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Patterns of microhabitat specialization and the consequences of coral degradation for coral-associated reef fishes

Thesis submitted by

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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 *National Statement on Ethics Conduct in Research Involving Human (*1999*),* the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997)*,* the *James Cook University Policy on Experimentation Ethics*. *Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001). The proposed research methodology received clearance from the James Cook University Experimentation Ethics Review Committee (approval number A1221).

Signature

Date

STATEMENT OF CONTRIBUTION OF OTHERS

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GENERAL ABSTRACT

Habitat loss is occurring at unprecedented rates in many ecosystems of the world and is considered a primary cause of the current extinction crisis. Species that are specialized on only a narrow range of habitats have been identified as highly susceptible to population decline and extinction in the face of habitat loss. On coral reefs, disturbances such as coral bleaching and tropical cyclones have already caused significant degradation to habitat-forming corals. Predictions that these disturbances will increase in frequency and intensity as a result of climate change have therefore raised concerns about the persistence of corals and the species that rely on them as habitat. This thesis uses a combination of observational and experimental research to investigate patterns of coral microhabitat specialization among reef fishes and examine the consequences of coral degradation for coral specialists.

Although the potential threats to coral-dependent reef fishes are widely acknowledged, the degree of coral specialization is still unknown among one of the most ubiquitous and abundant families of fishes on coral reefs, the Damselfishes (Pomacentridae). In Chapter 2, I used high taxonomic resolution surveys of coral microhabitat use and availability to provide the first species-level description of patterns of coral selectivity and specialization among recruits of 10 spp. of damselfish. In addition, surveys of the relative bleaching susceptibility of 16 common branching coral species are used to determine which of these critical recruitment microhabitats are at highest risk of decline as a result of chronic coral bleaching. The microhabitat use surveys revealed that four of these damselfish species—*Chrysiptera parasema*, *Pomacentrus moluccensis*, *Dascyllus melanurus* and *Chromis retrofasciata*—are highly vulnerable to the loss of branching coral habitats due to their specialized microhabitat requirements. More than 85% of recruits of all four species used only *Acropora*, *Pocillopora* and *Seriatopora* corals as microhabitat and these recruits primarily associated with only 2-4 coral species. The bleaching

surveys revealed that many of the fine-branching corals typically selected by these specialized recruits are also the microhabitats at highest risk of severe bleaching and mortality. The most severely susceptible coral species, the bottlebrush *Acropora subglabra*, suffered at least 40% mortality due to bleaching. This coral species is one of the preferred recruitment microhabitats of the specialist *C. parasema*, suggesting that this damselfish species in particular is likely to experience significant loss of critical habitat.

Coral bleaching is becoming an increasingly common disturbance on coral reefs that can lead to the degradation and loss of critical recruitment microhabitats. In Chapter 3 I examine the immediate effects of host coral degradation and mortality on the recruitment and persistence of coral specialist fishes during a natural coral bleaching event in Kimbe Bay, Papua New Guinea. Healthy (i.e. unbleached), severely bleached, and dying colonies of corymbose *Acropora* were tagged along the reef crest and the settlement and persistence of specialized *P. moluccensis* recruits were compared over time. Equal numbers of *P. moluccensis* settled to both healthy and severely bleached colonies during a settlement pulse, suggesting that recruits do not, or cannot, avoid settling onto microhabitats that are degraded by bleaching. The post-settlement persistence of these recruits was similar on healthy and bleached colonies over the next four weeks, although the frequency of recruit retention was significantly lower on corals that died from bleaching compared to both healthy and severely bleached colonies. The persistence of adult pairs of specialized coral-dwelling gobies (*Gobiodon* spp.) was also monitored throughout the bleaching event and the response to coral degradation was similar to that of *P. moluccensis* recruits. Gobies persisted in host corals that were severely bleached and only vacated these colonies when more than 50% of the colony had died. These results suggest a degree of resistance to the early stages of coral degradation in the coral associated fish community—coral specialists recruited to and persisted in microhabitats disturbed by bleaching. However the mortality of host corals clearly poses a problem for these specialists, highlighting the importance of live coral tissue as a critical feature of their microhabitat.

