (Dahlgren and Eggleston 2000, Jones et al. 2004, Feary et al. 2007a, Wilson et al 2008a, 2010). The selection of benthic habitat at settlement is critical for the survival and growth of larval fishes (Connell and Jones 1991, McCormick and Hoey 2004). Early post-settlement mortality of reef fishes is relatively high, largely due to very high rates of predation on small reef fishes (Hixon and Beets 1989, 1993, Hixon 1991). Several studies have shown that coral cover and habitat complexity have beneficial effects on population size of reef fishes, but the proximal causes of increased growth and survivorship are not always clear (Connell and Jones 1991, Almany 2004a). Reduced predation within complex coral habitats is the obvious explanation for higher survivorship of small reef fishes. Predation risk can also lead to sub-lethal effects through the reduction of foraging rates resulting in reduced growth rates (Holbrook and Schmitt 1988, Steele and Forrester 2002). Growth in juveniles is generally determined by food availability (Jones 1986, 1987, Forrester 1990) but can further be regulated by competition within the social hierarchy and the threat of predation (Forrester 1990). Selecting habitats that maximise growth rates also means that individual fishes will minimize the time spent in smaller size classes, which are disproportionately susceptible to higher predation rates (Post and Evans 1989). Therefore, live corals that offer the greatest level of protection (e.g., physical structure) and reduced competition should be favoured by fishes.

Of the 320 species recorded to use live coral habitat, I found that 39% (126 species) associated with live coral habitat during their juvenile stage (Figure 2.1). Conversely, Jones et al. (2004) found that 65% of all fishes in Kimbe Bay (PNG) settled onto live coral, yet only 11% of adults had an obligate association with living corals. Within the families Chaetodontidae, Pomacentridae and Labridae, more species associated with live coral habitats in their juvenile stage compared to the adult stage (Figure 2.1). This suggests that many fishes on the reef may be dependent on live coral habitat at settlement even if they don’t depend on live coral during their adult stage. Mortality of juvenile fishes is extremely high due to their small size and for many of these species (e.g., *Chaetodon ephippium, C. melannotus, Chrysiptera flavipinnis, Pomacentrus wardi* Table 2.1) settling to live coral habitats offers an essential shelter until they become larger. Cole and Pratchett (2011) found that juvenile butterflyfishes had a strong association with live coral habitats and remained within a single host coral until they were larger than 30mm. Following this, these fishes move across the reef feeding and showed less dependence on live coral for habitat. Acanthuridae and Scaridae showed equal association during juvenile and adult stages while other families had a lesser number of juveniles to adults (11 – 66%) (Figure 2.1). Our estimates of habitat association for juvenile fishes is still assumed to be under estimated considering it has been predicted that more fishes depend on live coral as recruits than adults (Jones et al. 2004) revealing how just little we know about the requirement of settling fishes.

Aside from those fishes that are found within live corals at settlement (e.g., Sale 1984, Feary et al. 2007a, Coker et al. 2012a, Chapter 6), it has also been suggested that live coral may provide an important settlement cue for a wide range of reef fishes (Kingsford et al. 2002, Gerlach et al. 2007). Research on the sensory cues used by larval fishes to find reef habitats for settlement are increasingly showing that olfaction (smell) is a critically important sense both at large (e.g., orientating towards a reef) and small-scales (e.g., choosing between alternative micro-habitats) (Kingsford et al. 2002, Gerlach et al. 2007, Munday et al. 2010). Additionally, this conspicuous olfactory cue may be utilised by fishes that do not necessarily settle within live corals. Furthermore, some species of fish may settle to areas of live coral cover even though in their adult stage they appear to have no obvious dependence on live coral (Wilson et al. 2010, Coker et al. 2012a, Chapter 6).

Fishes associate with live coral habitat during periods of their adult stage for shelter and reproductive needs (Munday and Jones 1998). Of the species associating with live coral habitat 57% (182/320) did so during their adulthood (Figure 2.1) suggesting that 18% (57%-39%) displayed ontogenetic shifts from coral to non-coral habitats. Many reef fishes are small bodied (Munday and Jones 1998) and may need to associate with coral throughout their life for shelter. Many small reef fishes from a range of families are demersal spawners (Munday and Jones 1998). For some species, live coral is essential for reproduction (e.g., Gobiidae) where eggs are laid within the structure of the reef (e.g., coral colony) and retained until hatching. This study found that 95% of adult Gobies associated with live coral (Figure 2.1.) These species rely on complex corals that provide the eggs and themselves with protection (Yamamoto 1980, Nakashima et al. 1996). Fishes that reproduce in live corals are generally coral-dwelling fishes and presumably reproduce within live coral colonies to reduce predation risk for their eggs and for themselves while they mate and tend to their nest and eggs.

2.6 Effects of coral loss

Coral reefs are subjected to disturbances from both natural and anthropogenic impacts (Hoegh-Guldberg 1999, Wilkinson 2008), which can significantly alter the biological and physical structure of coral reef habitats. Scleractinian corals are particularly vulnerability to ocean warming, acidification, outbreaks of coral predators and disease (Hoegh-Guldberg 1999, Gardiner et al. 2003, Willis et al. 2004, Bruno and Selig 2007). These sustained and ongoing disturbances have resulted in extensive declines in coral health, overall coral cover, coral composition and topographic complexity. Given their strong reliance on live corals, many fishes are being affected by these changes in reef habitats, both in the short term through the loss of healthy tissue cover and substantial coral loss and long term through the erosion of coral skeletons and degradation of topographic complexity of the reefs (Sano et al. 1987, Ohman and Rajasuriya 1998, Garpe et al. 2006, Graham et al. 2006, Wilson et al. 2006, Pratchett et al. 2008a).

Of the 320 species recorded in this study 39% (125 species) were found to show marked and consistent declines in abundance following acute disturbances (e.g., mass-bleaching, severe tropical storms) that resulted in significant loss of live coral cover (Table 2.1), reinforcing their strong dependence on live coral. However, this leaves a further 131 species of fishes that were shown to decline in abundance following extensive coral loss (Pratchett et al. 2011a) that are not recorded to use live coral habitats. This shows that the proportion of fishes that depend on live coral extends well beyond the small proportion of fishes known to rely on corals for food (Cole et al. 2008) or for habitat. This may be a result of the limited number of studies that implicitly look at the relationship between fish and coral. Alternatively, many fishes that depend on live corals may not have an obvious association with live coral. It is clear that small-bodied fishes rely on live coral for shelter (Munday and Jones 1998), but it is less obvious for larger fishes. While some larger fishes are found to shelter under large table corals (Kerry and Bellwood 2012) little is known about their dependence and the effects of coral loss on these species.

The general correlation between declining coral cover and declining fish abundance is often, but not always, accompanied by declines in the diversity of reef fishes (Pratchett et al. 2011a). Fish diversity and coral cover may be positively correlated (Sano et al. 1987, Booth and Beretta 2002, Jones et al. 2004, Graham et al. 2006, Feary et al. 2007b), although several studies have found no observable differences in species diversity following significant coral decline (Bellwood et al. 2006, Cheal et al. 2008). This apparent disparity may relate to instances where there has been no change in physical habitat structure, either due to structural integrity of dead corals, which often take 4-5 years to decompose and erode following tissue loss (Wilson et al. 2009), or because live corals contribute little to physical habitat structure. The effects of reduced habitat complexity vary among trophic groups from relatively little responses in invertivores to large responses in coral-dwelling fishes, but generally and overall decline in species diversity across depauperate reefs are observed (Sano et al. 1987, Graham et al. 2006, Wilson et al. 2006). Structural complexity of reef habitats is especially important for small-bodied fishes (Munday and Jones 1998) as well as functionally important groups of fishes (e.g., herbivores Garpe et al. 2006, Graham et al. 2006, Hoey et al. 2011). Recent research is showing that topographic complexity is just as important (if not more important) than live coral cover in structuring reef fish assemblages (Almany 2004b, Wilson et al. 2006, Graham et al., 2007), but it is often difficult to separate effects of coral loss and associated declines in topographic complexity (Pratchett et al. 2008a).

The greatest concern for reef scientist and managers is the impending threat of global climate change (Hoegh-Guldberg 1999, Wilson et al. 2006, Munday et al. 2007, Pratchett et al. 2008a), which compounds upon pre-existing and direct anthropogenic disturbances. For habitat-forming corals, effects of climate change are largely manifest as acute episodes of mass bleaching and coral mortality, and are expected to increase in frequency and severity with projected temperature increases (Donner et al. 2005). During mass-bleaching, the primary response in corals is the loss of pigmentation, turning them bright white (Hoegh-Guldber 1999). Most coral reef fishes exhibit bright colours and stand out against the pale and white bleached corals. This contrast has been shown to increase associated fishes visual vulnerability to predators (Coker et al. 2009, Chapter 3). Once corals die they are quickly colonised by turf algae, which eventually fills most available spaces among the branches of dead corals (McCook et al. 2001) reducing the ability of associated fishes to gain entry to the corals and effectively move among the physically intact branches. In time, often 4-5 years following extensive bleaching, dead coral colonies eventually break down and a decline in topographic complexity is observed (Hutchings 1986). In order to understand the consequences of coral bleaching and the sequence of events that follows coral mortality, consideration of the key processes (e.g., predation and competition) that structure coral reef fish assemblages is required.

2.6.1 Predation

Over half of the fishes recorded to associate with live coral habitat were less than 150mm total length (TL) (Figure 2.5). Therefore they are likely to be highly susceptible to predators suggesting that they associate with corals to avoid predators (Wen et al. *In review*). For small coral-dwelling fishes associated with impacted host colonies, predation rates may be higher during bleaching periods (Coker et al. 2009, Chapter 3). While large predators might benefit from bleaching through increased prey perception, this may influence smaller predators to avoid these habitats (Coker et al. 2009, Chapter 3). Aside from higher predation rates, coral-dwelling fishes will persist on bleached host colonies but will vacate these habitats once live tissue is lost and algal starts to colonize (Bonin et al. 2009a, Coker et al. 2012b, Chapter 4). Additionally, there is little evidence to support that bleached colonies will influence the recruitment of fishes to bleached habitats, although predation risk will still be high (Bonin et al. 2009a) and subsequent coral mortality will have a significant affect (Feary et al. 2007a, Coker et al. 2012a, Chapter 6).

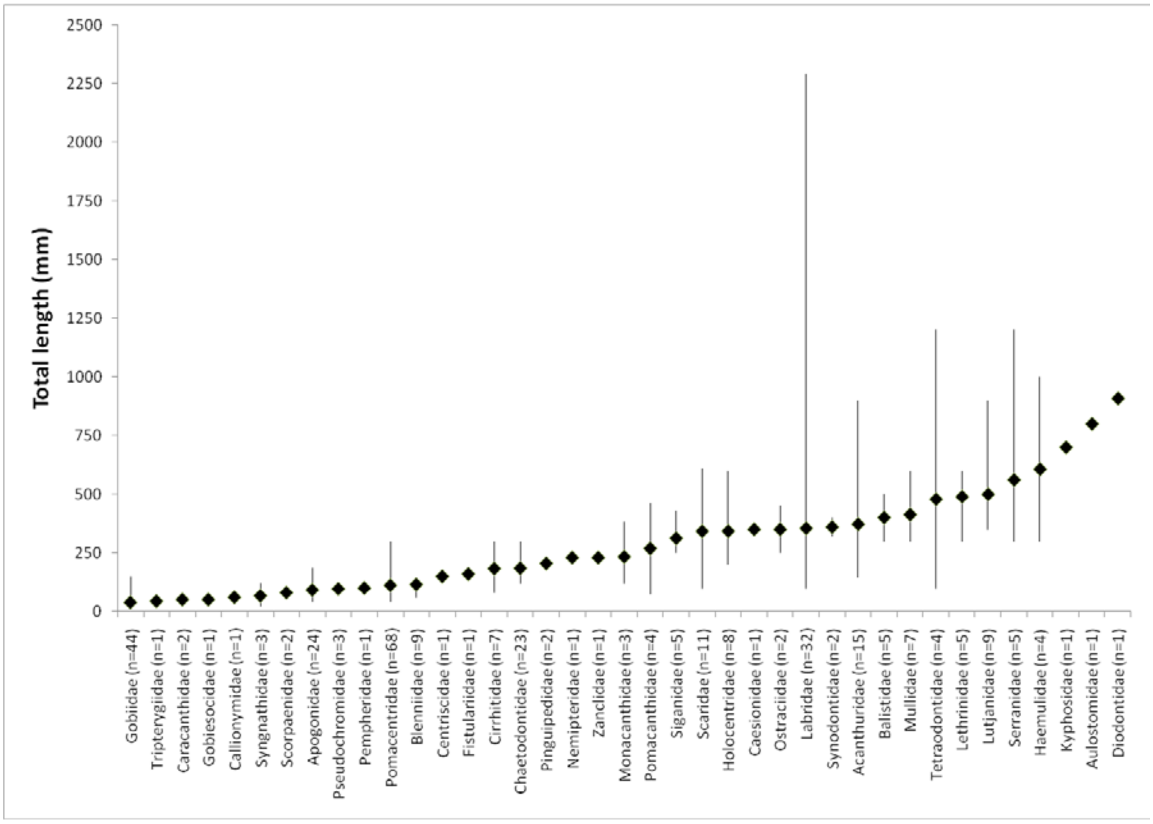

Figure 2.5: Length range (min, max, mean) of species associating with live coral habitat (n = number of species in each family).

Loss of live coral cover through coral mortality follows severe bleaching events, outbreaks of predatory starfish (*A. planci*) and coral disease (Sano et al 1987, Hoegh-Guldberg 2004, Willis et al. 2004). This decline in live coral cover has devastating effects on the abundance and distribution of reef fishes, including species that have no obvious dependence on live coral (Jones et al. 2004, Wilson et al. 2006). Fish that depend on live coral for food (e.g., *Chaetodon* spp.) experience significant declines in abundance (Wilson et al. 2006, Pratchett et al. 2008a) although sometimes these declines are not observed for a few years (Pratchett et al. 2006a). Many coral-dwelling fishes are only found associating with live coral colonies and actively avoid dead intact coral skeletons suggesting that dead colonies no longer provide adequate shelter. The majority of fishes in this study associate with branching morphologies (Figure 2.3), which allow small fishes to quickly retreat into and move through the complex structure avoiding larger predators. Once dead, colonies become over grown with algae, sponges and other invertebrates that take up valuable refuge spaces within the intrinsic of the branches and reduce the ability for fishes to shelter effectively (Coker et al. 2009, Chapter 3). Individuals are either subjected to higher levels of predation (Coker et al. 2009, Chapter 3) or relocate to alternative healthy colonies (Coker et al. 2012b, Chapter 4). Fishes that associate with plate morphologies for habitat will be less impacted by colony mortality in the short term as fish can still effectively shelter under them.

2.6.2 Competition

Many fish species that associate with live coral habitat live in hierarchical groups of conspecifics (e.g., Gobiidae, Pomacentridae) and pairs (e.g., Chaetodontodae, Pomacanthidae) within territorial host colonies or ranges (Coates 1980, Forrester 1991, Pratchett et al. 2006b, Wong et al. 2008a). Field surveys from Lizard Island revealed that 43% (230/537) of individual coral colonies contained more than one species of fish and 86% (461/537) contained more than one individual (Table 2.1). This shows that most fishes associated with individual colonies consist of single and mixed species groups. Here intra and interspecific competition for habitat resources (e.g., refuge space, feed sites) may play an important part in the ability of fishes to effectively use or inhabit colonys (Booth 1995). Following coral depletion, live coral habitat can become a limited resource for coral-dwelling fishes. Some reef fishes are very aggressive towards confamilial recruits and adults (Doherty 1982, Jones 1987, Forrester 1990, Chapter 5). This coupled with competition for a limited resource may reduce the ability of habitat displaced fishes to successfully colonise new habitats and may force species to associate with alternative and possibly unfavourable habitats (Coker et al. 2012b, Chapter 4, Chapter 5). Alternatively, the addition of new members will influence density-dependent processes on remaining colonies. In larger groups the average feeding success of individuals can be low as larger more dominant individuals denied smaller fish access to energetically profitable prey items (Coates 1980, Forrester 1991). Furthermore, studies on coral-dwelling Pomacentrids show fish in smaller groups ($\leq$ 3) consumed twice as much food as those living in larger groups (Kent et al. 2006). Changes in sex ratios through the addition of females can increase aggressive interactions by mothers there by increasing the levels of the stress hormone, cortisol, in their ovaries, which in turn reduces larval size (McCormick 2006).

2.6.3 Feedbacks

Live coral habitat is generally most important for small bodied reef fishes (Munday 2004, Wilson et al. 2008b), but many larger fishes also associate with live corals and serve critically important functions on coral reefs (Pratchett et al. 2011a, Figure 2.5, Table 2.1). On coral reefs, small coral-dwelling fishes (ca. < 150mm) are the most abundant and diverse, providing an important link in the food chain (Choat and Bellwood 1991, Randell et al. 1997, Munday and Jones 1998, Ackerman & Bellwood 2000). Many of the fishes that associate with live coral habitat do so because they are small and vulnerable to predators. I found that the majority of fishes associating with live coral habitat had a mean TL of < 150 mm (Figure 2.5). Smaller fishes therefore are generally more dependent on live coral habitats when they tend to associate with microhabitats, have a more restricted range (Warburton 1989) and have a closer proximity to reef habitat (Forrester 1991, Hobson 1991). Planktivores make up the largest tropic group (32%) associating with live coral habitat (Figure 2.2) and are the most abundant fishes on the reef (Williams and Hatcher 1983). This large biomass of small fishes is important to tropic web structures in reef ecosystems by providing prey for larger predators (Choat and Bellwood 1991, Graham et al. 2003). Furthermore a loss of coral related structural complexity can be associated with a decline in small-bodied fishes, which can include juveniles of ecologically important larger species (Wilson et al 2010) as well as important fisheries species (Graham et al 2007).

While most live corals provide small refuge spaces for small fishes, some open branching colonies (e.g., *Acropora formosa*, *A. pulchra*) and table colonies (e.g., *Acropora hyacinthus*) allow larger fishes to shelter with the branches or underneath (Table 2.1). In this study I found 118 species with a mean body size of >250 mm associated with live coral (Figure 2.5). Kerry and Bellwood (2012) recorded that the bulk of large fishes sheltering under large table corals were roving fishes. Live coral habitat may offer protection for these fishes against potential predators when resting (Munday and Jones 1998) and may offer concealment from prey when hunting (Samoilys 1997). While it appears that the physical structure of the habitat is the important factor for these fishes, the loss of large branching and table corals will result in a decline in available shelter sites for these larger fishes. Furthermore, these large corals are highly susceptible to both biological (Marshall and Baird 2000) and physical disturbances (Madin and Connolly 2006) and the loss of available habitat for these fishes will compound upon the threat of over fishing.

2.6.4 Recovery of fish communities

Recovery of impacted fish communities is dependent on the recovery of settlement habitat and the supply of larval fishes (Doherty and Williams 1988). Recovery of live coral habitat will vary in its ability to recover to pre disturbance levels based on the cover of existing coral colonies. Coral habitat will recover quicker if there are surviving colonies on the reef because extensions of remaining colonies through growth, increases live coral cover more rapidly than through settlement and growth of new recruiting colonies (Connell et al. 1997). Corals from the genus *Acropora* support the greatest number of fishes on the reef due to their complex structure (Figure 2.3). Fortunately for these fishes, corals in this genus are some of the fastest colonisers following disturbances due to their high recruitment and fast growth rates (Loya et al. 2001, Pratchett et al. 2009b).

Recovery of coral communities may have an influence on fish communities through shifts in coral composition if one species is removed and another persists and dominates the remaining space. Observations in the Arabian Gulf found that following a positive sea surface temperature anomaly, reefs dominated by *Acropora* species declined and shifted to the dominance of surviving massive taxa (mainly *Porities* and Faviids) (Riegl 1999). Riegl (2002) observed subtle changes in fish assemblages (Family and trophic level, but not species level following the shift in coral composition from *Acropora* to massive dominance in the Arabian Gulf. Similarly, Beruman and Pratchett (2006) observed a shift in coral composition from *Acropora* to *Pocillopora* dominated cover, which attributed to changes in *Acropora* dependent fish species (*Chaetodon trifascialis*) to *Pocillopora* dependent species (*Chaetodon lunulatus*). These two shifts were driven by differences in thermal sensitivities and crown-of-thorn (*A. planci*) preferences, but coral composition shifts can also occur from differences in physical susceptibility (e.g., wave energy, Madin and Connolly 2006). Shifts in coral composition on reefs will affect species of fish that depend on specific coral species but the greatest impact to coral inhabiting fishes will be the transformation from branching and plate morphologies to massive. Habitat complexity drives the association of many of these fishes with few fish species found to associate with non-complex morphologies (Figure 2.3).

2.7 Conclusions

Scleractinain corals have long been recognised as important habitat for coral reef fishes (Tyler 1971, Sale 1971), and this review shows just how important, revealing that 320 species of fishes (8% of all reef fishes) use live coral for habitat. In fact, this is an absolute minimum and there are likely to be an even greater range of fishes that are reliant on live coral habitats. Furthermore, there are inherent difficulties in establishing the strength of links between fishes and corals. While fishes are observed to associate closely with live coral cover or certain coral species, it does not necessarily mean that they won't associate with non-coral habitats following coral loss. Changes in fish communities following coral loss may indicate an obligate relationship, but this can be complicated because declines may not be observed in fish communities unless there are extensive changes in live coral cover. Greater estimates will not be revealed until specific surveys intended to quantify the diversity of fishes associated with coral versus non-coral habitats are conducted in a wider range of habitats and locations. This data is critically important for understanding the consequences of sustained and ongoing degradation of coral reef habitats (Wilkinson 2004) though it is already clear that the extensive loss of corals, combined with declines in topographic complexity of coral habitats, leads to major reductions in diversity of reef fishes on contemporary coral reefs (Wilson et al. 2006, Pratchett et al. 2011a).

Coral reef habitats are particularly susceptible to a wide range of natural and anthropogenic disturbances (Wilson et al. 2006, Wilkinson 2008). Unfortunately these disturbances are predicted to increase in frequency and severity over coming decades (Hughes et al. 2003, Bellwood et al. 2004) adding to the 54% of coral reefs that are already lost, critical or listed as threatened (Wilkinson 2008). This loss of habitat will compound on the loss of other critically important reef fish habitats (e.g., mangroves forests, seagrass meadows). While comprehensive loss of scleractinian corals is unlikely on many coral reefs (Hughes et al. 2012), we can expect to see a change in reefs that are dominated by coral species that are relatively susceptible to disturbances (e.g., *Acropora* spp. and *Pocillopora* spp.) to reefs dominated by more resistant species (e.g., *Favia* spp. and *Porities* spp.). Changes in species composition will have a dramatic affect on the topographic complexity of the reef and the loss of key habitat forming species and will have significant consequences for reef fish species rather than just the loss of live coral *per se*. Corresponding effects of coral loss on fishes will result in the decline of coralivores and coral-dwelling fishes through the loss of food and shelter (Wilson et al. 2006). As recorded in this study the majority of reef fishes associate with complex branching corals of the genus *Acropora*. Acroporid species are the first and worst affected by most agents of habitat disturbance (Coles and Fadlallah 1991, Gleason 1993, Wilkinson 1998, Marshall and Baird 2000, Madin and Connolly 2006) and experience serious declines (Aronson and Precht 1997). Given the high dependence of fishes on *Acropora* species a decline in these corals may have disproportionate impact on fish communities.

Chapter 3: Coral bleaching and habitat degradation increases susceptibility to predation for coral-dwelling fishes[3]

3.1 Abstract

Climate-induced coral bleaching frequently leads to declines in the abundance and diversity of coral associated fishes, though the proximate causes of these declines are largely unknown. In this study, I show that coral-dwelling damselfishes associated with bleached and dead coral hosts are more susceptible to predation compared to fishes associated with healthy coral colonies. Although the predator (*Pseudochromis fuscus*) actively avoided both bleached and recently dead corals, they were almost twice as likely to strike at prey associated with the stark white colonies of bleached corals. These results suggest that coral-dwelling fishes are much more conspicuous against the bleached-white background, increasing their susceptibility to predation. Direct estimates of predation rates in aquaria were 33% and 37% on bleached and recently dead coral colonies, respectively, compared to 25% on healthy coral colonies. However, predation rates were highest (42%) on algal-covered corals, reflective of colonies that have further degraded post-bleaching. I argue that increased susceptibility to predation may contribute to declines in abundance of coral-dwelling fishes following host coral bleaching. Even if predation does not cause increased *in situ* mortality, it is likely that increased exposure to predators will provide significant motivation for coral-dwelling fishes

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[3] This Chapter appears in the journal *Behavioural Ecology*: Coker, D.J., Pratchett, M.S., Munday, P.L. (2009) Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioural Ecology*, 20: 1204-1210. Reviewed in *Nature*.

to vacate bleached coral hosts

3.2 Introduction

Habitat structure exerts a major influence on the distribution and abundance of many organisms (Ehrlich and Roughgarden 1987), as well as moderating key biological processes, such as competition and predation (Menge 1976, Holt 1987, Hixon and Menge 1991). Structurally complex habitats typically support more species and individuals than less complex habitats and may reduce predation rates and the intensity of competitive interactions (Bell et al. 1991). Degradation of habitat structure due to declines in the abundance of key structural species invariably leads to population declines and the loss of biodiversity in terrestrial and aquatic environments (e.g., Andren 1994, Fahrig 1997, Syms and Jones 2000, Graham et al. 2006).

For coral reef fishes, critical features of benthic habitats include the relative abundance of scleractinian corals versus other habitat-forming species (Ohman and Rajasuriya 1998, Holbrook et al. 2000) as well as substrate topography, which is largely influenced by the species composition and respective growth forms of scleractinian corals (Gratwicke and Speight 2005, Graham et al. 2006, Pratchett et al. 2008a). For the most part, increased cover and diversity of scleractinian corals promotes increased abundance and diversity of coral reef fishes (Carpenter et al. 1981, Munday et al. 1997), partly because live corals represent an essential resource for many coral reef fishes (Jones et al. 2004, Pratchett et al. 2008a). At least 10% of fishes are directly reliant on live corals for food and/or shelter (Pratchett et al. 2008a), and up to 65% of fishes may need live coral at settlement (Jones et al. 2004). Moreover, live coral provides habitat that helps to mediate important biological interactions, such as competition (Munday 2001, Holbrook and Schmitt 2002) and predation

(Caley and St John 1996, Beukers and Jones 1997). Consequently, any change in the abundance or condition of coral habitat may have significant effects on biotic interactions, abundance and diversity of fishes (e.g., Munday 2004, Jones et al. 2004, Pratchett et al. 2004, Wilson et al. 2006).

3.2.1 Climate-induced coral bleaching

Global climate change represents the most significant and increasing threat to coral reef ecosystems, having already caused extensive and widespread habitat degradation (e.g., Wilkinson 2002). The geographic and taxonomic extent of coral bleaching has been increasing throughout the past 30 years, culminating in the global mass-bleaching event of 1998 (Hoegh-Guldberg 1999, Hughes et al. 2003). These changes in biological and habitat structure have devastating effects on the diversity and abundance of motile reef organisms resulting in significant and widespread declines in the abundance of coral reef fishes (e.g., Kokita and Nakazano 2001, Jones et al. 2004, Graham et al. 2006, Pratchett et al. 2006a), species extirpations and extinctions (Hawkins et al. 2000, Munday 2004), and dramatic shifts in community structure (e.g., Bellwood et al. 2006). Moreover, coral bleaching tends to have disproportionate impacts on coral species (e.g., *Acropora* spp. and *Pocillopora* spp.) that are used by coral-dependent fishes (Wilson et al. 2006, Pratchett et al. 2008a). Once dead, coral colonies are rapidly overgrown by turf algae and is highly susceptible to biological erosion (Hutchings 1986, Glynn 1997) leading to the structural collapse of dead coral skeletons (Sano et al. 1987, Sheppard et al. 2002).

3.2.2 Proximate causes of fish declines

Climate-induced coral bleaching often leads to declines in the abundance and diversity of coral-associated fishes (reviewed by Wilson et al. 2006, Munday et al. 2008, Pratchett et al.

2008a), but the proximate causes of these declines remain largely unknown. Coral-dwelling damselfishes are adversely affected by coral bleaching and rarely occupy bleached coral hosts (Feary et al. 2007b), but it is not known whether these fishes simply move to alternate coral habitats or succumb to increased mortality (e.g., predation) as a consequence of host coral bleaching. Predation is a major process on coral reefs influencing the size of populations and exerting considerable influence on the community structure of coral reef fishes (Hixon 1991, Hixon and Carr 1997), but previous studies have not considered the extent to which live corals offer increased protection against predators, compared to dead coral hosts with equivalent physical structure. Coral-dwelling fishes mainly rely on corals for physical protection from predators, so it is unclear why they would not utilise bleached or recently dead coral colonies where the complex structure of the habitat remains intact.

This study investigates whether predation rates on coral-dwelling damselfishes living on bleached coral colonies are significantly higher compared to damselfishes living on unbleached coral colonies. Predation rates are likely to be moderated by responses of both predators and prey fishes to coral bleaching. Firstly, predation rates on coral-dwelling fishes may decline if predators avoid bleached corals. Secondly, coral-dwelling damselfishes associated with white-bleached coral hosts may be more conspicuous compared to similar fishes associated with unbleached, dead, or algal covered colonies, and thus more susceptible to predation. Moreover, coral-dwelling fishes may become increasingly susceptible to predation following host-coral bleaching if they exhibit weaker associations with degraded coral hosts. A series of aquarium-based experiments were designed to test responses of coral-dwelling damselfishes as well as a common coral-associated predator to coral bleaching, culminating in a direct test for variation in susceptibility to predation among coral-dwelling damselfishes associated with corals at various stages of bleaching-induced habitat degradation.

3.3 METHODS

3.3.1 Study species

This study was conducted at Lizard Island Research Station (LIRS) on the northern Great Barrier Reef (GBR), Australia. *Pomacentrus moluccensis* and *Dascyllus aruanus* were chosen as the prey species for all experiments. Both these species are common in shallow reef habitat, where they associate with live colonies of complex branching corals (mostly *Acropora* and *Pocillopora* species) and take refuge in their respective coral hosts when approached by predators and at night (Allen 1991). The small size of these fishes (maximum size <80mm TL), strong host associations and rapid acclimation to aquarium conditions make them ideal candidates for experiments. *Pseudochromis fuscus,* a common small piscivore on coral reefs (McCormick and Holmes 2006) often associates with live coral, such as *Pocillopora damicornis* (Munday et al. 2003). *P. fuscus* is very amenable to experimentation and aquarium conditions, readily acclimating and exhibiting typical feeding behaviour within 1-2 days after collection (Messmer et al. 2005, McCormick and Holmes 2006).

Pocillopora damicornis, which has a complex branching structure and is the predominant coral used by many coral-dwelling fishes (Pratchett et al. 2004, Feary et al. 2007b), was used for all aquaria-based experiments. *P. damicornis* is highly susceptible to climate-induced coral bleaching (Marshall and Baird 2000). Approximately spherical (mean maximum diameter = 21.3cm ± 1.3 SE) intact and healthy colonies of *P. damicornis* were collected from near shore reef habitats close to LIRS. Algal-covered colonies of *P. damicornis* were also collected for use in aquarium experiments. These colonies were of equivalent size (mean maximum diameter = 20.5cm ± 1.2 SE) and appeared to have comparable levels of branching complexity, though many of the interstices between branches had been filled by thick algal growth, sponges and other non-coral sessile invertebrates.

Structurally equivalent healthy colonies were then randomly assigned to one of three different treatments (healthy, bleached and recently dead) to represent successive stages of bleaching-induced habitat degradation. Colonies assigned to the bleaching treatment were subject to osmotic stress until they exhibited conspicuous reductions in colour but still retained live tissue cover, indicative of zooxanthellae loss (Siebeck et al. 2006). Osmotic stress was used to induce bleaching because responses were much faster while still producing similar signs and symptoms as thermal stress (Kerswell and Jones 2003, D. Coker unpublished data). Remaining colonies were placed in a chlorine solution to systematically and rapidly remove all living tissue to represent colonies that had recently died from bleaching.

3.3.2 Experiment 1: Habitat associations of predatory fishes

Increased susceptibility of coral-dwelling fishes to predation following host coral bleaching will be partly conditional upon the willingness of reef-based piscivores to associate with bleached and recently dead coral colonies. *Pseudochromis fuscus* tend to have very specific habitat associations, which reflect individual colouration (Munday et al. 2003) and may avoid bright white colonies of bleached and recently dead coral colonies. To test this, habitat-choice experiments were undertaken to quantify the proportion of time that *P. fuscus* associated with i) healthy, ii) bleached, iii) dead, and iv) algal-covered colonies of *P. damicornis*. Individual fishes were placed in large, circular (113cm dia.) plastic tanks with equal opportunity to choose among these four alternate coral habitats. Four small glass aquaria were placed equal distances apart around the periphery of the tub and contained one of the four coral treatments. Each coral was placed in an aquarium to prevent the predator from sheltering within the nearest coral habitat and remaining there for the duration of the trial, as observed during a pilot test. Habitat preferences were inferred from the proportion of attempts to enter each habitat type.

After spending 5 minutes in an acclimation chamber in the centre of the tank each fish was observed for up to 20 minutes, recording the sequence with which it attempted to enter the four small glass aquaria containing the alternate habitat types. Each consecutive attempt to enter one of the four distinct habitats, characterised by circling or physically bumping the glass tank, was recorded and observations continued until each fish had made 50 independent attempts at entering one of the four coral habitats. A second consecutive attempt at the same tank was recorded only if the fish swam away (> 20cm) from the tank and then returned to make another attempt. Habitat associations of 30 individual *P. fuscus* were tested in 30 independent trials. A chi-squared goodness of fit was used to test whether the four habitats were visited in equal frequency by the predator (both colours pooled together).

3.3.3 Experiment 2: Strike rates in different habitats

To test whether background habitat influences the visual detection and thus the propensity to feed on coral-dwelling damselfishes, individual damselfishes were placed before laminated photographs of i) healthy, ii) bleached, iii) dead, and iv) algal-covered colonies of *P. damicornis*. Images of coral colonies were used instead of actual coral colonies to minimise any additional factors (e.g., olfactory stimuli, and variation in habitat complexity) that might otherwise influence predatory behaviour. Laminated life-size photographs (scale 1:1) of the four different coral treatments were placed equal distance around the perimeter of the tub. A small piece of *P. damicornis* was placed in the centre of the tub to offer shelter for the predator. The water level was adjusted to the top of the photos so that the fish remained within eye level of the image. A small clear zip-lock bag (50 x 100mm) containing a single prey fish was flooded with water and placed in front of each photograph.

Predators were introduced into the centre of the tub as described for experiment 1, and then observed for 20 minutes to record the number of strikes on each of the four prey fishes. Strikes were recorded if there was an obvious attempt from the predator to attack the prey within the bag. Predator and prey fishes were replaced between each trial to ensure that fishes were naive and to ensure that the health of the prey fishes in the bag did not decline. The predator was observed to take refuge within the coral colony at the centre of the tank and venture out to strike the prey and then return to the shelter of the coral. The trial was repeated 40 times (one trial per individual predator). Trials in which the predators did not strike a single prey fish were disregarded and the remaining 28 were analysed using a chi-squared goodness of fit to test whether frequency of strikes were significantly different among fishes placed before each the four different habitats.

3.3.4 Experiment 3: Predation rates

To directly test whether the condition of the coral habitat influences predation on coral-dwelling fish, predation experiments were conducted using different habitats in separate replicated aquaria. Four different coral treatments were used i) healthy, ii) bleached, iii) dead and iv) algal-covered colonies of the coral *P. damicornis* to simulate the degradation stages of coral. Ten replicate 60 x 30 x 40 cm glass aquariums were used, two for each of the four coral treatments and two for controls (no habitat, no predator). Each aquarium contained one coral colony, one predator (*P. fuscus*) and four prey fish (2 x *D. aruanus*, 2 x *P. moluccensis*). The entire experiment was repeated three times over ten days, giving a total of six replicates per habitat type.

At the start of each trial all prey fish were placed with their assigned habitat into the tanks one hour before the predator, to allow them to acclimate to the surrounding habitat. Prey fish were haphazardly selected from a pool of 120 individuals (FL = 22.1mm ± SE 0.3) and predators from a pool of 40 individuals (FL = 63.0mm ± SE 1.0). Due to the small variation in FL of both fishes it would be expected that predator prey length would not influence predator/prey interactions. Each trial was started at 17:00 and survivorship was recorded at set time intervals 30-180 minutes apart over a 75 hour period. Predation rates were expected to be highest during crepuscular periods (dawn and dusk) (Collette and Talbot 1972, Helfman 1986) therefore; the survivorship was monitored at 30-minute intervals from 17:00 to 19:00, but much less frequently at night and during the day.

Logrank (Mantel-Cox) analysis of survival was used to analyse variation in survivorship across four different treatments over time (Pyke and Thompson 1986). This analysis tests the shape of the survivorship curve over time rather than simply comparing mean survivorship at the termination of the experiment. The analysis also takes into consideration censored and uncensored data due to the fact that the trials often end before all individuals die. Observed variation in predation rates of fishes within contrasting habitat types was presumed to reflect differences in the visual detection of prey fishes by the predator, *P. fuscus*, and differences in the behaviour of prey fishes associated with each different habitat-type. Importantly, predation rates may vary with differences in the strength of habitat-associations among prey fishes assigned to different habitat treatments. To test this, the proportion of time that prey fishes spent in proximity to the coral host was recorded and compared among the four treatments (healthy versus bleached, dead and algal-covered colonies of *P. damicornis*). To estimate proximity of prey fish to the coral, the tank was divided into three zones: i) within the coral, ii) close to the coral (approx 10 cm), and iii) away from the coral host (farther than 10 cm from the coral). A total of 26 fish were observed, 7 associated with healthy coral, 8 associated with bleached coral, 7 associated with dead coral and 4 associated with algal-covered coral. After 10 minutes of acclimation with the observer present, the fish were observed for 5 minutes and the total time spent in each of the three zones were recorded and analysed using ANOVA to test the variance between different habitat conditions.

3.4 RESULTS

3.4.1 Experiment 1: Habitat associations of predatory fishes

There were significant differences in the proportion of times that *P. fuscus* visited the alternate habitat-types (X^2=61.45, *df*=3, p<0.001). Significant differences in the proportion of times that fishes visited alternate habitat-types (Figure 3.1) were assumed to reflect relative habitat preferences. Foremost, there was no different in the mean number of times that *P. fuscus* visited healthy versus algal-covered corals, reflecting approximately equal preference for both these highly pigmented habitats. In contrast, *P. fuscus* made significantly fewer attempts to enter stark white corals that were either bleached or recently killed. Contrary to expectations of differential habitat associations for yellow versus brown colour morphs of *P. fuscus* (Munday et al. 2003), there was no significant difference in the proportion of times that yellow versus brown colour morphs visited each of the four alternate habitat types (MANOVA: $F_{3,26}$=1.043, P=0.39), therefore, no distinction was made between colour morphs for the remaining experiments.

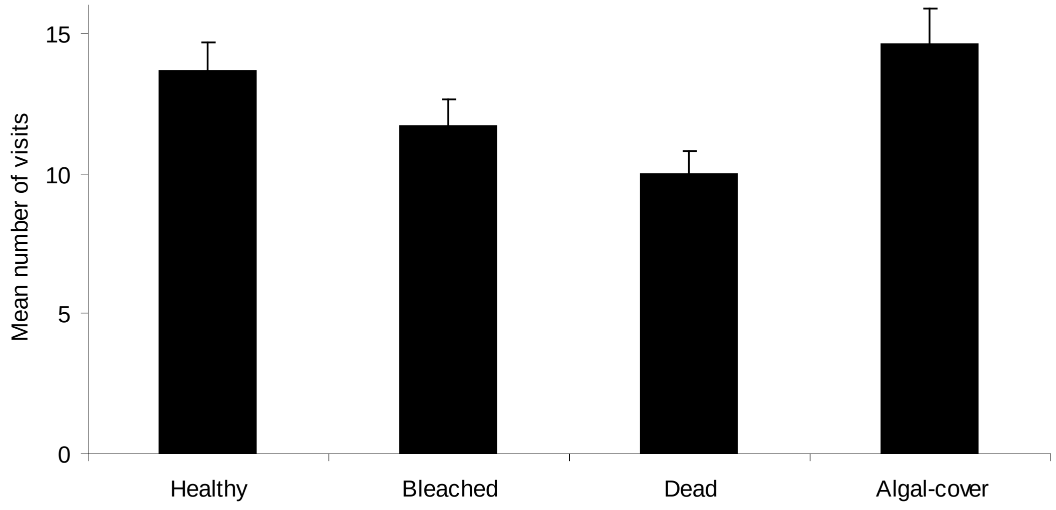

Figure 3.1: Mean number of visits (±SE) of *Pseudochromis fuscus* to four different habitat treatments

3.4.2 Experiment 2: Strike rates in different habitats

Given the choice of four equal sized prey fishes (specifically, juvenile *P. moluccensis and D. aruanus*) placed in front of contrasting habitats, *P. fuscus* revealed a difference in the frequency of attempts to feed on fishes in front of different habitat conditions (X^2=17.50, *df*=3, p<0.001) showing preference to prey associated with photographs of recently dead coral colonies much more than either healthy, bleached or algal-covered colonies (Figure 3.2.).

The relative strikes rates of *P. fuscus* on prey fishes in front of alternate coral habitats were assumed to reflect differences in the ability of predators to perceive prey fishes against different backgrounds. Importantly, prey selection was independent of specific habitat selection of the predatory fish because *P. fuscus* made extensive use of habitat provided in the centre of experimental aquaria. Almost invariably, *P. fuscus* would swim directly from this habitat to strike at the prey fishes before one of the four backgrounds and then swim back to the central habitat before the next strike.

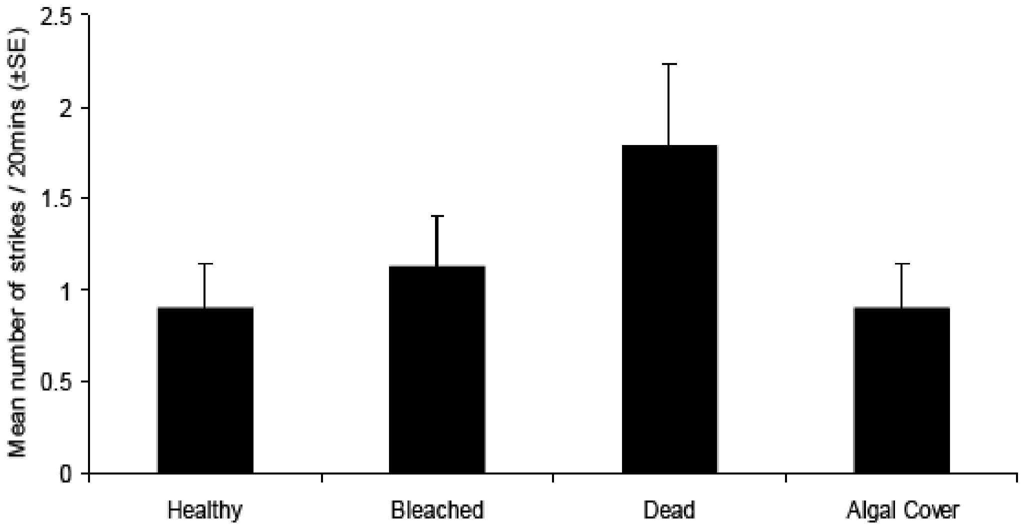

Figure 3.2: Mean number of predator strikes on prey associated with four different habitat treatments over a 20min period.

3.4.3 Experiment 3: Predation rates

Direct comparisons of predation rates on prey fishes associated with alternate habitats (healthy, bleached, dead and algal-covered colonies of the coral *P. damicornis*) indicate that habitat quality has some influence on predatory interactions between *P. fuscus* and coral-dwelling damselfishes where survivorship declines with habitat degradation (Figure 3.3). Mortality rates of coral-dwelling damselfishes, in the presence of *P. fuscus*, were highest on algal covered colonies, where 42% (10/ 24 fishes) of damselfishes disappeared over the course of the experiment. In contrast, only 25% (6/ 24 fishes) of damselfishes disappeared in tanks with healthy coral hosts. Although there is a clear pattern showing mortality rates increasing with increasing degradation of coral hosts (Healthy<Bleached<Recently dead<Algal-covered), mortality rates between the four treatments were statistically non-significant over the 75 hours (X^2=1.95, *df*=3, *P*=0.58).