Competition for space is likely to play an increasingly important role in determining the local distribution and abundance of species in degraded coral reef environments, yet little is known about how these interactions influence recruit survival. In Chapter 4 I investigate the effects of intra- and interspecific competition for microhabitat space on early post-settlement survival in two different microhabitats. Observations of recruit microhabitat use in Chapter 2 revealed that two of the specialists, *C. parasema* and *D. melanurus*, both commonly occur on structurally complex bottlebrush *Acropora* but only *D. melanurus* occurs on less complex *Pocillopora* microhabitats. I hypothesized that competition with *D. melanurus* excludes *C. parasema* recruits from occupying *Pocillopora* corals, and that the higher complexity of bottlebrush *Acropora* microhabitats allows these competitors to co-exist. These predictions were tested using a patch reef experiment in which the density of intra- and interspecific competitors was manipulated on both *Acropora* and *Pocillopora* reefs and the survival of recruits was monitored over 5 days. Both microhabitat and interspecific competition significantly influenced the survival of recently settled *C. parasema*, although the effects of competition were not modified by the microhabitat on which they occurred. The presence of interspecific competitor *D. melanurus* significantly reduced survival of *C. parasema* recruits on both *Acropora* and *Pocillopora* reefs, whereas increasing conspecific densities did not negatively affect survival. Microhabitat had an even stronger effect on *C. parasema* survival than interspecific competition. In the absence of *D. melanurus*, only 25% of *C. parasema* recruits survived on *Pocillopora* reefs compared to 85% survival on higher complexity bottlebrush *Acropora*. These results suggest that the primary reason *C. parasema* rarely occurs on *Pocillopora* microhabitats is high predator-induced mortality, not competitive exclusion. Higher complexity bottlebrush *Acropora* microhabitats provided *C. parasema* recruits with much greater protection from predators and the results of this study suggest that these recruits are unlikely to outcompete other species for space in these critical microhabitats if they become scarce.

Numerous disturbances, including coral bleaching, can result in the loss and fragmentation of coral habitats. Although habitat loss is clearly expected to have negative consequences for the associated fish community, the potential effects of habitat fragmentation are not well understood. The aim of Chapter 5 was to examine the independent and interactive effects of habitat loss and fragmentation on the survival of *C. parasema* recruits, as well as the abundance and species richness of other coral specialized recruits. To achieve this aim, 20 *C. parasema* recruits were transplanted to each of 30 large experimental reefs that offered 1 m^2 of bottlebrush *A. subglabra* habitat. Following a 1 week acclimation period, these coral habitats were experimentally manipulated and the response of the fish community was monitored over the next four months. As expected, few *C. parasema* recruits survived on reefs with 75% habitat loss and these reefs also accumulated the lowest abundance and richness of other recruits over the four months following disturbance. In contrast, separating the experimental reefs into three equal fragments did not have negative effects on *C. parasema* survival and resulted in significantly higher abundance and species richness of other recruits relative to the control reefs. These positive effects of fragmentation were at least four times stronger than the negative effects of habitat loss in the first six weeks following disturbance, and were most pronounced on reefs in which 75% of the coral habitat had been lost. I hypothesize that these positive fragmentation effects arise due to the separation of competitors onto discrete habitat fragments, which effectively reduces competition for shelter space within and between species. The loss of coral habitats due to disturbance will clearly have significant consequences for the survival of *C. parasema* recruits and the recruitment and diversity of other coral specialists. Habitat fragmentation, on the other hand, may actually buffer against the negative effects of habitat loss and contribute to the resistance of reef fish populations to declines in habitat availability.

This thesis provides the first report of patterns of species-level associations between damselfishes and the corals they use as recruitment microhabitat and has revealed that the level of coral specialization exhibited by some damselfish recruits is on par with that observed in other highly coral-dependent fishes (e.g. coral gobies, butterflyfishes). These coral specialists will be highly sensitive to declines in the availability of critical recruitment microhabitats brought about by chronic disturbance, and this project has highlighted several mechanisms likely to cause population declines among coral specialists in degraded reef habitats. Foremost among these is increased competition over the few remaining high quality recruitment microhabitats, which may lead to the eventual demise of species that are poor competitors. Future research into patterns of coral specialization among a wider range of coral reef fish species as well as into the sub-lethal consequences of coral degradation will significantly improve our understanding of the consequences of habitat loss on reef fish communities.