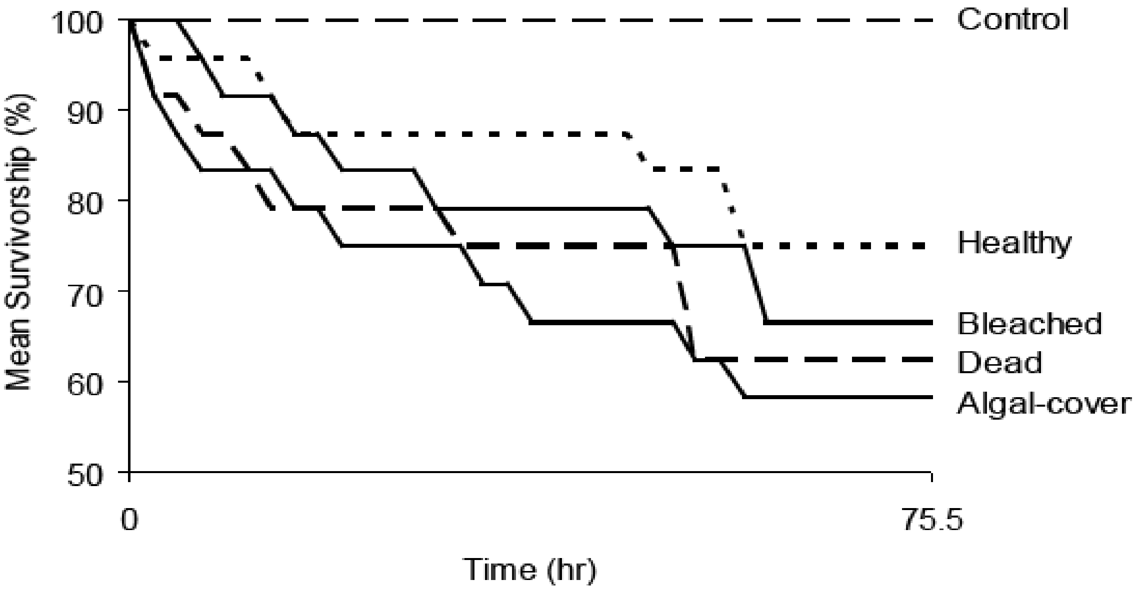

Figure 3.3: Mean survivorship of four prey fish associated with different habitat treatments (n=6 for each treatment) i) healthy, ii) bleached, iii) dead, iv) algal-cover, v) control (no predator) after being exposed to a predator for 75 hours. Mean Std Error = 6.5%, 4.3%, 4.2% and 3.7% respectively.

Habitat-associations of coral-dwelling damselfishes did not vary with respect to habitat quality (ANOVA *F*=1.48, *df*=6, *P*=0.20). More specifically, the proportion of time that individual prey fishes spent inside, on the edge, or well-outside of host coral colonies did not vary among habitat treatments (Figure 3.4). Consequently, it does not appear that differences in susceptibility to predation were due to changes in habitat-use or habitat-affinity by coral-dwelling damselfishes.

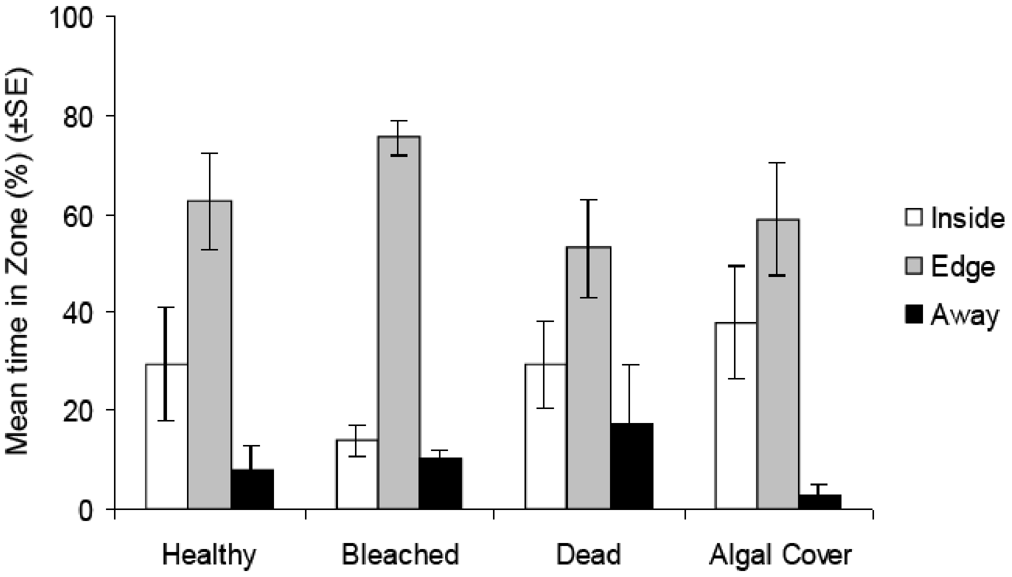

Figure 3.4: Mean percentage time (±SE) prey fish spent inside the coral colony, within 10cm of the coral colony, or more than 10cm away from the coral colony in the presence of a predator during a five minute observation period (Healthy n=7, bleached n=8, dead n=7, algal-cover n=4).

3.5 DISCUSSION

Predation exerts a major influence on population and community structure of coral reef fishes (Hixon and Menge 1991, Hixon and Carr 1997, Almany 2003) and outcomes of predatory interactions can be affected by habitat complexity (e.g., Beukers and Jones 1997, Almany 2004a) and habitat quality (Main 1987). In this study, I found that predation rates on obligate coral-dwelling damselfishes were up to 17% higher on bleached or dead coral colonies compared to healthy coral colonies. These findings suggest that increased exposure and susceptibility to predation may contribute to observed declines in the abundance of coral-dwelling fishes immediately following coral bleaching (reviewed by Wilson et al. 2006, Pratchett et al. 2008a), either contributing directly to increased mortality or providing significant motivation for coral-dwelling fishes to rapidly vacate bleached coral hosts.

Increases in predation rates on coral-dwelling fishes on bleached or dead coral colonies versus healthy coral hosts could be attributable to either increased conspicuousness of prey fishes on bleached and degraded coral habitats, and/or changes in the behaviour of prey fishes in a way that increases susceptibility to predation. In this study, *P. fuscus* selected both healthy and algal-covered *P. damicornis* colonies over bleached and recently dead colonies, suggesting that damselfishes on these corals might be less susceptible to predation. However, when offered a choice of prey in front of coral colonies in various stages of degradation, *P. fuscus* attempted to feed more often on prey in front of bleached or dead coral colonies. These contrasting results suggest that *P. fuscus* prefers to associate with live coral or algal covered habitat (as described by Munday et al. 2003), but prefers to feed near bleached and dead corals where prey are more conspicuous.

Most predators have visual systems that rely on contrasting colouration and movement to detect potential prey (Lythgoe 1988). It seems intuitive that coral-dwelling damselfishes would be more conspicuous against the white background of bleached or recently killed coral hosts, compared to the pink hues of live coral hosts or the dark brown coloration of dead algal-covered coral skeletons. The intensity of light reflected by a white object will also be much greater than from a dark object (coral substrates do not reflect a large proportion of incident light) and the large amplitude difference results in maximal luminance contrast (Barry and Hawrsyhyn 1999). Thus, as I observed in our experiments, predators are more likely to perceive, and strike at, prey fishes that are residing on bleached and recently dead coral habitats.

Observations of predation rates of prey fish residing on different habitats confirmed that mortality is higher on bleached and dead corals compared to healthy corals. In the final experiment, mortality of prey fishes increased from healthy to bleached, to dead and finally algal-covered skeletons of *P. damicornis*, reflecting successive stages in the degradation of bleached coral hosts. This result suggests that predation will increasingly contribute to declines in the abundance of coral-dwelling fishes as host corals bleach and subsequently die. The pervasive view in the literature investigating the effects of climate-induced coral bleaching on coral associated fishes is that declines in the abundance of fishes result from declines in the structural complexity of coral hosts (Sano et al. 1987, McCormick 1994, Nanami and Nishihira 2002) as biological and physical erosion contributed to structural collapse of the algal-covered skeletons (Sano et al. 1984, Lewis 1997, Halford et al. 2004). By contrast this study shows that predation may have a significant influence in survivorship of coral-dwelling fishes even while structural integrity of coral habitats is retained.

One likely mechanism contributing to the increased mortality of coral-associated fishes on bleached and dead corals is their increased prominence to potential predators. However, in predation trials mortality rates were highest for fishes associated with algal-covered corals. One possible explanation for this could be that the algal-covered habitat offered less shelter as refuge spaces between the branches are taken up with algal growth and invertebrates such as sponges. While there were no apparent differences in habitat – associations by coral-dwelling on algal covered colonies in experimental conditions, the invasion of algae and sponges would be expected to limit the available shelter space for coral-dwelling fishes rendering them more susceptible to predation. In field conditions, obligate coral-dwelling damselfishes are almost never found living on completely dead and algal covered colonies (Wilson et al. 2008a), suggesting that there is strong preference for live corals. Aside from visual protection, live coral tissue may offer increased protection from potential predators by providing chemical concealment and stinging nematocysts might further deter potential predators from entering live corals. *Pseudochromis fuscus* is regularly found living among live corals and so may be immune to nematocysts, but odours produced by live coral tissue and other associated organisms may reduce olfactory detection of prey fishes within coral branches, especially at night. The recruitment of territorially aggressive herbivores to the algal-covered coral habitat could also drive the live coral-dwelling fishes out of the area.

Aside from increases in their conspicuousness, increasing predation on coral-dwelling fishes in bleached and dead coral hosts may be attributable to changes in the behaviour of prey fishes, such as declines in the strength of their habitat-associations. It is conceivable that coral-dwelling damselfishes would respond to the death of their host coral by attempting to move to an alternate coral host (Feary 2007), or if they maintain associations with their original coral hosts they may spend less time sheltering within their host colony. In this study, coral colony health had no effect on prey fish behaviour. Consequently, there was no apparent difference in the strength of habitat-association that might account for the variation in predation rates among habitats. Subtle changes in the behaviour of prey fishes may nonetheless increase susceptibility to predation as habitat quality is compromised, and may be much more important under field conditions.

This study shows that increasing susceptibility to predation may contribute rapid and dramatic increases in the mortality of coral associated fishes immediately following host coral bleaching. These effects will be further compounded by longer-term declines in the abundance of coral associated fishes attributable to increasing sub-lethal impacts (Wilson et al. 2006, Pratchett et al. 2009a). For example, Pratchett et al. (2006a) showed that declines in the abundance of coral-feeding butterflyfishes occurred >2 years after initial coral loss, following gradual declines in physiological condition and survivorship of butterflyfishes. Similarly, coral-dwelling fishes that remain within bleached coral hosts may experience significant sub-lethal impacts that contribute to reduced survivorship. Moreover, fishes that remain on bleached corals may be further impacted by the eventual declines in the physical structure of these habitats (Lindahl et al. 2001), whereby structurally complex coral habitats may be reduced to rubble (Steneck 1988). Structural collapse of bleached corals can take several years, but will have pronounced effects on remaining fishes (Sano et al. 1987, Graham et al. 2006). Some coral-dwelling fishes may escape the immediate effects of coral mortality by moving to alternative coral habitats, however, this could have long-term impacts on population sustainability if growth, survival or reproductive rates of the fishes is lower in less preferred coral habitats (Munday 2001, Munday et al. 2008). This study does not consider the potential movement of prey fishes among habitats, though it is important to recognise that these fishes are likely to be highly susceptible to predation during their relocation (Stewart and Jones 2001). Moreover, the increasing severity and geographic extent of coral bleaching events make the likelihood of finding alternate coral habitats very remote.

Climate change is having significant impacts on coral associated fishes, largely due to the loss of resources associated with bleaching-induced coral depletion (Lindahl et al. 2001, Booth and Beretta 2002, Sano 2004, Pratchett et al. 2004, 2006a, Wilson et al. 2006). This study shows that predation may have a significant influence on the abundance of small coral-associated fishes following host coral bleaching. Predation is a critical process affecting the structure and dynamics of reef fish populations, and any increases in rates of predation (attribute to changes in habitat area or habitat quality) could have significant impacts on prey populations as well as overall productivity and trophodynamics of coral reef ecosystems (Munday et al. 2008). Experiments conducted in this study now need to be repeated under field conditions to incorporate added complexities of multiple predators (Almany 2003), potential movement of prey fishes among alternate habitats (Lewis 1997). Importantly, the risk of predation may provide significant motivation for damselfishes to rapidly vacate bleached coral hosts, even if it is not the proximate cause of declines in their abundance.

Chapter 4: Influence of coral bleaching, coral mortality and conspecific aggression on movement and distribution of coral-dwelling fish[4]

4.1 ABSTRACT

Changes in coral health may have significant impacts on fishes that shelter within live coral habitats. However, disturbances can be spatially patchy and it is unclear whether fishes subject to degradation of their immediate habitat are able to move and exploit alternative nearby healthy habitat patches. This study experimentally investigated the response of a common coral-dwelling damselfish (*Dascyllus aruanus*) to bleaching and mortality of host coral colonies. Three factors were considered that may influence the initiation and success of movement among habitat patches; i) condition of the host colony, ii) the availability of preferred habitat, and iii) the presence of conspecifics on alternative coral habitat. *Dascyllus aruanus* remained associated with bleached coral colonies and only moved to alternate habitats once the host coral died. On colonies that suffered complete mortality, 67% of associated fish vacated and migrated to healthy coral colonies. The remaining individuals persisted on dead colonies as a result of competition from aggressive resident fish on neighbouring healthy colonies, but relocated once offered an alternative colony without any

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competitive resident fish. When relocating in degraded reefs, 64% of the fish were successful in migrating to alternative healthy habitats. For these fish the selection of new habitat was based mostly on the presence of conspecifics, with 91% of fish relocating to healthy coral colonies containing conspecifics. The importance of conspecifics presence was further demonstrated by tank experiments where fish selected to associate with habitat containing conspecifics over unoccupied dead or healthy habitat. Movement of coral-dwelling fishes following disturbances will allow individuals to mediate the impact of host coral degradation by re-locating to more suitable habitats. However, the potential for relocation will decline as disturbances become more severe and widespread, thereby increasing the distance to suitable habitats and reducing the availability of preferred habitat types. Furthermore, increased densities within habitat patches may increase competitive effects, with potential consequences for growth, survival and reproductive success.

4.2 Introduction

Understanding how species respond to disturbances is critical, especially given predicted increases in the severity, frequency and spatial extent of disturbances over coming decades (Vitousek et al. 1997, Dulvy et al. 2003, Wilson et al. 2006). While disturbances are a natural component of ecosystem dynamics (Connell 1978), increasing anthropogenic pressure and climate change are compounding upon natural disturbances and thereby threaten biodiversity and ecosystem function (Walther et al. 2002, Thomas et al. 2004, Pratchett et al. 2011a). The greatest threat to species diversity is the degradation and loss of critical habitat (Vitousek et al. 1997, Dirzo and Raven 2003), often caused by declines in the abundance of key habitat-forming species. The effects of habitat degradation are particularly evident in coral reefs, where environmentally sensitive reef-building corals provide complex living habitat that is essential for the persistence of many species of fishes and motile invertebrates (Jones et al. 2004, Pratchett et al. 2008a, Stella et al. 2011). The effects of disturbance on coral reefs are not usually homogenous, with some corals suffering greater impacts than others, even within the same reef area (Marshall and Baird 2000). This patchiness in coral degradation and mortality provides opportunities for coral associated species to move and recolonise remaining healthy habitat patches. However, there could be consequences for social organisation and demographic rates if recolonisation is associated with increased density within habitat patches (Hixon and Webster 2002, Holbrook and Schmitt 2002). Organisms that have a strong association with live coral habitat experience the greatest impact to coral loss and degradation (Munday 2004, Wilson et al. 2006, Feary et al. 2007b, Pratchett et al. 2008a). While there is substantial evidence of a direct effect on the coral associated fishes brought on by the loss of live coral habitat, it has only been speculated about whether these fishes are declining in abundance in these impacted habitats, or if they are moving to alternative healthy habitats (Wilson et al. 2006, Coker et al. 2009, Chapter 3).

Habitat formed by branching scleractinian corals is an essential resource for many small-bodied reef fishes, providing refuge spaces among the complex matrix of branches (Munday and Jones 1998). However, this branching morphology is highly sensitive to disturbances, such as thermally-induced coral bleaching (Marshall and Baird 2000). While mass bleaching events can cause considerable coral mortality (Hoegh-Guldberg 1999, Wilkinson 2000), bleaching is typically patchy; even on a small scale some colonies will show signs of bleaching while neighbouring corals will appear healthy (Marshall and Baird 2000, Clark et al. 2009). Physical disturbances (e.g., tropical storms) break down the complex reef framework, but bleached and recently dead corals retain their physical structure (Sano et al. 1987). Although it appears that the physical structure of these corals is important for their survival, many fishes will only associate with live corals and are not found associated with dead coral skeletons (Feary et al. 2007b, Pratchett et al. 2008a, Bonin et al. 2009a). This suggests that live coral habitat is more important for these fishes than just the physical structure it provides.

Complex branching corals can support large social groups of coral-dwelling fishes (Sale 1972, Holbrook et al. 2000, Thompson et al. 2007, Jordan et al. 2010) and many fish take refuge between coral branches at night, or during the day when threatened by predators. Some coral-associated fishes exhibit such fidelity to their host coral that they rarely venture more than a few meters from the coral and remain within the same social group for the majority of their life (Sale 1971, Forrester 1991, Wall and Herler 2008). However, by living in a group these fish experience a trade-off between; i) reduced predation risk through increased vigilance and dilution of predation risk and ii) increased intra-group competition for food, shelter and reproduction (Jones 1987, Forrester 1990, Booth 1992, Hobbs and Munday 2004). Within social groups there can be strong size-based social hierarchies that mediate competition for essential resources, such as food and breeding partners (Forrester 1991, Buston and Cant 2006, Wong et al. 2007). Here, larger individuals (relative to other group members) are generally higher in the ranking than smaller individuals because of their dominance and superior competitiveness (Forrester 1991, Wong et al. 2008b). Stability of social groups and persistence of individuals within groups can depend on the maintenance of these size-based hierarchies (Wong et al. 2007, 2008b). However, habitat degradation may cause social groups to break down, potentially leading to changes in social hierarchies and increases in competitive interactions.

Historical data shows that coral cover is declining in many geographical regions (e.g., Caribbean, Great Barrier Reef) due to a range of disturbances, including mass coral bleaching (Hoegh-Guldberg 1999, Gardiner et al. 2003, Hughes et al. 2003, Bruno and Sielg 2007). While bleached and recently dead corals should still offer suitable physical habitat, there is often a rapid and dramatic decline in the local abundance of coral-dwelling fishes following coral bleaching (e.g., Booth and Beretta 2002, Spalding and Jarvis 2002, Jones et al. 2004, Munday 2004, Pratchett et al. 2009a). Studies showing declines in coral-dwelling fishes are often conducted long after coral mortality revealing a significant gap in our knowledge in the timing and mechanisms that are driving these observed declines. We know that fishes that remain on bleached coral habitats can become visually more vulnerable to predators against the bleached background and suffer lower survivorship as a result (Coker et al. 2009, Chapter 3). Furthermore, as the coral dies, invasion of algae, sponges and other invertebrates reduces refuge spaces for fish, further reducing their survivorship (Coker et al. 2009, Chapter 3). Although many coral-dwelling fishes are strongly site attached, this increased exposure might motivate them to vacate their host corals and search for alternative healthy habitats (Wilson et al. 2006, Coker et al. 2009, Chapter 3). Neighbouring healthy coral colonies might provide alternative habitat. However, successful relocation will depend on the willingness of individuals to move among habitat patches and their ability to invade social groups already present on the remaining healthy coral colonies.

The objective of this study was to test if and when coral-dwelling fishes vacate their host colonies following coral bleaching, and to assess the factors that influence successful relocation to alternative coral hosts. Previous studies have documented localised declines in the abundance of coral-dwelling damselfishes following severe coral bleaching (e.g., Booth and Beretta 2002, Spalding and Jarvis 2002, Jones et al. 2004), however these fishes may vacate host corals as soon as bleaching occurs, or only after the host coral actually dies (Bonin et al. 2009a). In this study I first examined the timing of movement by coral-associated damselfish after coral bleaching to determine if they move from host corals immediately following bleaching or coral mortality, or if they persist with degraded coral hosts. Secondly, I determined the success of fish at finding alternative habitat and if the presence of conspecifics influences selection of new colonies. I predicted that the success of re-locating fish would depend on; i) the availability of alternative healthy habitats, and ii) the presence of conspecifics on alternative coral habitats. I tested these predictions for a common coral-dwelling fish *Dascyllus aruanus* following host degradation in the natural reef environment, and used experiments in aquaria, where the presence of conspecifics could be manipulated in association with varying habitat conditions.

4.3 Materials and Methods

4.3.1 Location and study species

This study was conducted at Lizard Island (14°40’S, 145°28’E), northern Great Barrier Reef, Australia. The study species was *Dascyllus aruanus* (Family Pomacentridae), a small (ca. 8cm TL) planktivorous damselfish common on Indo-Pacific reefs. Individual damselfish rarely venture more than 0.5m from their specific host colonies and retreat into the branches of their colony when threatened by predators and at night (Allen 1991, Forrester, 1991). *Dascyllus aruanus* live in size-structured social communities (Coates 1980). Within each coral colony, there is a hierarchical harem structure, which is comprised of a dominant male, smaller females, and nonbreeders (Cole 2002, Asoh 2003). *Dascyllus aruanus* associate closely with branching coral colonies (Sale 1972, Holbrook et al. 2000) and within the Lizard Island lagoon approximately 70% of social groups associate with healthy colonies of *Seriatopora hystrix* (Family Pocilloporidae) (D.Coker unpublished data). This branching coral has a 3-dimensional network of fine branches that provides ideal refuge spaces for small fishes; however, it is highly susceptible to temperature-induced coral bleaching (Marshall and Baird 2000).

4.3.2 Experiment 1: Movement of resident fish following host coral bleaching.

To assess if, and when *D. auranus* vacate host colonies following bleaching, individual fishes were tagged and monitored for 12 days following experimentally induced bleaching of coral colonies. Coral colonies were collected from the field along with the full complement of resident *D. aruanus* (mean fish/colony = 3.11 ± 0.39 SE). Resident fish were removed following anaesthetisation using a dilute solution of clove oil (Munday and Wilson 1997) and placed into labelled zip lock bags. Coral colonies were labelled with a small plastic tag, carefully removed from the substrate, and placed into a basket for transportation to the boat (<20m). The location of the removed colony was marked with a numbered visual tag so the colony could be placed back to its original position following the bleaching protocol. Fish were transported to and from the boat in clear zip lock bags and stored on the boat in holding buckets containing fresh seawater for tagging while their host coral were subjected to osmotic stress. Resident fish were separated from their host coral for transportation and while colonies were subjected to stress (< 15 mins). All commensal fish and invertebrates (e.g., coral gobies and Trapezia crabs) associated with the collected colonies were retained and returned to their host colony following colony stress along with the resident tagged *D. aruanus*. All associated fish were tagged using a subcutaneous fluorescent elastomer tag (Northest Marine Technologies Inc.) to identify fish to their host colony. The 10 treatment colonies were subjected to osmotic stress to induce bleaching (loss of pigmentation but not live tissue). Osmotic stress was used to induce bleaching because it produces similar signs and symptoms to thermal bleaching but in a considerably shorted period (Kerswell and Jones 2003, Coker et al. 2009, Chapter 3, Cole et al. 2009). Osmotic stress was accomplished by submerging each vacant colony into water with reduced salinity. Experimentally bleached colonies lost pigmentation over 2 days and remained white for 2 weeks and then rapidly started to recover and regain pigmentation. To control for movement of corals and tagging of fishes, an additional 4 colonies and resident fish (mean fish/colony = 2.75 ± 0.39 SE) were collected and handled in a similar manner, but were not subjected to osmotic stress. Coral colonies and resident damselfish were returned to their original location on the reefs after the bleaching treatment and surveyed daily for 12 days. The experiment was concluded after 12 days because pigmentation had started to return to the bleached colonies and no movement was recorded from the treatment or control colonies.

4.3.3 Experiment 2: Movement of resident fish following host coral mortality.

To explicitly test if fishes will move following host coral mortality (as distinct from host coral bleaching), 28 replicate colonies of *S. hystrix* and associated *D. aruanus* were collected from the reef and transported to a nearby sand flat where no other coral colonies were present. This allowed us to have a controlled environment to monitor any movement. All colonies were approximately the same size (mean maximum diameter = 32.9 cm ± 0.8 SE), and due to all colonies being collected from the same habitat (shallow sheltered lagoon), colony morphology (e.g., branch thickness, space and depth) was observed to be similar between all colonies. All colonies collected contained a minimum of three *D. aruanus* individuals per colony (Mean number/colony 3.4 ± 0.2 SE) and were sub adults and adults (approx 4–8cm) due to the absence of any recent recruitment. All coral colonies were numbered with small plastic tags and all resident fish were visually tagged with elastomer tags to identify them to their host colony (see above). The 28 colonies and resident fish were randomly placed into 14 pairs on the sand flat. Each coral colony was placed 1.5m apart within the pair, and each pair 10m from the nearest pair and >20m from the nearby continuous reef. Prior to this study, I ran some trials which showed that putting two healthy colonies 1.5m apart did not influence movement or mixing of the two resident social groups, demonstrating their strong site attachment to host colonies and reluctance to move off healthy colonies. Both coral colonies in a pair contained resident fish because literature suggests that coral-dwelling fish settle to and are more likely to migrate to coral colonies that already contain conspecifics (Fredwick 1997, Feary 2007, Bonin et al. 2009a).

For nine of the 14 coral pairs, one colony from the pair was randomly chosen and subjected to osmotic stress to induce bleaching and eventually the loss of live tissue. This method was similar to experiment 1 except colonies were subjected to osmotic stress for a slightly longer period of time. Stressed colonies lost their pigmentation within 48 hours resulting in a white appearance. Colonies died approximately 4 days post stress and were slowly colonised by algae. The remaining five pairs were used as controls to account for movement and handling of both corals and fish. For two of the control pairs, both colonies remained in a healthy condition. For the other three control pairs, both colonies in the pair were subjected to stress to induce bleaching and mortality. The number of fish on each colony was surveyed after 21 days. Since fish were tagged to correspond to their host colony, the colonies were checked for moving fish and the nearby reef was searched for tagged fish that might have relocated there. To examine whether there were significant differences between the abundance of fish associated with colonies before and after coral mortality, raw data meet the assumptions of ANOVA and was analysed using one-way ANOVA.

4.3.4 Experiment 3: Competition for healthy habitat.

At the end of the 21 day survey period some *D. aruanus* were still associated with dead coral colonies. To test if competition for the remaining healthy habitats by resident fish was forcing them to remain on the degraded habitat, an additional vacant healthy colony was added to each treatment pair. Colonies were then surveyed the following day to record the location of all fishes. It was predicted that if resident fish on the healthy colonies were preventing fish on the dead coral from relocating (aggressive competition) then they would take up residence on the additional vacant healthy colony.

4.3.5 Experiment 4: Relocation of migrating fish.

To test whether fish associated with a degraded coral colony could successfully relocate to an alternative healthy colony, individual fish were released onto dead branching corals in an area of degraded reef benthos and monitored to see if they would move across unsuitable reef matrix and find a suitable colony in which to occupy. Thirty six adult *D. aruanus* of varying size (mean size 42.4 mm ± 1.2 SE) were randomly collected from live coral colonies, tagged, measured and released individually onto a selected reef. The degraded reef consisted of dead corals and rubble with well-dispersed suitable live coral habitats and sparse individuals or communities of conspecifics. Over the period of one month, four fish at a time were collected off healthy coral colonies from a nearby reef, measured, tagged and released 20m apart onto dead coral colonies. Each fish was followed for 10 mins after release and the distance, microhabitat and interactions with other fishes were recorded. The location of release was marked with flagging tape and a number to correspond to the released fish. Following 24, hours the surrounding reef was extensively searched for the tagged fish.

4.3.6 Experiment 5: Influence of conspecifics on habitat selection.

A habitat choice experiment was used to test the influence of habitat quality and conspecific presence on the decision making of relocating fish. Choice experiments were conducted in 1000 litre plastic tanks (2.2 m x 1.2 m x 0.5 m deep) at Lizard Island research station. Individual *D. aruanus* were presented with the choice of habitat patches in different stages of degradation, with or without conspecifics present. Each fish was offered four pairwise choices: i) Healthy without conspecifics vs Dead without conspecifics, ii) Healthy with conspecifics vs Dead with conspecifics, iii) Healthy without conspecifics vs Healthy with conspecifics, iv) Healthy without conspecifics vs Dead with conspecifics. The tank base was covered in a thin layer of marine sand and coral habitat was placed at either end of the tank. Healthy and dead coral colonies of similar size and shape were collected from reefs in the Lizard Island lagoon. In trials with habitat containing associated conspecifics, a single individual *D. aruanus* was placed on the coral colonies. Conspecifics were placed in small, water tight, clear ziplock bag (50 X 100mm) containing fresh seawater and a small weight to ensure they remained with the necessary colony for the duration of the trial. Conspecifics were chosen to be slightly smaller than the introduced trial fish and in the trial where there was a conspecific associated with both coral colonies in the experimental arena the fish were within 1mm in size to each other.

Individual fish (n = 28) were trialled (each fish was run once in each of the 4 treatments and treatments were presented randomly to each fish) after a 5 min acclimation period in a perforated plastic cylinder in the middle of the tank. Once the cylinder was removed the fish was discretely monitored for 1 hour and the habitat that it was associating with was recorded every 5 mins. The choice of habitat based on the proportion of time that each habitat was associated with was compared for each of the pairwise choices using a Kolmogorov-Smirnov test.

4.4 Results

4.4.1 Experiment 1: Movement of resident fish following host coral bleaching.

The mean abundance of *D. aruanus* associated with the 10 artificially bleached colonies of *S. hystrix* was 3.11 (± 0.48 SE). No fish moved or were lost from corals following bleaching.

Similarly, all fish associated with the four non-bleached control colonies remained with their host corals over the survey period.

4.4.2 Experiment 2: Movement of resident fish following host coral mortality.

In contrast to absence of movement or mortality of *D. aruanus* on bleached colonies that were still alive (above), densities of *D. aruanus* declined by 67% on coral colonies that were subject to bleaching induced mortality (F_1, 8.00, $P<0.001$ Figure 4.1). Despite declines in fish abundance associated with the dead colonies in coral-pairs, there was no significant change in *D. aruanus* abundance on the neighbouring healthy colonies (F_1, 0.47, $P = 0.65$ Figure 4.1). Furthermore, abundances were unchanged on controls where both corals were healthy (F_1, 1.00, $P = 0.36$), and where both coral were subject to bleaching induced mortality (F_1, 0.42, $P = 0.70$), indicating that handling and being situated out on the sand flat did not influence movement patterns.

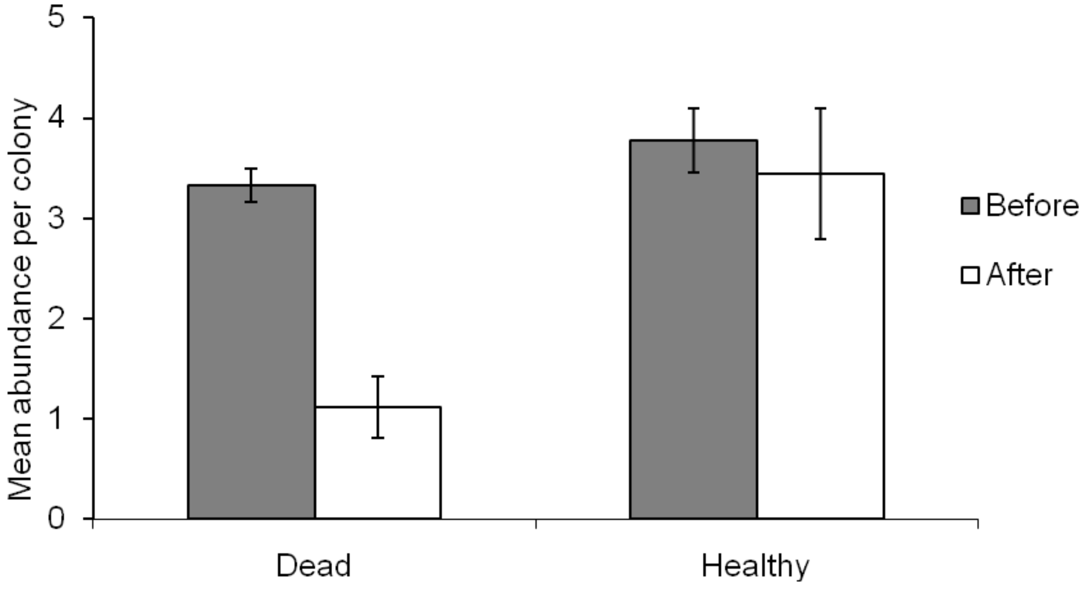

Figure 4.1: Mean number of *D. aruanus* per coral colony before and after on patch reefs that remained healthy and patch reefs that were subjected to bleaching and coral mortality.

Of the fish that vacated dead corals in treatment pairs half (n=11) moved the short distance to neighbouring healthy colonies while the other half (n=10) were found associated with live corals in the nearby reef matrix (Figure 4.2). Tagged fish on the nearby reef were associated with live branching corals from the families Acroporidae, Faviidae and Pocilloporidae.

Although there was no overall increase in the abundance of fish associated with the healthy colonies in the dead-healthy coral pairs, a significant number of fish moved from the dead colony to healthy colony (Figure 4.2). Abundances remained stable on the healthy colony because a similar number of fish left the healthy colonies (n=15) as the number of colonising fish from degraded colonies (n=11).

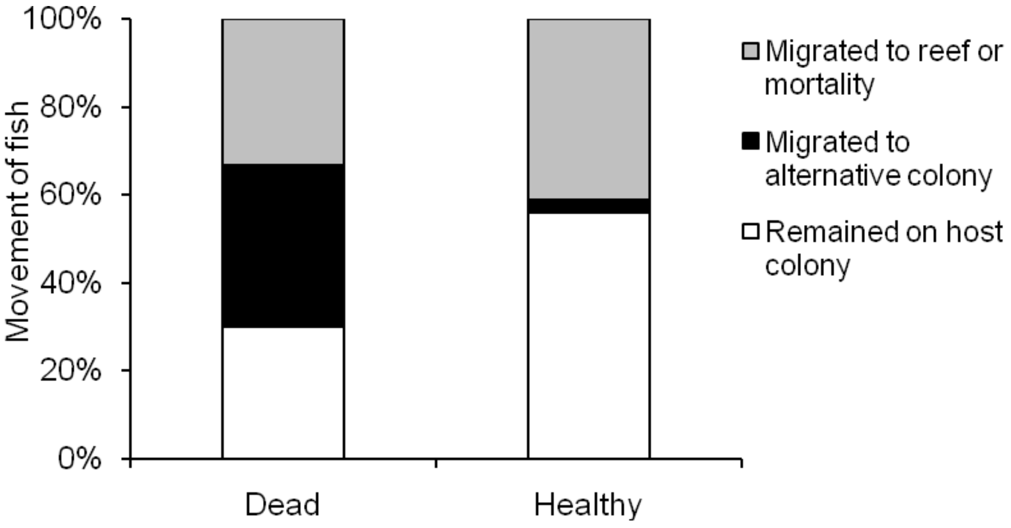

Figure 4.2: Movement of fish post mortality of a colony within treatments pairs (Healthy, n = 34, Dead, n = 30). Percentage of fish that persisted on their host coral, migrated to the alternative colony in the pair or migrated back to the reef.

4.4.3 Experiment 3: Competition for healthy habitat.

Fish that remained on degraded host corals (above) repeatedly swam away from the colony towards the neighbouring healthy colony in an attempt to relocate to the alternative colony. When an additional vacant healthy colony was added, all but one fish moved from the degraded colony to the additional colony within 24 hr (Figure 4.3). This along with observations indicates that agonistic interactions from the resident fish on healthy colonies were impeding fish from relocating from the dead coral. No fish moved from the healthy colonies to the new healthy colony placed nearby (Figure 4.3).

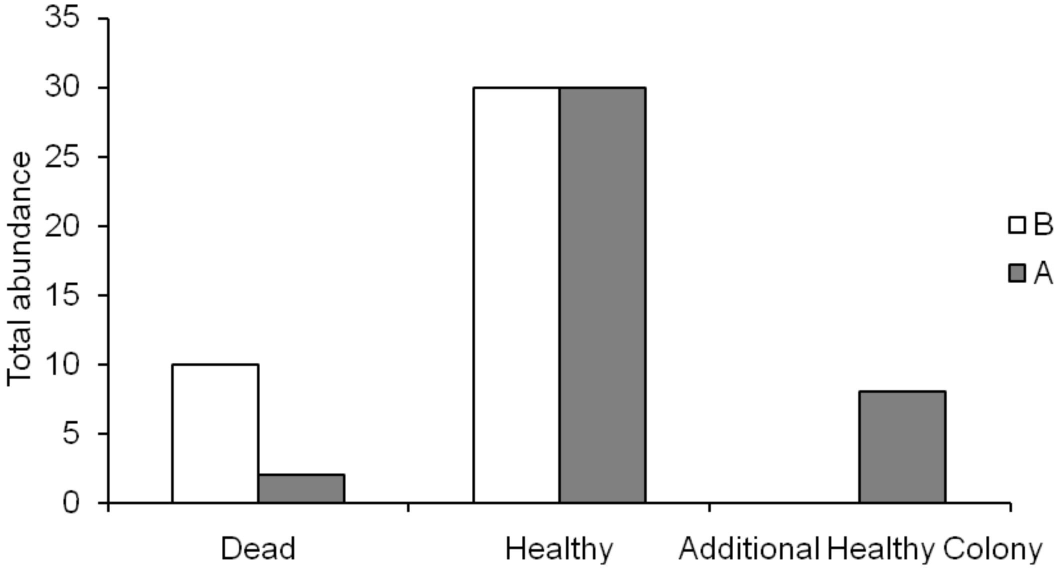

Figure 4.3: Movement of fish following the addition of an extra healthy vacant colony to each treatment pair (24 hour period).

4.4.4 Experiment 4: Relocation of migrating fish.

Of the 36 fish released onto the degraded reef, 23 were found the following day with the remaining 13 unaccounted for and presumed to have been removed through predation. Of the fish that were successful in finding suitable habitat (64%), all but 2 individuals were associated with healthy coral habitat containing conspecifics (Figure 4.4). Individuals were found up to 40m from where they were released.

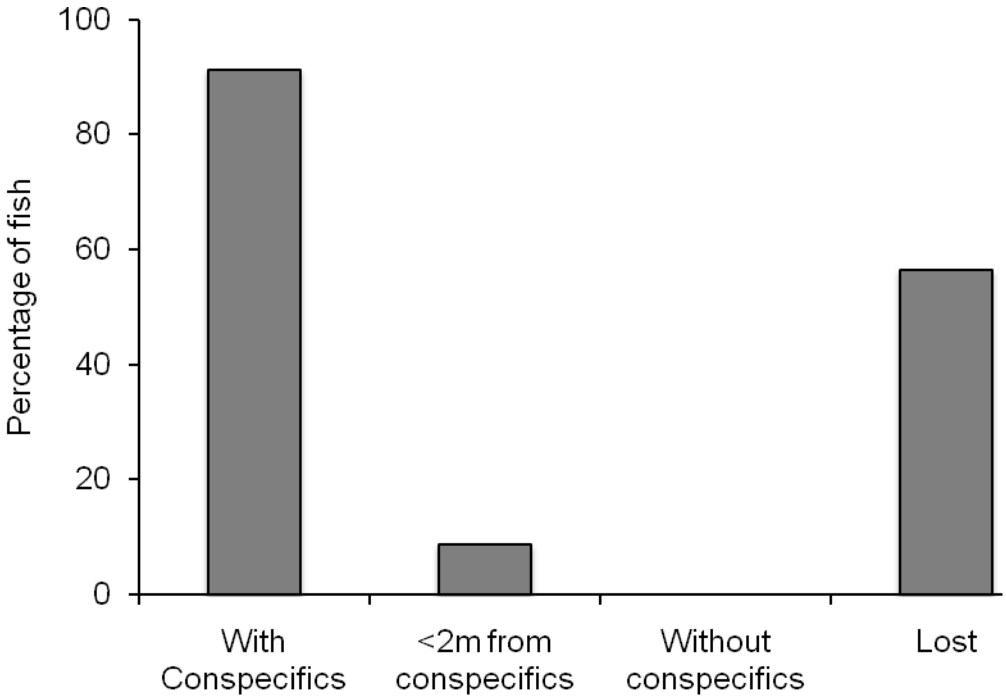

Figure 4.4: Total number of released individuals (n = 36) lost and found. If found whether associated with or without conspecifics.

4.4.5 Experiment 5: Influence of conspecifics on habitat selection.

Habitat choice experiments revealed that the presence of conspecifics on habitats drove habitat selection of relocating fish. Fish associated more often with healthy colonies if neither (*P*<0.05 for both comparisons) or both (*P* < 0.01 for both comparisons) colonies had conspecifics associated (Figure 4.5a,b). When presented with two healthy habitats, fish associated more with the colony containing conspecifics (*P*<0.001 for both comparisons Figure 4.5c). This attraction to associate with conspecifics over just a suitable habitat was so influential that fish would associate with dead corals over healthy corals if they contained conspecifics (*P*<0.001 for both comparisons Figure 4.5d).

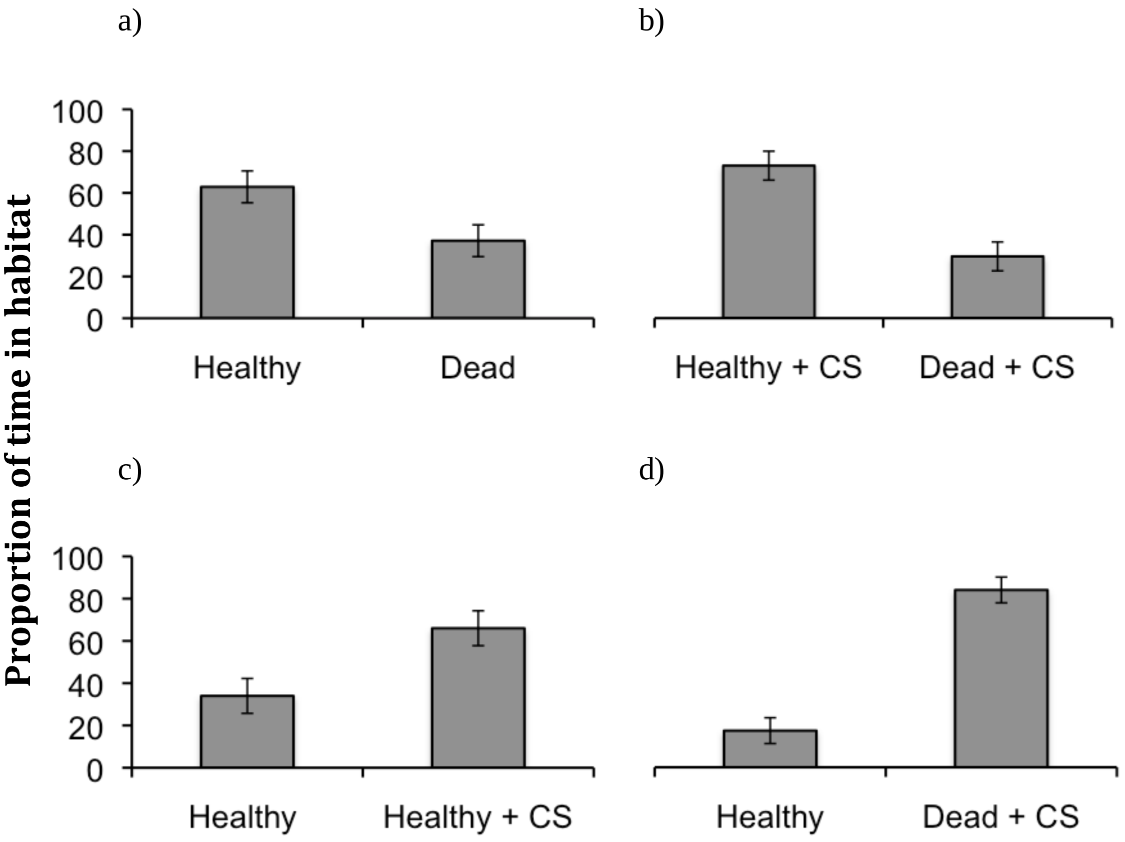

Figure 4.5: Mean percentage of habitat visits by fish (n = 28) in four pairwise trials (+CS = containing conspecifics).

4.5 Discussion

Previous studies have shown that coral-dwelling fishes decline in abundance following bleaching and loss of live coral cover (e.g., Lindahl et al. 2001, Bellwood et al. 2006, Wilson et al. 2006), but these studies lacked the temporal resolution to assess whether declines in abundance of fishes occur during coral bleaching or only after host corals actually die. Our study has shown that *Dascyllus auranus* will persist in bleached habitats, and that there was no change in the structure of fish assemblages throughout subsequent recovery of bleached corals. Conversely, fish associated with host colonies that suffer mortality will readily vacate and relocate to alternative healthy colonies where they use the presence of conspecifics as a cue for suitable habitat.

Abundance of *D. aruanus* was unchanged in colonies of *Seriatopora hystrix* that were subject to experimental bleaching, but that ultimately recovered. Bonin et al. (2009a) found similar results when investigating the persistence of newly settled *Pomacentrus moluccensis* recruits. They found no significant difference in the abundance of new recruits associated with healthy and bleached colonies, although there was high mortality associated with fish of both treatments. These results suggest that coral-dwelling fishes will be unaffected by mild episodes of coral bleaching, where bleached corals eventually recover. Although staying on a bleached colony will still offer physical protection they might be more conspicuous to predators and suffer higher predation rates due to an increase in their contrast with the pale background (Coker et al. 2009, Chapter 3). Regardless of the increased threat in predation, these fish remain associated with their host corals while bleached. However, following a severe bleaching event, coral colonies will eventually die and quickly become colonized by turf algae (McCook 2001). This study revealed that *D. aruanus* would vacate their dead host colony. This has also been observed in adult gobies that persisted within bleached but not dead host corals (Feary 2007, Bonin et al. 2009a). It appears that once dead, even though host corals retain the same physical structure, they no longer provide these fish with a suitable habitat. While live coral habitats offer an important physical structure for coral-dwelling fishes to shelter from predators, several studies have shown declines in these fishes following the loss of live coral cover but before the collapse or decline in structural complexity of coral hosts (Lindahl et al. 2001, Bellwood et al. 2006). These studies suggest that live coral cover is more important that just providing a physical structure for these fishes. Dead coral habitats offer limited protection against predators as the growth of algae and other sessile invertebrates reduces refuge space among the coral branches (Coker et al. 2009, Chapter 3).

Coral-dwelling fishes often associate with a single host coral for the majority of their life (Sale 1971, Munday 2002). I found that once their host coral is devoid of living tissue, two-thirds of the resident fish moved to an alternative healthy colony. The majority of the fish that left their dead habitat moved to the neighbouring healthy colony, while the other half relocated to healthy branching colonies within the nearby reef. Garpe et al. (2006) found that the abundance of coral-dwelling fishes on healthy habitats was higher following a large bleaching event than before suggesting that some fish had relocated. In our experiments, the overall abundance of fish on healthy coral colonies remained unchanged because a similar number of fish that moved to the neighbouring healthy colony moved off the healthy colonies and moved to nearby contiguous reef. This suggests that relocating individuals displaced resident subordinates from their social group, as has been observed in coral-dwelling gobies (Wong et al. 2007).

Individuals that vacated their host colony moved to nearby healthy habitats already occupied by conspecifics. There were a small number of individuals that remained associated with the degraded habitats possibly because they were unsuccessful at joining the resident community on the neighbouring healthy colony. It was observed that these fish would frequently approach the neighbouring healthy colony and attempt to enter the colony. Resident fish from the healthy coral colony would then defensively chase the fish back to the degraded habitat. When an empty healthy coral colony was placed nearby, all but one fish moved from the degraded colony to the new additional habitat by the next survey (24 hrs). This shows that these fish were associated with these degraded colonies because they were unsuccessful at joining the neighbouring resident community, probably due to aggression from resident fish. Resident fish maybe aggressive towards intruding fish because additional fish may be aggressive or socially dominant and therefore compete for refuge space, food and mating position within the established community (Booth 1995, Webster and Hixon, 2000, Holbrook and Schmitt 2002). Due to competition being the greatest between individuals of similar size (Booth and Wellington 1998) it is plausible that larger dominant fish, or smaller fish that don't compete directly with resident fish for social position, are likely to be more successful at relocating and joining a new social group although this needs to be tested.

In order for fish to successfully relocate to alternative healthy colonies, they must be able to move across degraded areas of reef and detect suitable habitats. Individuals and groups of *D. aruanus* commonly associate with colonies of live branching *Acropora spp*. and *Pocillopra spp*. (Forrester 1991, Holbrook et al. 2000), therefore, the availability of these colonies is predicted to influence their success. Of the fish that were released onto a degraded reef, all but two fish were found on healthy colonies containing conspecifics the next day even though there were vacant live branching coral colonies in the area. The other two fish were found on empty colonies within 2m of colonies containing conspecifics suggesting that they were attempting to join the community, but faced resistance from the resident fish. Furthermore, during the observations of re-locating fish on a degraded reef, fish swam past suitable empty colonies (branching *Acropora*, *Pocilliopora* and *Porites*) but attempted to remain close or on colonies that supported resident conspecifics. Our results suggest that the presence of conspecifics is an important indicator of suitable habitat for these fish. This was further supported by the laboratory experiments where individuals associated more with healthy colonies with conspecifics than without conspecifics, and dead colonies with conspecifics than healthy colonies without conspecifics. Migrating to habitats containing conspecifics would provide benefits like reduced risk of predation (Booth 1995, Kent et al. 2006). Also, joining a social community of conspecifics would increase the chance of mating (Sweatman 1985). Conversely, competition for shelter, food and rank with established resident individuals might have a negative impact on the growth or survivorship of the intruding fish. There is plenty of evidence that the presence of conspecifics influences the settlement of larval fishes and the benefits it offers these fishes (Sweatman 1985, 1988, Booth 1991, 1992), but the attraction of adult fishes to habitats containing conspecifics has not been widely reported.

Our results show that successful movement may be possible following small scale bleaching events where only parts of the reef are affected. Bleaching is often spatially patchy, with some coral species and individual coral colonies bleaching while neighbouring species and colonies remain healthy (Marshall and Baird 2000). This patchiness would allow fish to move short distances to healthy colonies or to healthy sections of the reef. But as bleaching events become more frequent and severe (Sheppard 2003, Donner et al. 2005) and other impacts like coral disease, terrestrial runoff and predatory starfish compound coral mortality (Sano et al. 1987, Willis et al. 2004, Pratchett et al. 2009a), migrating fish will have greater distance to travel in order to seek out healthy habitats. Fish associated with a narrow range of live corals would have a lower probability of success compared to more generalist coral dwelling species (Munday 2004, Feary et al. 2007b). It is conceivable that the recorded observed declines in coral-dwelling fishes following disturbances are a combination of fishes moving from degraded areas to healthier suitable habitats and *in situ* mortality rather than just the observed decline being a direct result of declining fish abundance through mortality.

This study is consistent with previous observations that loss of live coral habitat has a significant impact on small coral-dwelling fishes (Wilson et al. 2006, Munday et al. 2008, Pratchett et al. 2009a). However, this study also shows that coral-dwelling fish are strongly site attached and will remain associated with the host colony if subjected to bleaching, such that mild bleaching (from which coral hosts eventually recover) is unlikely to greatly affect resident fish communities. Nevertheless, coral-dwelling fish vacate following coral mortality, and they do so before the loss of structural complexity. A greater understanding is needed of how the relative size of colonising and resident fish influence the success of relocating fish, and if and what individuals (size, sex) are forcibly evicted from the colony. Furthermore, if relocating fish displace resident fish then the net result on disturbed reefs is still a decline in abundance. While having the ability to vacate a degraded habitat and move to alternative live habitats might sound promising, vacating fish will be exposed to predators as they leave the safety of their structure and try to seek out and join resident communities of conspecifics. This vulnerability will further increase if there are no suitable corals nearby (desired species, morphology or occupied colonies with residents). Bleaching events are predicted to increase in severity and spatial extent with a greater proportion of colonies being affected across reefs. This will lead to fewer healthy habitats for fish to relocate to and force displaced individuals to move greater distances across the reef in search of suitable healthy habitats.

Chapter 5: Intra-specific aggression limits group joining for displaced coral-dwelling fish[5]

5.1 Abstract

Habitat degradation via natural or anthropogenic disturbances often results in the displacement of resident organisms. One important determinant of the lethality of such displacement is the nature of the interactions between displaced individuals and the occupants of alternative habitats. Here, I show that displaced individuals of the group forming coral-dwelling fish *Dascyllus aruanus* have a very low probability of joining a new group of conspecifics due to cooperative aggression from resident group members. Resident group size and the body-size distribution of resident group members failed to predict group entry success by displaced individuals, however, the smallest displaced individuals tended to be more successful than larger displaced individuals. Pair-wise contestant size-ratio did not affect absolute aggression by residents towards displaced intruders, but did affect the relative attack rate by individuals within groups, whereby equal-sized and relatively larger residents accounted for a greater proportion of total group attacks compared to smaller residents. Despite the aggression towards unfamiliar intruders, group members readily accepted group re-entry by displaced familiar group members. This study shows that aggression by group members towards intruding displaced individuals is dependent on group size, size ratio and

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[5] A manuscript of this chapter is in preparation for submission to the journal *Biological Letters.*

familiarity, with similar sized group members disproportionately contributing to group and habitat defence. The implication is that social and group dynamics may lead to greater habitat-displacement lethality than would be predicted by mobility-potential and alternative-habitat availability alone.

5.2 Introduction

Group living occurs in a wide range of animals, including mammals, birds, insects, and fishes. Living in a group involves a trade-off between the potential costs (e.g., increased disease, competition) and benefits (e.g., reduced predation risk, increased foraging) of group living versus solitary living (Krause and Ruxton 2002). In fishes, preference to live in conspecifics groups has been documented for many fishes that form schools, at recruitment time where recruiting fishes prefer to settle to coral colonies containing conspecifics (Sweatman 1983, Ben-Tzvi et al. 2009) and for displaced adults relocating to coral colonies that support conspecifics (Coker et al. 2012b, Chapter 4). Dominance hierarchies are present in many groups, especially when resources (e.g., shelter, mating partners) are limited (Rubenstein 1981, Forester 1991, Buston and Cant 2006). Hierarchies are generally size related, with larger or more dominant individuals at the top (Coates 1980, Forrester 1991, Buston and Cant 2006), and are suggested to indicate the existence of competition within the group of individuals (Rubenstein 1981, Jones 1987, Booth 1995). Individuals within the social group may compete for refuge space, access to food and breeding rights (Munday et al. 2001, Holbrook and Schmitt 2002, Wong et al. 2008a). Despite competition for these limited resources, individuals in the group benefit from reduced predation risk through increased vigilance (Morgan 1988), dilution effect, (Krause and Ruxton 2002) and confusion of predators (Pitcher et al. 1982) as well as increased foraging success (Krause and Ruxon 2002) and access to breeding partners (Buston 2003a, Wong et al. 2008b). In some groups, size-based hierarchies function as a queue for dominant status (e.g., breeding), where individuals move up the rank following the loss of higher ranked individuals (Buston 2003b, 2004, Mitchell 2005, Wong et al. 2007).

For reef fishes, groups are often restricted to territorial areas or individual coral colonies (Forrester 1991, Wong et al. 2008a). Groups of small-bodied reef fishes associate with live coral colonies because they provide food, reproduction sites (Thresher 1984, Munday and Jones 1998, Cole et al. 2008) and habitat that helps mediate predation interactions (Caley and St John 1996, Beukers and Jones 1998, Holbrook and Schmitt 2002). The continued loss of live coral from natural and anthropogenic disturbances are a threat to coral reefs and the many fishes that depend on this structure for habitat (Wilson et al. 2006, Pratchett et al. 2008a). Thus, future loss of live coral habitat as a result of predicted increases in disturbances through climate change (Hoegh-Guldberg 1999) is expected to cause significant net reductions in the abundance and diversity of coral-dwelling fishes (Jones et al. 2004, Munday 2004, Bonin et al. 2009b). However, predicting the magnitude of these reductions is difficult without knowledge of how surviving inhabitants respond to habitat disturbance and loss (Wilson et al. 2006, Pratchett et al. 2008a). Coral-dwelling fishes associated with degraded corals will vacate their host colony (Feary 2007, Coker et al. 2012b, Chapter 4) and attempt to relocate to alternative healthy habitats, whereby they often preferentially select habitat containing conspecifics as opposed to vacant healthy habitats when provided with a choice (Coker et al. 2012b, Chapter 4). Therefore, the success of mediating habitat loss through relocation for displaced coral-dwelling fishes will depend on the probability that individuals can join established groups of conspecifics (assuming that at least some suitable habitat remains intact).

For habitat-displaced coral-dwelling fishes, the probability of relocation success maybe low if established groups on alternative healthy colonies show resistance and aggression towards intruding fishes. Sale (1972) suggested that aggression towards intruders might prevent the addition of members in order to reduce overcrowding. For established groups, increased density through new members would lead to increased competition within the group for social rank, breeding status, shelter and feeding sites (Booth 1995, 2004, Holbrook and Schmitt 2002, Buston 2003a, Wong et al. 2008a). Therefore resident group members with over lapping resources may be aggressive in order to protect essential resources. Furthermore, increased within-group aggression as a result of new individuals joining a social group may lead to the expulsion of less dominant group members (Wong et al. 2007).

Research on group dynamics and the introduction of new members has largely focused on ‘free entry’ groups, whereby individuals are readily permitted to join groups of their choice (Krause and Ruxton 2002). For ‘restricted entry’ group dynamics, research is more limited. Success and aggression may be driven by territorial aggression whereby the largest member of the group is predicted to be the most aggressive or the aggressor through size-based aggression, where invaders are competing with individuals for a place in the hierarchy or for resources. Jordan et al. (2010) examined which group members restricted the entry of new members through aggression based on intruder size and the size of members in the group for a common coral-dwelling damselfish. They revealed that larger residents were more aggressive towards intruders than smaller group members, while Wong et al. (2007) showed that individual resident coral gobies were most aggressive to individuals of similar size (i.e., size-ratio ≈ 1). Individuals in a group may be separated by body size ratios (Buston and Cant 2006). In order to maintain a stable hierarchy, individuals may diet so as to not approach the size of their immediate subordinate in order to avoid competition for food and conflict over social rank (Wong et al. 2008b). Knowledge is still lacking on entry success of intruders to natural groups and which resident members attempt to prevent entry into the group. These are important because fish displaced through habitat loss will be forced to relocate and attempt to join new groups.

I tested the success of a common coral-dwelling fish, the humbug damsel, *Dascyllus aruanus* (Family Pomacentridae) in joining a new social group following habitat degradation. *Dascyllus aruanus* live in hierarchical social groups associated with complex live coral habitat (Coates 1980, Cole 2002, Asoh 2003). In this study I investigated i) the success of foreign individuals at joining established social groups, ii) what group demographics influence the level of aggression towards intruders, and iii) which individuals within the resident group are eliciting the aggression as a function of intruder size. This will provide insight into the probability of success for relocating individuals of varying size. Because fish may vacate their degraded host colony at different times, it is possible that some individuals that leave later may encounter a group that comprises of past group members. Therefore, I also tested iv) the acceptance of removed individuals back into their group over time to see if they will remember and accept or reject past group members back into the group.

5.3 Methods

5.3.1 Study species and collection

This study was conducted at Lizard Island Research Station (LIRS) (14^{o}40’S, 145^{o}28’E), Northern Great Barrier Reef, Australia. *Dascyllus aruanus* was used as the model organism because they form tight social hierarchical groups and have a strong dependence on live complex coral for habitat, often associating with single colonies from the genus *Acropora* spp., *Stylophora* spp. *Pocillopora* spp. for the majority of their life (Chapter 2, Sale 1971, Shpigel and Fishelson 1986). Live coral habitat is important for these small-bodied fish (max 65mm TL) for reducing competition and predation through the availability of refuge spaces and discrete resources (Murdoch and Oaten 1975, Hixon 1987, Hixon and Menge 1991). *Dascyllus aruanus* recruit to colonies containing conspecifics (Sweatman 1983) where they occur in groups averaging two to five individuals (Sale 1972). Here strict dominance hierarchies exist within the stable groups, with larger individuals dominating smaller individuals (Coates 1980). In small groups, sexual composition is in the form of a heterosexual pair or a single-male polygynous group, while in less common larger groups (< 25) associated with large coral thickets, multi-male multi-female groups can exist (Fricke 1977).

Established groups of *D. aruanus* (2 – 10 members) were collected using a dilute solution of clove oil (Munday and Wilson 1997) and transported back to LIRS in their groups. Their host colony (*Stylophora pistilata*) was removed from the substrate at the base, measured, tagged for identification and transported back to LIRS. Once back at LIRS the host colonies (n=12) were placed into separate 1000 litre plastic flow through tanks (2.2 m x 1.2 m x 0.5 m deep). All group members were measured and tagged for individual recognition using a subcutaneous fluorescent elastomer tag (Northwest Marine Technologies Inc) and then placed back with their host colony. A separate batch of *D. aruanus* (n=66) of varying sizes were caught from reefs distinct from the previously collected groups and transported back to LIRS to function as intruders. Group member's ranged from 18mm to 59mm and intruding fish ranged from 16mm to 59 mm in size. All fish were left to acclimate for two days before the commencement of trials.

5.3.2 Entry into new groups

To directly test the success rate of relocating individuals joining a resident group a randomly selected individual was placed on a dead coral colony at the opposite end of the tank from a randomly selected resident-group and host colony. Success in joining the group and aggressive interactions were visually recorded by observers for one hour. During the trial, intruding fish were recorded as successful (gaining and maintaining entry) or unsuccessful. During this period the group members that expressed aggression towards the intruder was noted (based on visual tag) and the number of aggressive attacks recorded. Aggressive attacks were identified as chasing and bitting (Katzir 1981). Group members were also observed to regularly exhibit frontal-displays (attacker swims towards the intruder with fins spread wide and body axis slightly tilted down, Katzir 1981) and signal jumps (attacker rises and descends in the water column, Katzir 1981) but these were not recorded as an attack. Although disputes and interaction can be resolved through non physical aggression, it was not always possibly to distinguish if a display was directed towards the intruder or towards group members (e.g. intra-group dominance display or a mating display). At the end of the trial, the intruder was removed from the tank and the study. This process was repeated with at least 24 hours between trials and with no more than six intruders introduced to each group.

5.3.3 Entry into familiar groups

To test whether group members would act aggressively towards a removed group member after time, eight coral colonies and associated *D. arunaus* were collected and placed in large flow through tanks (see above). After five days of acclimation a group member was removed and held in a separate tank. The individual (n = 26) was re-entered to the tank after 1 hour, 7 hours, 24 hours and 48 hours. For each introduction, aggressive interactions were recorded for 1 hour and if successful at entering and maintaining membership during the observation then the fish was removed for the following time period. This was repeated for each member of the group until the fish was rejected from the group or it had reached the 48 hour period.

5.3.4 Statistical analysis

Statistical analyses were conducted in R. Individual aggression was ln(x+1) transformed prior to statistical analysis to reduce heteroscedasticity. Due to apparent non-linear relationships between individual aggression and predictor variables, we employed generalized additive models with Gaussian error to derive the best-fit model for individual aggression (rate per hour) (VGAM package) (Hastie and Tibshirani 1986). The best-fit model incorporated non-parametric smoothing functions for resident-intruder size similarity (ln (intruder size mm TL)-ln(resident size mm TL)) and resident group dominance rank, and included group size and individual group ID as parametric factors.

Predictors of group entry success for unfamiliar habitat seekers were examined for significance using logistic regression. Predictors included were; total group aggression (ln(x+1) transformed), group size, intruder size (ln(mmTL)), and size-similarity between the intruder and the next largest habitat resident (as above). Predictors of group entry success for familiar habitat seekers were not explored due to a lack of variance in group entry success (100% success rate).

5.4 Results

5.4.1 Entry into new groups

All individuals on dead coral colonies were observed to try and relocate to healthy coral occupied by conspecific residents. Aggression from habitat residents towards familiar displaced habitat seekers was found to be limited to conventional dominance signals (i.e.

frontal displays and jumps) with zero physical attacks being recorded during group re-entry trials. In contrast, aggression from habitat residents towards unfamiliar habitat seekers was found to be highly physical (Figure 5.1a,b). Total group physical aggression towards unfamiliar habitat seekers was relatively curensistent across group sizes, but slightly peaked at intermediate group sizes. Individual group ID had a non-significant effect on resident aggression (GAM; Group ID: $t = 0.34$, $p = 0.75$; Figure 5.1a). Mean resident aggression towards unfamiliar habitat seekers significantly declined as a function of group size (GAM; Group size: $t = 4.06$, $p < 0.01$; Figure 5.1b), and significantly increased as a function of resident-intruder size-similarity (GAM; s(Size similarity): $F_{6,3,7.5} = 12.77$, $p < 0.01$; Figure 5.1c) and within resident-group dominance-rank (GAM; s(Rank): $F_{2.03,2.6} = 4.8$, $p < 0.01$; Figure 5.1d).

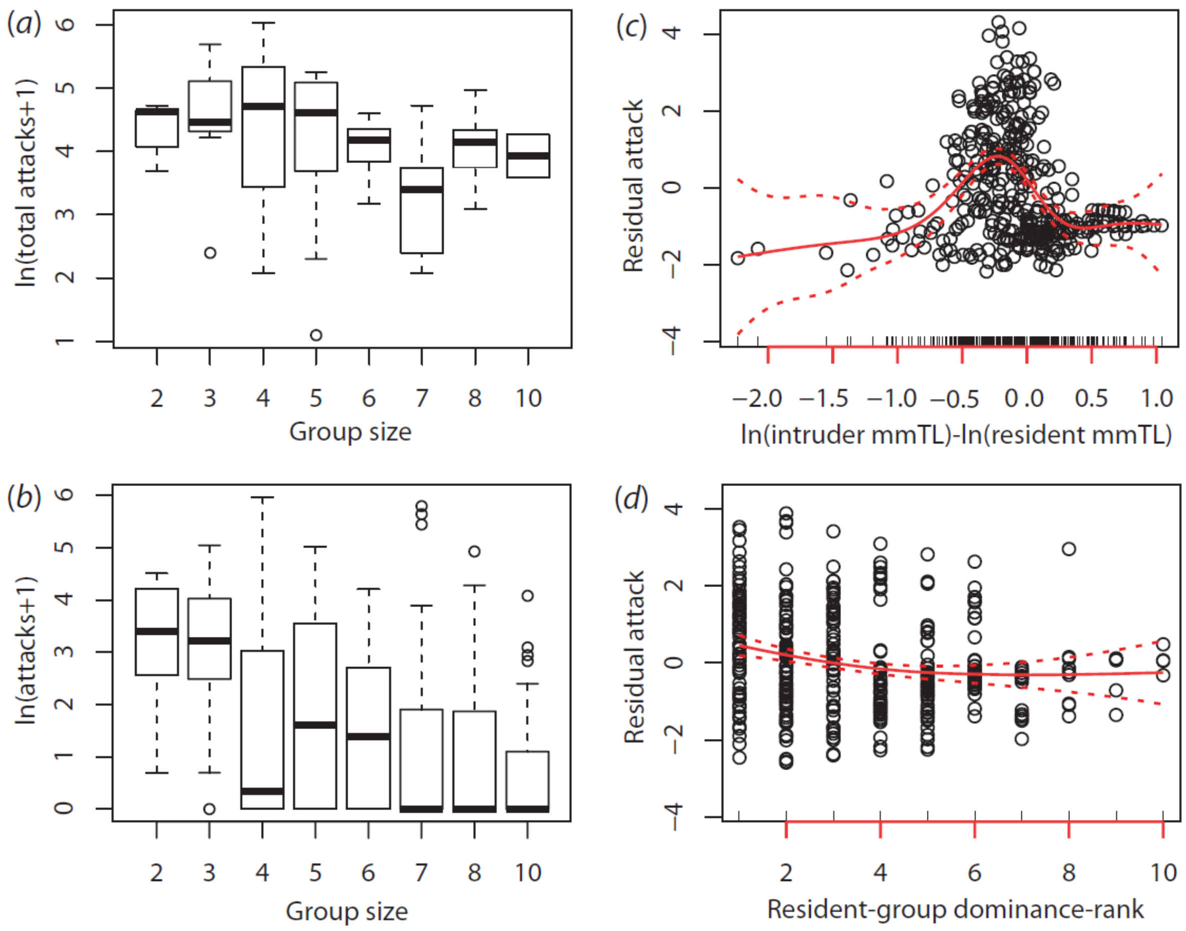

Figure 5.1: Relationship between attacks and a) total group aggressio, b) group size, c) intruder size and d) size-similarity between the intruder and the next largest habitat resident.

Consistent with patterns of aggression, all displaced familiar habitat and social group seekers (*n* = 26) achieved group re-entry over a 48h time period, while only 18% (12/66) of relocating unfamiliar individuals were successful in joining a new social group within the same time frame. The absolute size of the intruder was found to be the only significant predictor of group entry success for unfamiliar habitat and social group seekers (Logistic regression; Body size: z = 2.46, *p* = 0.014, Table 5.1), with smaller fish having a higher rate of success compared to larger fish (Figure 5.2).

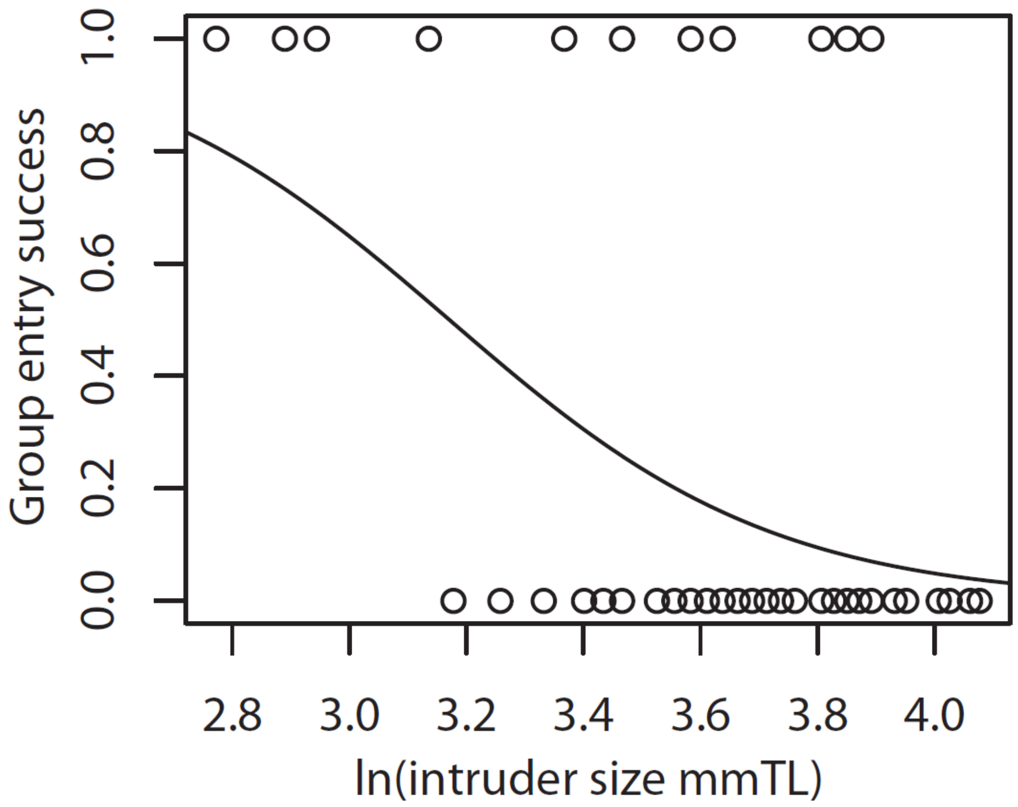

Figure 5.2: Binary outcome of individual (n=66) group entry success (1.0 = successfully gained and maintained group entry, 0.0 = unsuccessful).

Table 5.1: Probability of fish successfully joining a group of conspecifics based on group demographics.

	Estimate Std.	Error	z value	Pr(>[z])
(Intercept)	13.3666	6.58209	2.031	0.0423
Ln.Intruder.size	-4.02695	1.63445	-2.464	0.0137
Size.dif.large	-1.84863	4.21809	-0.438	0.6612
Group.size	-0.03315	0.19313	-0.172	0.8637

5.4.2 Entry into familiar groups

All individual group members that were removed (1, 7, 24, 48 hours) and then re-introduced back to their group were accepted. Resident group size and size-similarity between intruder and next largest resident (NLR) had no significant effect on unfamiliar-individual group-entry success (Logistic regression; Size-similarity (NLR): z = 0.44, p = 0.66; Group size: z = 0.17, *p* = 0.86). There were no aggressive attacks from the resident members towards the intruder, but in three cases there were some dominant displays (frontal displays, signal jumps) from the largest member of the group.

5.5 Discussion

The success of many coral-dwelling fishes following habitat loss will depend on the ability of displaced individuals to form or join new social groups. Although relocating individuals prefer to associate with coral colonies containing conspecifics (Coker et al. 2012b, Chapter 4) this study shows that resident group members are highly aggressive towards intruders resulting in a low success rate. Levels of aggression are influenced by group size and individual size of residents, whereby resident fish that are similar or slightly larger in size are most aggressive towards intruding fishes. This suggests that for these coral-dwelling fish, aggression is driven by size-based competition and not just a group territorial response. Furthermore, this aggression will limit the relocation of displaced individuals following habitat degradation.

The success of joining a group appears to be slightly higher for smaller individuals than for that of larger individuals, suggesting that the resident group members control entry success rather than relocating fish forcing their way in. Hierarchies function as queues for subordinates waiting to move into breeding status (Buston 2004, Mitchell 2005, Wong et al. 2007) therefore smaller individuals may be more successful compared to larger individuals because they are further down the breeding hierarchy and therefore less of a threat to resident individuals for breeding status. Large individuals will be in close competition for breeding status because they will enter further up the queue and will have to out compete dominant breeding members in order to gain entry. It would be expected that larger individuals are able to force their way into new groups based on their size alone, but this study found that intruding individuals that were larger than dominant group member were not always successful at gaining entry. A study by Whiteman and Côte (2004) on group living gobies found that larger individuals still failed to gain access to new territories despite some also coming from a prior dominant position (but see Beaugrand et al. 1996). The success of resident fish in keeping intruders out may be influenced by differences in individual aggression, size, outnumbering or prior-resident effect. Prior-resident effect has been shown in brown trout where studies found that territory owners win 86% of sized matched contests against intruders (Johnsson et al. 2000). For coral-dwelling gobies, Munday et al. (2001) showed that an inferior competitor species was able to competitively win contests for preferred habitat against similar sized dominant species if they were prior residents of the coral colony. This effect can be driven by greater knowledge of the habitat or associated resources by the residents (Davis and Houston 1981, Eason and Hannon 1994) and the cognitive disadvantage inflicted on intruders that are trying to evaluate the quality of habitat or group and the received aggression (Johnsson et al. 1999).

Overall, larger group members were more aggressive towards intruding fishes than smaller members. Smaller fish are physically unable to defend against larger fish and therefore show little to no aggression towards larger intruders, but were still aggressive towards smaller fish. Larger damselfishes are aggressive towards recruits and smaller damselfishes (Doherty 1982, Jones 1987, Forrester 1990, Jordan et al. 2010), although in this study aggression from larger individuals was only towards intruders that were similar or slightly smaller in size and not just towards all smaller fish. This reveals that rather than all fish larger than the intruder and therefore able to have a competitive edge displaying aggression, it was limited to a few individuals within the group. This suggests that aggression is related to position in the size hierarchy, which has benefits in terms of access to shelter, food and mates and not just a territorial response. The individuals eliciting the attacks change with changing intruder size, showing that members of the group that have the most to lose from a successful entry elicit the defence, while members that will not be disadvantaged show little or no aggression. As for much larger individuals in the group, the addition of a lower ranked member will not have any effect on their status and therefore they don’t need to waste energy or risk injury in aggressive interactions. Although intrasexual aggression is predicted to be highest among dominant individuals (Wong et al. 2008b), we were not able to assess sex-specific effects in this study.

The observed decline in the number of attacks on intruders with increasing group size may be influenced a decreasing negative cost of having another individual join. For larger groups, the addition of another individual may be less of a cost than for groups containing fewer members. For larger groups, intergroup competition may be higher for refuge spaces and the best feeding spots between individuals, which may take away from their priorities of defending against intruders (Coats 1980, Forrester 1991, Booth 1995). Many groups of coral-dwelling fishes under normal conditions have significantly lower numbers per coral head than expected under random distribution (Kent et al. 2006) suggesting that high densities are not favourable. Furthermore, fishes in larger groups are recorded to consume half the amount of food compared to fishes in smaller groups (Kent et al. 2006). If more than one fish is allowed to enter the colony, density-dependent processes may impact on mortality rates and competitive interactions for resources caused by the enhanced crowding within the colony (Sale 1972, Booth 1995). Competition would increase between the intruder and group members that have over lapping niches (e.g., rank, breeding status, shelter, feeding sites) (Booth 1995, 2004, Holbrook and Schmitt 2002) and may also result in the forcible eviction of less dominant members.

Unsuccessful fishes are predicted to be forced to live solitary on nearby colonies and experience a decline in survivorship without the added security of group members. Holbrook and Schmitt (2002) found that less aggressive individuals can be displaced to less desirable habitats where they are more susceptible to predators. Additionally, movement across the reef and constantly getting chased away from a colony into the open by resident fishes is likely to increase their vulnerability to predators (Lassig 1981, Shpigel and Fishelson 1986, Stewart and Jones 2001). For some species, solitary individuals may initially miss out on the opportunity to mate and for some individuals, this may influence a change in sex with the absence of the dominant group member (Shpigel and Fishelson 1986). Fortunately, *D. aruanus* are known to settle to habitats containing conspecifics (Sweatman 1985), so over time this many attract additional members and help form a new social group through recruitment.

While group members aggressively defend against intruding foreigners, previous group members are welcomed back into the group without aggression. This study found that even after a group member had been removed for up to 48 hours, the remaining members would readily accept them back into the group. Furthermore, although these fish appear visually identical to us, group members are able to distinguish between familiar and foreign intruders. Mode of identification is unknown but possibly involves chemical cues, UV body patterns or slight variations in patterns and markings. The acceptance of past members suggest that if group members vacate their degraded host colony at different times but relocate to the same healthy colony then they will reform their group and maintain the same stable hierarchy as before.

For many coral-dwelling fishes the benefits of living in a group far outweighs solitary life. This study shows that relocating individuals are unlikely to successfully join another group, and resident group individuals with the most to lose from the addition of another group member aggressively defend against intruders of the same species. While *D. aruanus* acts aggressively towards intruding conspecifics, they are also aggressive towards other coral-dwelling species (e.g., Sale 1977, Katzir 1981, Sweatman 1988). Furthermore, aggression between reef fishes for territory and habitat is wide spread (e.g., Low 1971, Myberg and Threasher 1974, Munday et al. 2001) suggesting that competition plays an important role in fish communities with both positive and negative outcomes. While aquaria experiments proved suitable for accurately collecting behavioural data, we must also acknowledge that relocating and defending fishes on the reef would also be exposed to predators that may reduce their persistence, survivorship and levels of aggression. Additionally, this study only looked at single coral colonies. While these fish commonly associate with small isolated colonies, numerous continuous colonies extending over a much larger area would possibly aid in the intruders ability to gain entry by sneaking in or avoiding aggression by moving among the joining colonies. Therefore, habitat displacement lethality driven by social and group dynamics will be high for displaces coral-dwelling fishes reducing their ability to mediate habitat disturbances through relocation.

Chapter 6: Interactive effects of live coral and structural complexity on the recruitment of reef fishes[6]

6.1 Abstract

Corals reefs are subjected to multiple disturbances that modify levels of coral cover and structural complexity of the reef matrix, and in turn influence the structure of associated fish communities. With disturbances predicted to increase, insight into how changes in substrate condition will influence the recruitment of many fishes is essential for understanding the recovery of reef fish populations following biological and physical disturbances. While studies have revealed that both live coral cover and structural complexity are important for many fishes, there is a lack of understanding regarding how a combination of these changes will impact the recruitment of fishes. This study used experimentally constructed patch reefs consisting of six different habitat treatments; three levels of live coral cover (high, medium, low) crossed with two levels of structural complexity (high, low), to test the independent and combined effects of live coral cover and structural complexity on the recruitment and recovery of fish communities. The abundance and species diversity of fishes varied significantly among the six habitat treatments, but differences were not clearly associated with either coral cover or structural complexity and varied through time. More striking, however, was a significant difference in the composition of fish assemblages among

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treatments, due mostly to disproportionate abundance of coral-dwelling fishes on high coral cover, high complexity reefs. Overall, it appears that coral cover had a more important influence than structural complexity, at least for the contrasting levels of structural complexity achieved on experimental patch reefs. Furthermore, I found that live coral cover is important for the recruitment of some non-coral dependent fishes. This study confirms that live coral cover is critical for the maintenance of high biodiversity on tropical coral reefs, and that sustained and ongoing declines in coral cover will adversely affect recruitment for many different species of reef fishes.

6.2 Introduction

Coral reef ecosystems are subjected to a multitude of different disturbances that vary in scale and intensity. It is predicted that coral reefs will experience an increase in anthropogenic disturbances over coming decades resulting in declines of quality and quantity of coral dominated habitats (Hoegh-Guldberg 2004, Wilson et al. 2006, Hughes et al. 2010). Cyclones, storms and bioeroders change the physical architecture of reefs while mass coral bleaching, outbreaks of crown-of-thorns starfish (*Acanthaster planci*) and coral disease reduce live coral cover (Sano et al. 1987, Willis et al. 2004, Garpe et al. 2006). Reductions in live coral cover and structural complexity of the benthos can lead to fundamental changes in reef fish communities. Coral dependent fishes typically experience the greatest declines in abundance, but structural complexity loss can further affect other groups of fishes (Luckhurst & Luckhurst 1978, Munday 2004, Gratwicke and Speight 2005, Wilson et al. 2006, Pratchett et al. 2008a, Graham et al. 2009). While disturbances to coral habitats can have a strong effect on adult fishes, studies have also observed long-term population declines as a result of the decline of suitable settlement habitats (Jones et al. 2004). Therefore, it is important to understand how changes in live coral cover and structural complexity influence the recruitment of fish larvae, especially given settling fish have very specific habitat requirements (Sale et al. 1984, Öhman et al. 1998, Holbrook et al. 2000, Booth and Beretta 2002).

The substrate of coral reefs is important for the survivorship of existing fishes, but also for the replenishment of fish communities to reefs (Jones et al. 2004, Feary et al. 2007a). Live coral cover and structurally complex reefs provide essential resources for fishes by supplying them with food, refuge space and helping to mediate important biological interactions such as competition and predation (Syms and Jones 2000, Cole et al. 2008, Coker et al. 2009, Chapter 3). Following multiple disturbances and declines in fish abundances, replenishment of fishes to these impacted reefs is essential for recovery processes and maintenance of key functional groups that help sustain reef health, promote recovery and provide resilience by preventing phase shifts (Bellwood et al. 2004, Hughes et al. 2010).

Recovery of fish communities can occur through the emigration of fishes from surrounding reefs or through the recruitment of larval fishes from the pelagic environment. While emigration of fishes is limited to small scales and only relevant to local disturbances, recovery through recruitment is, while an infrequent demographic event, able to repopulate communities over larger distances. Live coral cover and structural complexity are important for settling fishes through the provision of settlement cues and shelter (Sweatman 1988, Jones and Syms 1998, McCormick et al. 2010). Furthermore, some juvenile fish require specific dietary requirements (e.g. algae, live coral tissue), which influence their settlement site. An understanding of how impacts through the change in substrate health and complexity will influence the recruitment of many fishes is essential. Studies have shown that live coral and structural complexity are important for many juvenile fishes (e.g., Caley and St John 1996, Booth and Beretta 2002, Feary et al. 2007a, McCormick et al. 2010), but we still lack a solid understanding of how biological and physical changes in habitat combine to impact fish recruitment.

While it is important to understand how substrate condition influences the replenishment of reef fish communities, this is difficult to study on natural reefs. Factors like larvae supply, coral composition and existing fish communities can confound differences in recruitment (Cowen 1985, Booth 1992, Messmer et al. 2011). Patch reefs are a natural component on many reefs, especially in lagoons and back reefs, and can be easily constructed and manipulated. As such, patch reefs have been used extensively to study the relationship between substrate and fish recruitment, diversity indices, mortality and offer the ability to control variables (e.g., Williams 1980, Sale et al. 1984, Syms and Jones 2000, Almany 2004ab, Feary et al. 2007a, Bonin et al. 2011, Messmer et al. 2011). Furthermore, removal of all fish prior to an experiment allows assessment of replenishment of fish due to substrate characteristics without the influence of resident fish which may vary between patch reefs, influencing recruitment through settlement cues, competition and predation (Booth 1995, Sweatman 1985, Kent et al. 2006). While some studies have looked at the recruitment of fishes to reefs with varying coral cover (e.g., Feary et al. 2007a, McCormick et al. 2010) and structural complexity (e.g., Caley and St John 1996), the interactive effects of these two attributes have not been investigated. While some species of fishes are dependent on live coral (Munday et al. 1997, Cole et al. 2008), and structural complexity can influence competition and predation (e.g., Hixon and Beets 1993), the effect of disturbances on the recovery of degraded reefs may be determined by disturbances that differentially or in combination modify both coral cover and structural complexity (Graham et al. 2011a).

The presence of living coral tissue is considered by many to be a critical factor in shaping patterns of recruitment or early postsettlement survivorship (Beukers and Jones 1998, Öhman et al. 1998, Holbrook et al. 2000). Conversely, structural complexity is important in increasing survivorship of larval fishes, providing increased number of refuge sites from predators and competitors (Syms and Jones 2000) and some authors perceive that live coral is largely irrelevant, except in providing habitat diversity (Lindahl et al. 2001, Garpe et al. 2006). Ultimately, both coral cover and topographic complexity may both be critical elements of coral-reef habitats, although they may influence different components of reef fish assemblages (Graham et al. 2009). This study used experimental manipulations to examine the recruitment of fishes to patch reefs with varying levels of live coral cover and structural complexity, to test the relative importance of these two features of coral habitats in modifying the structure of fish assemblages.

6.3 Methods

6.3.1 Study location and experimental design

Experimental patch reefs were constructed on a shallow sand flat situated in the lagoon behind an exposed reef flat at Lizard Island (LI) on the Great Barrier Reef, Australia (14^{o} 41’S, 145^{o} 27’E). All patch reefs were constructed from four species of live and recently dead (algal covered) but still structurally intact branching corals (*Acropora nasuta, Acropora formosa* (Fam. Acropoidae), *Pocillopora damicornis* (Fam. Pocolloporidae) and *Porities cylindrical* (Fam. Poritidae)) from nearby reefs. Coral species were the same on all reefs because studies have shown that coral diversity can influence the diversity and abundance of fishes on reefs (Munday et al. 1997, Messmer et al. 2011). These four species of corals were selected for their high abundance on surrounding reefs as well as their high susceptibility to both physical and biological disturbances (e.g., cyclones, crown of thorns, bleaching) (Marshall and Baird 2000). All reefs were 1m^{2} and constructed with an equal volume of rubble base and live and dead coral structure. Reefs were constructed to six different treatments of high, medium and low coral cover crossed with high and low structural complexity. The six treatments are labelled as; High H, High L, Med H, Med L, Low H and Low L with High, Med and Low representing three levels of coral cover and H and L representing high and low complexity respectively. A block design was used where each of the six treatments were replicated five times and mixed across the sand flat. All reefs were first constructed as high complexity reefs and then reefs were selected as low complexity treatments were physically degraded with the use of a hammer and chisel until the desired complexity was achieved. Patch reefs were situated in two rows running parallel to the reef crest at a depth of approximately 3m. Patch reefs were 10m apart and 30-50m from the nearby reef edge.

To confirm distinct differences in coral cover and structural complexity at the start and throughout the course of the experiment, measurements of coral cover and substrate composition were made using a 100 point grid on an aerial photograph to calculate a percentage cover. Coral cover for the three levels were: High = 56.5% (SE +/- 2.0), Med = 33.5 (SE +/- 2.0) and Low = 10.6 (SE +/- 0.9). Substrate was recorded as live coral, algal, soft coral, sand and rubble. Habitat complexity was measured by recording the height of the reef at five random points (Wilson et al. 2007), rugosity as the linear distance covered by a 3m chain fitted to the patch reef contour (replicated 3 times) (Risk 1972), and the number of refuge holes (diameters <5cm, 5-10cm, >10 cm) (Graham et al. 2003) of each individual patch reef (Table 1).

Table 6.1: Measurements of habitat complexity for high and low complexity patch reefs (mean ± SE).

	High	Low
Height (cm)	43.5 ± 2.4	19.6 ± 0.7
Rugosity (m)	0.71 ± 0.03	0.48 ± 0.01
Holes <5cm	185 ± 15	123 ± 10
Holes 5-10cm	23 ± 2	35 ± 6
Holes >10cm	12 ± 1	14 ± 1

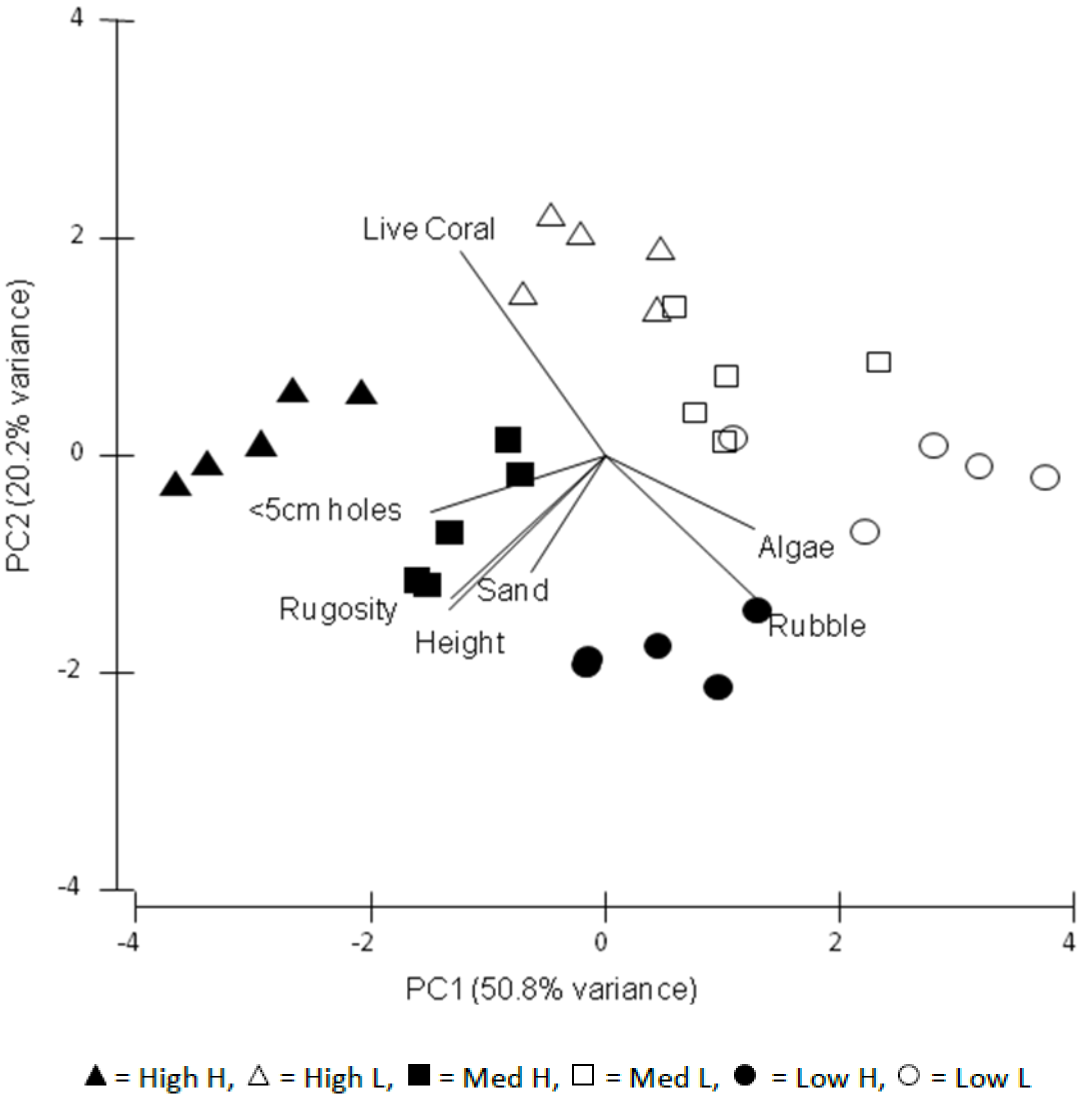

Figure 6.1: Separation of six groups of patch reefs based on coral cover and structural complexity indices. Each symbol represents an individual patch reef.

To display measures of patch reef complexity and composition, measures of rugosity, refuge holes (<5 cm), reef height and benthic composition were entered into a Principal Component Analysis (PCA), based on correlation matrices (Figure 6.1). High and low complexity patch reefs fall out separately with high complexity reefs containing higher levels of rugosity, sand, number of small holes and reefs were also higher. Patch reefs were also separated on a gradient driven by levels of live coral cover, algae and rubble.

6.3.2 Surveys

Fish surveys were conducted periodically on scuba from 13th November through to 14th December. All patch reefs were constructed a few days before surveying commenced and were devoid of fish upon construction. For all patch reefs, recently recruited fish that were visible were counted and identified to species. Fish were classified as recruits by their size and lack of pigmentation. Because recruitment of fishes at LI is patchy in time, reefs were surveyed approximately every two days over this period to try and capture all species of fishes recruiting to the different patch reefs. During this period the majority of fish recruit to the reefs and settle during the night (Victor 1991) and I attempted to capture that recruitment the following day. Patch reefs were all surveyed nondestructively by visual recording on the same day by the same observer for consistency (DJC). Reefs were surveyed in three stages; i) from a distance of ≈ 3m to capture shy species as well as fish swimming in the water column and around the fringes of the reefs, ii) from the immediate edge of the reef to record the majority of species residing on the reefs, and iii) reefs were searched intensively with the aid of an underwater torch to capture fishes within the intrinsic structure of the reef framework. Each reef was surveyed until no new individuals were identified and the reef had been meticulously searched (approx 10 mins per reef). Although this method may not capture cryptic species, most species would be captured visually and any missed species would be consistent among treatments. Due to the high numbers (approx 1000) of Apogoniidae that would recruit and school above some of the patch reefs they were omitted from analyses as they would significantly skew the data.

6.3.3 Analysis

To examine common indices of fish assemblages among the different reef treatments, abundance and species diversity were compared over the survey period by repeated measures ANOVAs (RMANOVA) in SPSS V19. Measures of abundance and diversity (Shannon diversity index *H'*) for each survey were effectively paired and a repeated measure was undertaken. Sphericity, assumptions of normality and homogeneity of variance were examined using residual analysis. Following RMANOVA a Tukey's HSD was conducted to explore significant differences among the six reef treatments. Ordination analysis was performed in PRIMER V6. Data were square root transformed to down weight highly abundant fishes. The final five survey dates were used to represent the most advanced community of juvenile fishes and because Bray Curtis values and an exploratory multi-dimensional scaling (MDS) plot indicated that dissimilarities in fish communities were greater between time intervals early on in the experiment than towards the end. This MDS plot of the final five survey dates was fitted with similarity slices grouping patch reefs with 70 and 75 Bray-Curtis similarity of reef fish community composition based on a hierarchical clustering analysis (Clarke 1993). All differences were analysed using ANOSIM to assess statistical difference among the treatments. SIMPER was run on the last five surveys to assess which species of fish were driving the differences and ranked in order according to their contribution (%) to the difference. From this the species that contributed accumulatively 50% of the differences were plotted as vectors to illustrate the differences according to the six different treatments.

6.4 Results

6.4.1 Patch reef indices

Across the 30 patch reefs I recorded a total of 75 species of fishes from 23 families by the end of the survey period. There were some significant differences in the accumulation of fishes among the treatments (F=23.842, df=5, P<0.001) but differences attributable to coral cover versus structural complexity were not consistent through time (Figure 6.2A). Overall abundance was higher on reefs with high coral cover and low complexity (High L) with the highest abundance recorded at the end of the survey period (mean 136.6 +/- 31.3 SE) and lowest on low coral cover and high complexity (Low H) with the greatest abundance recorded at the end of the survey (mean 91.6 +/- 14.5 SE). Abundance for both treatments was significantly different (P<0.05) to the other five habitat treatments based on Pairwise comparisons. Significant differences were also detected among the six treatments for species diversity over time (F=4.954, df=5, P=0.013) (Figure 6.2B). This difference was driven by patch reefs with high coral cover and high complexity (High H) showing significantly higher species diversity compared to all other treatments (P<0.05, Pairwise comparisons). The difference among treatments was variable through time and was particularly apparent during surveys conducted on the 4th, 6th and 8th of December where diversity was higher on high coral cover and high complexity (High H).

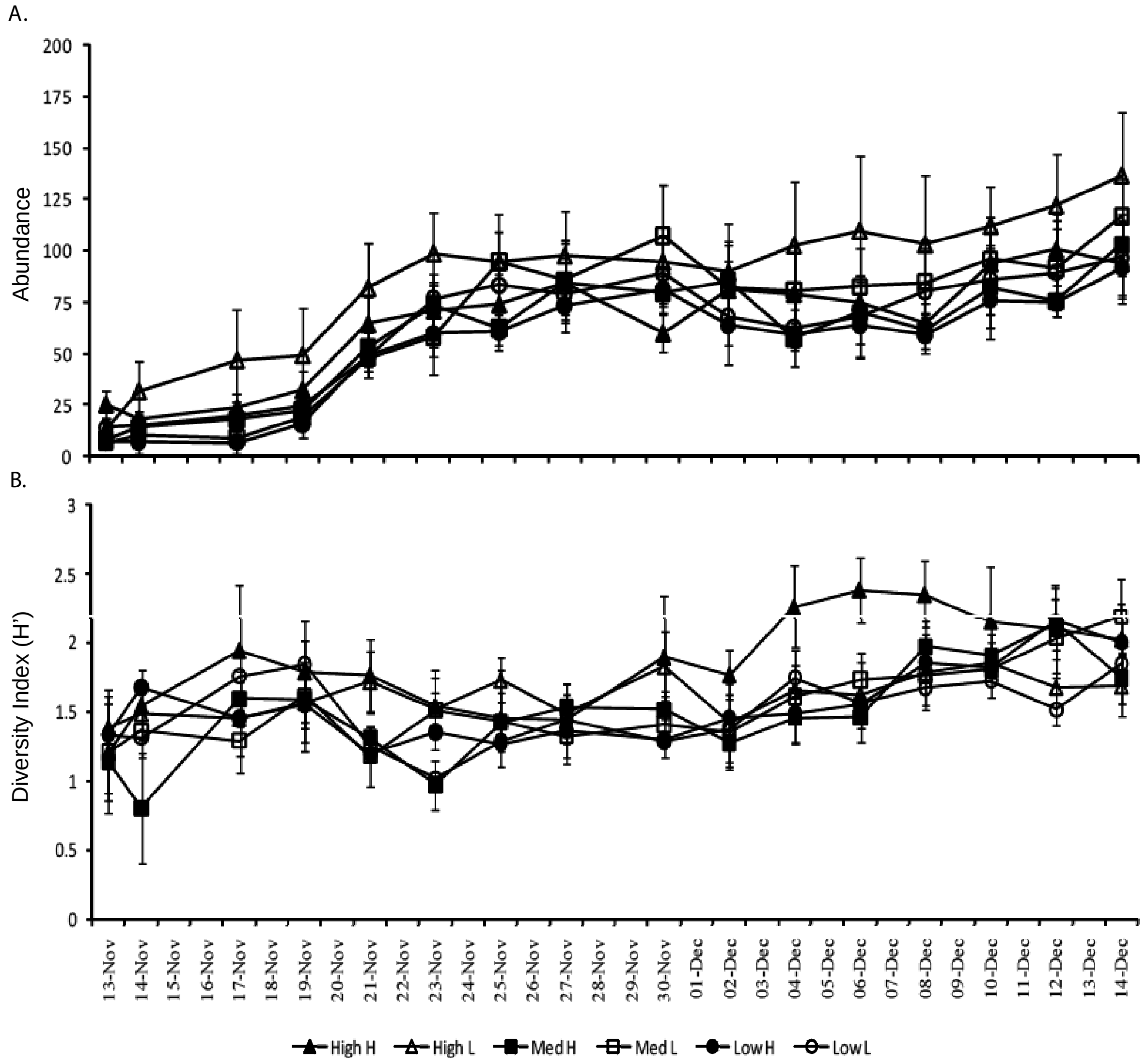

Figure 6.2: Changes in mean (+/-SE) fish A abundance and B Shannon diversity index (H') associated with six patch reef treatments over time.

6.4.2 Patch reef fish communities

The MDS plot of the fish community composition shows clear differences among the treatments where hierarchical agglomerative clustering (70% and 75% similarity) groups replicates within habitat treatments (Figure 6.3A). An ANOSIM test of difference in community structure between the six treatments where an R value of 0 states that there is no difference between groups, while an R value of 1 states that between-group differences are larger than all within-group differences (Clarke and Warwick 2001), revealed strong

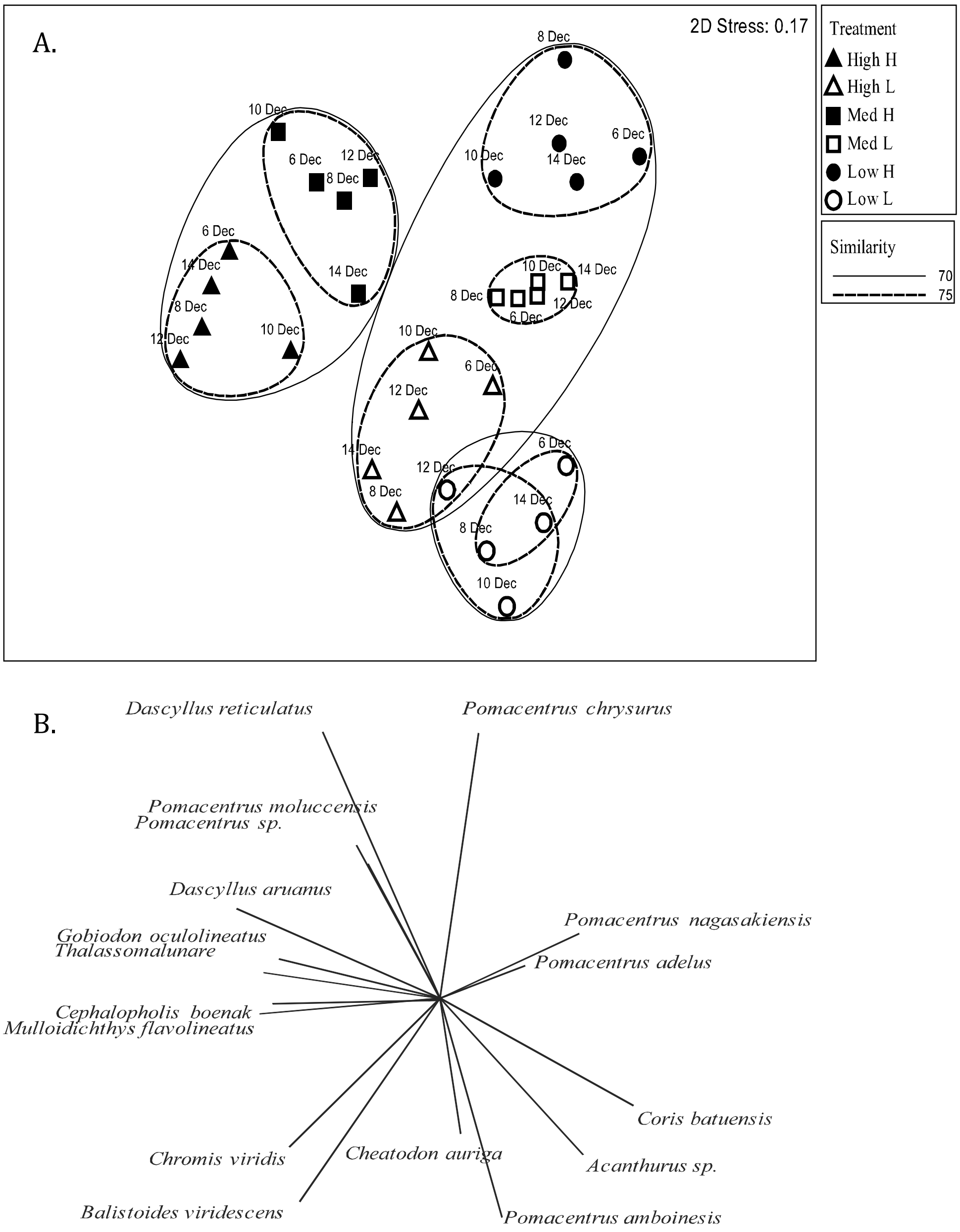

Figure 6.3: Last five surveys following community stability. A Bi-plot of first two components of PCA with 70 and 75% similarity groups showing a clustering of patch reefs based on fish communities. B Eigenvectors of fish species (top 50% contribution), using the same Bray Curtis similarity matrix as used for panel.

differences between treatments of high, medium and low coral cover (R= 0.95, P<0.001) and high and low complexity (R=1, P<0.001). SIMPER analysis results of species contribution (%) to these dissimilarities in communities between treatments showed that the species contributing accumulatively 50% of the differences were associated with different reef treatments (Figure 6.3B). SIMPER yielded 17 species that clearly discriminated between coral cover and habitat complexity, with nine species from the family Pomacentridae contributing to the list (Figure 6.3B). Of the species contributing to the differences, 82% were associated with reefs with high or medium coral cover, including *Dascyllus aruanus, D. retriculatus, Gobiodon oculolineatus, Pomacentrus sp.* and *P. moluccensis*. Conversely, there were three species associating with low coral cover reefs: *Acanthurus sp., Pomacentrus amboinensis* and *P. chrysurus*. One piscivore, *Cephalopholis boenak* and a common species of goatfish (*Mulloidichthys flavolineatus*) were associated with reefs of high coral cover and complexity showing a dependence of live coral cover at recruitment. Species contributing to differences based on the complexity of the reefs were: *Chaetodon auriga, Coris batuensis, Pomacentrus adelus, P. amboinensis* and *P. nagasakiensis*.

6.5 Discussion

Scleractinian corals are the fundamental habitat-forming organisms on coral reefs and it is well known that adult stages of many reef fishes are critically dependent on live corals for food and shelter (Munday et al. 2008, Pratchett et al. 2008a). This study shows that live coral is also important in the recruitment of many reef fishes, significantly expanding on the number of fishes that appear to be reliant on live corals. Previous studies have shown that live coral is an important settlement substrate for fishes that rely on corals as adults (Booth and Beretta 2002, Feary et al. 2007a, Pratchett et al. 2008b, McCormick et al. 2010). This study revealed that differences in fish abundance and species diversity among treatments were fairly subtle and not consistent through time, probably due to underlying stochasticity in recruitment patterns and differential survivorship. However, the abundance of fishes was highest on patch reefs with high coral cover and low complexity reefs, while diversity was highest on patch reefs with high coral cover and high complexity. This suggests that levels of live coral cover have a stronger influence on abundance and diversity than the complexity of the reef. Similarly, Caley and St John (1996), with the use of artificial reefs, found that changes in structural complexity of habitat had no effect on the abundance of new recruits, while other studies have revealed differences in abundance driven by live coral cover (Feary et al. 2007a, McCormick et al. 2010). For cryptobenthic reef fish, Bellwood et al. (2006) found that extensive coral loss through bleaching had no effect on abundance or diversity. For our study the observed differences among habitat treatments were not consistent through time. Due to this inconsistency I cannot confidently say that coral cover or habitat complexity influences fish abundance or species diversity. Some of this variation in abundance and species diversity could be due to fluctuations in recruitment over time and post-settlement processes (Sweatman 1983, 1985, Cowen 1985, Booth 1992).

While I found small fluctuating differences in abundance and diversity among treatments, it is important to also understand species composition among treatments. Marked variation in the composition of fish assemblages associated with each of the distinct treatments was present and largely attributable to higher abundances of coral-dependent species on patch reefs with high coral cover. Over half of the species contributing to the difference were planktivorus damselfish (Fam. Pomacentridae) with coral-dependent species associating with reefs of high and medium coral cover and high complexity, and rubble associated species clustering with low coral cover and low complexity reefs. This shows that these fishes have the same habitat requirements at settlement as they do in adulthood. Interestingly I found a common piscivore and a goatfish associated with high coral cover and high complexity even though both these fishes are not dependent on live coral as adults. This result suggests that these fishes depend on live coral for shelter or possibly prey attracted to this habitat, and that live coral is important for fishes at settlement even if they do not depend on it later in life. Fish communities recruiting to reefs with low levels of live coral cover and structural complexity were significantly different than those recruiting to reefs with high levels of live coral cover and structural complexity and these treatments were dominated by a similar species complex that generally dominates as adults (Wilson et al. 2008a). This suggests that coral dependent and some non-coral dependent fishes will not recruit in high numbers to reefs with low coral cover and structural complexity and will not replenish and replace existing species or species that declined from disturbances.

Notable differences in the abundance of fishes among experimental treatments, may be driven by settlement preferences of fishes (Gutièrrez 1998), or differential survivorship on patch reefs with high versus low coral cover, and high versus low complexity. Habitat characteristics have a strong influence on juvenile fishes and settling to unsuitable habitat could result in significant effects on growth and survivorship through increased predation, competition or a decline in essential food resources (Caley and St. John 1996, Beukers and Jones 1997, Munday 2001, Feary et al. 2009). Therefore, the persistence and survivorship of juvenile fish on reefs needs to be monitored through time. Furthermore, some reef fishes undergo ontogenetic shifts in habitat as they grow, with some species dependent on live corals during their early juvenile stage but become less dependent as adults (Jones et al. 2004, Feary et al. 2007a, Pratchett et al. 2008b). Further monitoring of patch reefs such as those used in this study would be necessary to answer questions regarding the persistence of fishes post-settlement and through to adulthood based on ontogenetic shifts, competition (intaspecific, interspecific) and mortality through predation and/or lack of essential resources (food, shelter).

On coral reefs, certain functional groups (e.g, herbivorous fishes) play an important role in conserving ecosystem function and resilience of coral reef habitats (Bellwood et al. 2004, Graham et al. 2011b). Herbivorous fishes are of great importance in enhancing ecosystem resilience by regulating abundance of macroalgae, which might otherwise inhibit settlement, and growth of coral recruits (Hughes et al. 2007, 2010). In this study I found only one species that contributed to differences in community structure that plays an important role in ecosystem function. A common herbivore *Acanthurus sp.* (Fam. Acanthuridae) was found to have strong associations with patch reefs that have low coral cover and low complexity, suggesting that recruitment of this species will be resilient to most major episodes of coral loss and habitat degradation. If this species also survives to adulthood, it may help play a role in reducing algae on these reefs and facilitate the return of live coral by reducing competition between algae and coral recruits. While one species might have limited capacity in promoting the recovery of reefs, particularly if they only form one functional group, the scale of the patch reefs may not have provided adequate space for other functionally important species to be recorded. Furthermore, this survey was only undertaken for 1 month and therefore I may not have captured the recruitment of other important functional species.

Declines in coral cover and structural complexity on reefs following disturbances vary dramatically depending on pre-disturbance levels and the magnitude of the impact. While some intact reefs have upwards of 95% coral cover (Sano 2004) levels of around 50% are more common (Sheppard et al. 2002). The levels of coral cover and structural complexity on our patch reefs represent realistic levels with respect to healthy, moderately and substantially impacted reefs. This study found that with changes in coral cover of 23% and 46%, differences in fish composition were significantly different. Although these communities were different, treatments with low coral cover and low complexity still supported similar numbers of fish and diversity to other treatments. While low coral cover treatments had only 10.6% coral cover and low complexity treatments were significantly degraded this might be enough to support some species that depend on live coral for recruitment. Ultimately there will be a threshold where reefs degrade to a point where their condition affects the recruitment of some fish species. Therefore further degradation of our reefs to zero coral cover and pavement (flat substrate) would further increase our understanding of how disturbances will impact the recruitment of reef fishes and the importance of live coral and structural complexity.

Results from this study suggest that declines in coral cover and structural complexity will not necessarily lead to declines in overall abundance and species diversity despite coral cover being 81% lower on low coral cover reefs than high coral cover reefs and structural complexity being significantly lower. Differences were found in species composition with the use of multivariate ordination techniques, illustrating the importance of investigating changes in species composition with habitat changes and not just basic population indices. Differences in communities are driven by coral dependent fishes associating with reefs of high and medium coral cover and high complexity and rubble associated fishes associating with heavily degraded reefs. Furthermore, two non-coral dependent species were found associated with high coral cover reefs showing the importance of live coral for fishes that are non-obligately coral dependent as adults.

Globally coral reefs are experiencing an increase in the frequency and severity of a range of disturbances resulting in significant degradation of the benthos. This study shows that fishes will recruit and settle to degraded reefs in high numbers and high diversity following coral degradation, but that these fish communities will be significantly different compared to healthy complex reefs. These results suggest that recruiting fish communities following reef degradation will shift in composition and are unlikely to reflect pre-disturbance communities unless coral cover recovers. It is not clear from our study how longer-term survivorship of species may vary among the different treatments examined here. Some species may settle to degraded habitats but either show ontogenetic shifts or increased mortality through a lack of essential resources. It is also unclear how these changes will influence the delivery of ecosystem functions, which should be a priority area for future research.

Chapter 7: General Discussion

Scleractinain corals are a key component of coral reef habitats providing both physical and biological structure for a large number of reef fishes. This relationship means that declines in coral health, abundance and diversity has a significant impact on the communities of fishes that associate with coral reefs (Graham et al. 2006, Wilson et al. 2006, Munday et al. 2007, Pratchett et al. 2008a). While links between disturbances and reef fishes have been studied in depth, we still lack knowledge of what species are associating with live coral habitat, and why. Approximately a quarter of all marine fish species are reported to associate with coral reefs (Spalding et al. 2001). For many coral reef fishes, live coral is an important resource providing food, habitat, recruitment cues (Sweatman 1985, Munday 2002, Cole et al. 2008) and helping to mediate predation and competition interactions (Beuker and Jones 1997, Munday 2001, Holbrook and Schmitt 2002,). For reef fishes, the strength of dependence ranges from highly specialist fishes (Munday 2004, Pratchett 2005) through to fishes that rarely associate with live coral (Sano et al. 1984, Wilson et al. 2008a). While many of these coral-dwelling fishes suffer declines in abundance following significant coral bleaching events, the processes driving this have only been until now speculated on (Wilson et al. 2006, Pratchett et al. 2008a).

7.1 Corals as habitat

Documenting the relationship between reef fishes and live corals is essential for understanding the ramifications of ongoing coral loss and coral reef degradation occurring throughout the world (Gardner et al. 2003, Bellwood et al. 2004, Bruno and Sleig 2007). Previous estimates of the number of fishes that will be adversely affected by extensive coral loss are limited to those species within an obligate association with living corals for food (Cole et al. 2008) or habitat (Jones et al. 2004, Munday et al. 2007). It has been estimated that 9-11% of fishes are obligately dependent on live corals for food or shelter (Pratchett et al. 2008a), but these estimates are incongruent with the range of fishes that exhibit declines in abundance following extensive coral loss (Pratchett et al. 2011a). Loss of live coral cover and habitat degradation has a significant impact on the abundance and diversity of coral reef fishes (Graham et al. 2006, Wilson et al. 2006). In a meta-analysis of 17 independent studies, 62% of reef fishes declined in abundance following a decline in coral cover of >10% (Wilson et al. 2006). This is most evident for small bodied coral-dwelling and coral-feeding reef fishes. While some short-term studies reveal variation in fish diversities and often a lag response (Pratchett et al. 2004, Graham et al. 2007), long term studies explicitly show declines in fish abundance and diversity decline across a range of fish taxa (Jones et al. 2004, Garpe et al. 2006, Graham et al. 2006, Cheal et al. 2008).

Documented declines in the abundance of fishes following extensive coral loss point to diverse associations between reef fishes and scleractinian corals, but it is also clear that the number of fishes that rely on corals (e.g., for habitat) has been greatly underestimated. This thesis combined global evidence from published literature and field based surveys to establish that at least 8% of coral reef fishes from around the world (320 of 4000 sp.) have been recorded living on or in scleractinian corals (Chapter 2). While this expands on the number of species known to associate with live coral for habitat, this proportion is only an absolute minimum due to a lack of fish and coral association knowledge. It is possible that this proportion is greatly higher due to the number of species that are affected by declines in coral cover (see Jones et al. 2004, Wilson et al. 2006, Pratchett et al. 2008). Moreover, many of the fishes that utilise live coral habitat are among the most abundant fishes on coral reefs (e.g., damselfishes). The majority of fishes associate with structurally complex habitats (e.g., branching, table, and corymbose growth forms), mostly from the genus *Acropora* and family Pocilloporidae (Chapter 2), which strongly suggests that these fishes are utilising coral habitats mainly to evade predators. Predation on small reef fishes is often mediated by structurally complex habitats whereby small fishes shelter within the refuge spaces and move between the small gaps and holes in the structure (Syms and Jones 2000). If however, small reef fishes are reliant on host coral colonies simply for the physical structure they provide, it seems that these fishes would be unaffected by the loss of live coral tissues (e.g., due to climate-induced coral bleaching), at least in the short term. Following bleaching, dead coral colonies remain physically intact for at least 2-4 years (Pratchett et al. 2008a), after which, natural decomposition and erosion of the exposed carbonate will greatly reduce structural integrity.

7.2 Corals as predation refugia

The relative importance of live coral cover versus topographic complexity is critical to understanding the effects of coral loss on coral reef fishes (Wilson et al. 2006). While some types of disturbances (e.g., severe tropical storms) simultaneously reduce both live coral cover and topographic complexity, coral bleaching will remove the live coral tissue but leave structural complexity unchanged in the short term (e.g., Sano et al. 1987, Wilson et al. 2006). Despite this, coral bleaching has been shown to have rapid and dramatic effects on a range of coral-dwelling fishes (Feary et al. 2007b), whereby fishes decline in abundance on bleached corals long before any change in structural integrity. Two theories have been presented to explain this phenomenon. Either fishes may move as soon as the health of the host corals has been compromised because they are pre-empting the ultimate loss of habitat structure, or live corals are more effective predator refuges than dead coral colonies with equivalent structure. This study showed that a common coral-dwelling fish *Dascyllus aruanus* do indeed experience an increase in predation intensity immediately after hosts corals are bleached (Coker et al. 2009, Chapter 3). This can be attributed to increases in the visual appearance of these fishes on bleached versus healthy coral colonies. This is because coral-dwelling fishes associated with host colonies that have reduced or absent pigmentation elicit more strike rates than fish associated with pigmented healthy and algal covered colonies (Coker et al. 2009, Chapter 3).

Experimental tests of actual predation rates on fishes associated with live, bleached, dead and algal covered coral colonies showed that survivorship was always highest on live coral hosts (Coker et al. 2009, Chapter 3). Interestingly, the lowest survivorship was observed for fish associating with algal covered habitat while strike rates were recorded to be equal to healthy habitats. While coral-dwelling fishes may be less visually vulnerable to predators on algal covered habitats, as colonies die, algae, sponges and other invertebrates begin to colonise the skeleton and the amount of refuge spaces diminish further increasing their risk to predators. This finding may suggest that an increase in predation risk associated with bleached and recently dead corals maybe contributing to the documented declines in abundance of coral-dwelling fishes post bleaching (e.g., Wilson et al. 2006, Munday et al. 2008, Pratchett et al. 2008a) through *in situ* mortality as well as providing motivation for fishes to vacate their degraded host colony. It also proposes that fish either actively avoids algal covered colonies because they no longer offer adequate protection (difficulty to access and shelter within the branches) or are removed through predation

7.3 Movement among coral habitats

While it is often assumed that rapid declines in the abundance of damselfishes on bleached or dead coral colonies are attributable to increased rates of *in situ* mortality (presumably due to predation), it is also possible that fishes leave degraded coral colonies and recolonise alternative coral hosts. Bleaching events are often patchy, with marked variation in the timing or extent of bleaching within and among different coral species (Marshall and Baird 2000). If coral-associated fishes were able to relocate to alternative healthy coral hosts then this would greatly increase their resilience to acute disturbances, such as coral bleaching. Explicit tests of movement among coral colonies revealed that *D. aruanus*, will remain associated with bleached host colonies, but will rapidly vacate host corals when the colony dies (Coker et al. 2012b, Chapter 4). Displaced fishes nearly always colonised corals that already supported one or more conspecifics, rather than occupying seemingly suitable and healthy (and often closer) coral colonies that were unoccupied (Coker et al. 2012b, Chapter 4). As such, movement and recolonisation of coral-dwelling damselfishes will be strongly influenced by inter-specific competition for coral hosts.

In the absence of any disturbances, coral-dwelling damselfishes mostly remain closely associated with a single coral host, and co-existence among conspecifics is maintained through a size-based hierarchy of social status (Sale 1972, Coates 1980, Forrester 1991). When displaced from their original coral hosts and attempting to join other groups of conspecifics, damselfishes are met with intense resistance from established resident individuals (Coker et al. 2012b, Chapter 4). In experimental tests of relocation with *D. aruanus*, only 12 out of 66 fishes (18%) were successful in gaining entry into a new group of conspecifics (Chapter 5). Within the group, hierarchy functions as a queue for subordinates waiting to move into breeding status (Buston 2004, Mitchell 2005, Wong et al. 2007).

Therefore, smaller individuals may be more successful compared to larger individuals because they are further down the breeding hierarchy and therefore pose less of a threat to resident individuals for breeding status. Aggression towards intruding individuals was not displayed by the entire group or from just the largest dominant resident but from one or two individuals that were similar or slightly larger in size to the intruding fish (Chapter 5). This suggests that aggression towards these coral-dwelling fishes is driven by resource competition (e.g., shelter site, breeding rank) and not just a group territorial response. Similarly, Holbrook and Schmitt (2002) found that less aggressive individuals can be displaced to less desirable habitats where they are more susceptible to predators. Therefore, fishes that are excluded from joining a new group may be forced to occupy nearby vacant colonies where they will be more vulnerable to predators without the added security of group members. While group members aggressively defend against intruding foreigners, this study found that even after a group member had been removed for up to 48 hours, the remaining members would readily accept them back into the group. Therefore, if group members vacate a degraded host coral and relocate to the same colony but at different times, then they will readily re-establish their group. Survivorship for relocating fishes is predicted to be extremely low on reefs because competing for habitat would expose individuals to predators and if unsuccessful they may have to associate with less favourable habitats that could result in lower growth rates and even higher levels of predation.

7.4 Corals as recruitment habitat

Scleractinian corals provide an essential habitat for many species of reef fishes (Chapter 2) but even fishes that do not live on or in live corals appear to benefit from good coral growth (e.g., Lindahl et al. 2001, Bellwood et al. 2006, Wilson et al. 2006). For example, many fishes that do not otherwise live in corals utilise live corals at settlement, presumably to evade predators (Leis and Carson-Ewart 1999). As such, live corals are essential for recruitment, recovery and replenishment of fish populations. I recorded a total of 75 species of fishes from 23 different families recruiting to experimentally constructed patch reefs including species that do not otherwise use coral habitats as adults (Coker et al. 2012a, Chapter 6). These patch reefs may be used not only because they are comprised of live coral, but also because they are topographically complex.

While studies have looked at the independent influence of changing live coral cover and structural complexity (e.g., Caley and St John 1996, Booth and Beretta 2002, Feary et al. 2007b, McCormick et al. 2010) little is known how a combined effect of these two disturbances impact the recruitment of fishes. Changes in live coral cover (high, medium, low) and structural complexity (high, low) had little effect on the abundance and diversity of associated newly recruited fish communities but had marked affects on species composition. Differences in communities were driven by coral dependent fishes recruiting to reefs of high and medium coral cover and high complexity while rubble associated fishes recruited to heavily degraded reefs (Coker et al. 2012a, Chapter 6). In addition we found some fishes that are not coral dependent as adults contributing to differences for high coral cover reefs. This shows that some fishes may depend on live coral for recruitment, even if they show no obvious dependence on live coral as adults. There is also the possibility that this range of species is much greater than observed in this study. This shows that pre disturbance fish communities will not recover until the recovery of live coral habitats.

7.5 Conclusions

This thesis emphasises the importance of live coral in providing live coral habitat and topographic complexity for many small species of fish. Branching and table morphologies are used disproportionally more than other coral types, presumably because they provide an increased number of small refuges among the matrix of branches and under large horizontal structures (Kerry and Bellwood 2011). These morphologies are especially important in the replenishment of fish communities through providing a valuable settlement site for new recruits. Fish species that associate with live coral habitat as adults, and some non-coral dependent species, settle to reef sites with high levels of live coral cover. With a significant proportion of fishes associating will live coral for habitat, impacts to coral cover will have pronounced effects on abundance, diversity and functional structure of reef fish communities (Bellwood et al. 2006, Graham et al. 2006, Wilson et al. 2006, Messmer et al. 2011, Pratchett et al. 2011a). While topographic complexity of habitats appears to play a critical role in maintaining fish communities, changes in predation rates on coral-dwelling fishes occur before the demise of structural complexity. Furthermore, coral-dwelling fishes will vacate their host colony once devoid of living tissue cover. This reveals that live coral habitats are more important for these fishes than just providing physical habitat structure.

Habitat loss represents the greatest impact to reef fishes and compounds on fishes that are already exposed to a range of other disturbances. While climate change posses a considerable threat through climate induced coral bleaching, other impacts are also reducing live coral cover (disease, predatory starfish) and topographic complexity (tropical storms). Importantly, climate change and other acute disturbances are already producing changes in the structure of coral assemblages (e.g., Reigl 1999, Pratchett et al. 2011b), which may have significant effects on reef fishes long before extensive loss of all habitat-forming corals.

While many fishes are versatile enough in their habitat use to associate with multiple species of corals, the vast majority of these key habitat forming species are highly susceptible to disturbances (Marshall and Baird 2000, Madin and Connolly 2006). Key habitat species (e.g., *Acropora* spp.) will be replaced by relatively less susceptible habitats (e.g., *Favia* spp. *and Porities* spp.). Not only will coral dependent fishes decline, it is also expected to have a flow on effect to larger predatory fishes that depend on these fishes for prey.

This study emphasises the value of intact coral habitats for reef fish assemblages and the importance of live coral cover and structural complexity in maintaining reef fish communities. In order to conserve reef fish communities, it is crucial that measurements are implemented to protect essential features of habitat structure (e.g., complexity) and key habitat species (e.g., *Acropora* spp.) from further degradation. Managing the effects of climate change is a global task but managing other local threats to coral reefs should include reducing terrestrial disturbances (e.g., pollution, sedimentation), protecting functionally important fish species (e.g., parrotfishes) and banning any activities that degrade reef benthos (e.g., destructive fishing, anchoring). Coral loss through climate-induced changes and pre-existing natural stresses is already occurring and needs to be reversed in order to maintain reef fishes and associated fisheries.

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Appendix:

Appendix 2.1: Reference numbers and corresponding references (author, year).

	Corresponding reference	No.	Corresponding reference	No.	Corresponding reference
1	Allen and Randall 1980	39	Gratwicke et al. 2006	77	Munday et al. 2003
2	Allen et al. 1991	40	Gutierrez 1998	78	Munday et al. 2004
3	Allen and Randall 1993	41	Herler 2007	79	Myers 1999
4	Allen et al. 2003	42	Hiatt and Strasburg 1960	80	Nilsson et al. 2007
5	Almany 2004	43	Hixon and Jones 2005	81	Nanami & Nishihira 2002
6	Bean et al. 2002	44	Hobson 1974	82	Nanami et al. 2005
7	Bellwood et al. 2006	45	Hoey and McCormack, 2004	83	Ohman et al. 1998
8	Belmaker et al. 2007	46	Holbrook and Schmitt 2002	84	Oritz and Tissot 2008
9	Belmaker et al. 2008	47	Holbrook et al. 2000	85	Ormond et al. 1996
10	Bergman et al. 2000	48	Itzkowitz 1977	86	Patton 1994
11	Beuker and Jones 1997	49	Jennings et al. 1996	87	Pratchett et al. 2008
12	Bonin 2012	50	Johnson et al. 2011	88	Pratchett et al. 2011
13	Bonin et al. 2009	51	Jones 1988	89	Randall 2005
14	Booth 2002	52	Kane et al. 2009	90	Randall et al. 1997
15	Booth and Beretta 1994	53	Karplus et al. 2006	91	Sale et al. 1984
16	Booth and Beretta 2002	54	Kent et al. 2006	92	Sale et al. 2005
17	Booth and Beretta 2004	55	Kerry et al. unpublished data	93	Schmitt and Holbrook 1997
18	Buston 2003	56	Kumamura et al. 1994	94	Schmitt and Holbrook 1999
19	Buston and Cant 2006	57	Lassig 1976	95	Shpigel and Fishelson 1986
20	Chabanet et al. 1995	58	Lecchini 2003	96	Shulman 1984
21	Danilowicz et al. 2001	59	Lecchini 2005	97	Srinivasan 2002
22	DeMartini and Donaldson 1996	60	Lecchini 2006	98	Sweatman 1983
23	DeMarini and Anderson 2007	61	Lecchini and Galzin 2005	99	Sweatman 1985
24	DeMartini et al. 2010	62	Lecchini et al. 2006	100	This study
25	Dirnwober and Herler, 2007	63	Lecchini et al. 2007	101	Thompson et al. 2007
26	Ebersole 1985	64	Lieske and Myers 1994	102	Tolimieri 1995
27	Feary 2007	65	Limbourn et al. 2007	103	Tolimieri 1998
28	Feary et al. 2007	66	Lirman 1994	104	Tyler 1971
29	Feary et al. 2009	67	Lirman 1999	105	Walsh 1983
30	Fishelson et al. 1974	68	Losey 2003	106	Webster 2002
31	Fowler 1988	69	McCormick 1994	107	Williams 1978
32	Forrester 1991	70	McFarland 1980	108	Williams and Sale 1981
33	Fricke 1980	71	Messmer et al. 2011	109	Williams et al. 2009
34	Gardiner and Jones 2005	72	Munday 2000	110	Wilson 2001
35	Gardiner and Jones 2010	73	Munday 2001	111	Wilson et al. 2008
36	Garpe and Ohman 2007	74	Munday 2002	112	Wilson et al. 2010
37	Geange and Stier 2009	75	Munday et al. 1997	113	Wong et al. 2008a
38	Gonzalez et al. 2006	76	Munday et al. 1999	114	Wong et al. 2008b

Other papers published during my candidature:

Pratchett, M.S., **Coker D.J**., Jones G.P., Munday P.L. (2012) Specialization in habitat use by coral reef damselfishes and their susceptibility to habitat loss. Ecology and Evolution doi: 10.1002/ece3.321

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