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CHAPTER 1: GENERAL INTRODUCTION

The importance of habitats for species persistence

One of the fundamental goals of ecology is to understand associations between organisms and their environment (Ehrlich and Roughgarden 1979; Putman and Wratten 1984). A key component of an organism's environment includes the local habitat – the biotic and abiotic features that support critical resources including food, shelter and sites for reproduction (Bell et al. 1991). Because certain habitats provide higher quality resources than others, variations in the structure and dynamics of habitats are likely to have a direct influence on the distribution and abundance of species (Pagel et al. 1991; Pulliam et al. 1992; Venier and Fahrig 1996). Moreover, the configuration of available habitat patches can also have an important impact on species distribution and abundance (Hanski 1999; Flather and Bevers 2002). Finally, the range of suitable habitats occupied by a species may also be influenced by interspecific interactions among organisms that use the same habitats (Rosenzweig 1991). Some habitats that have all the resources required by a species may therefore remain unoccupied due to the negative effects of predation (Paine 1974; Werner et al. 1983) or competition (Connell 1961; Hairston 1980). Changes in the availability and configuration of critical habitats may therefore significantly influence demographic processes and ultimately impact species persistence.

Habitat availability and quality are in decline in almost every ecosystem on the planet as a result of human activities (Vitousek et al. 1997). Half of the world's tropical forests have been destroyed, and these ecosystems are home to more than two-thirds of all terrestrial species (Pimm et al. 2001). Habitat loss has also been extensive in temperate grasslands, Mediterranean forests and freshwater ecosystems (Hoekstra et al. 2005; Revenga et al. 2005). Such degradation of habitats leads not only to habitat loss but habitat fragmentation as well, and this loss and fragmentation of habitats is considered the primary cause of the current extinction crisis (Brooks et al. 2002; Dirzo and Raven 2003). As a result of the extinction crisis, a major goal of conservation biology in recent years has been to identify the traits that put a species at risk following habitat degradation. Habitat specialization has been identified as a key trait that increases vulnerability to extinction (Julliard et al. 2004; Koh et al. 2004; Safi and Kerth 2004). Consistent with theory (e.g. McKinney 2007), specialists seem to be less able to adapt to rapidly changing environmental conditions, while the greater flexibility of generalist species makes them less vulnerable to changes in habitat availability and configuration. Although habitat specialization may have once been an ecological strategy that provided a species with a competitive edge (Futuyma and Moreno 1988), in this era of extensive habitat destruction it is now more likely to be a hindrance than a boon.

Habitat degradation, habitat specialization and extinction risk in coral reef fishes

Coral bleaching, crown-of-thorns starfish outbreaks, tropical cyclones and increased sedimentation are just a few of the numerous disturbances currently degrading coral reef habitats across the world. As a consequence of these disturbances, 20% of the world's coral reefs have already been damaged beyond repair and 50% of the remaining reefs are threatened with the same fate if disturbances continue (Wilkinson 2004). It is currently estimated that one third of all reef-building corals now face an elevated risk of extinction due to climate change, making corals one of the most at-risk groups of animals in the world (Carpenter et al. 2008). Coral bleaching is undoubtedly one of the most concerning disturbances impacting corals and as a result of bleaching we are already beginning to see shifts in coral community structure due to the greater susceptibility of certain coral taxa (Marshall and Baird 2000; Loya et al. 2001). Ironically, many of the coral taxa that are highly susceptible to bleaching (e.g. *Acropora*, *Seriatopora*, and *Pocillopora* spp. corals) are also important microhabitats for the coral reef fish community. Given the degradation to coral habitats that we have already observed (Wilkinson 2004; Baker et al. 2008) and the predicted rise in the frequency and intensity of disturbances that cause coral loss in the decades to come (Donner et al. 2005; Emanuel 2005; Hoegh-Guldberg et al. 2007) it has now become critical to understand how degradation to corals will impact on reef fish communities.

Although dependence on corals for microhabitat and sites for settlement appears to be common across a wide range of reef fishes (Pratchett et al. 2008), the degree of specialization on particular coral microhabitats is still unknown for the vast majority of coral reef fish species, despite the fact that this information is likely to be important in predicting their vulnerability to habitat loss. This gap in knowledge exists in large part because the metrics historically used by researchers to survey coral reef habitats are well not suited to the investigation of fine-scale patterns of microhabitat association. Many studies have used very broad microhabitat groupings in which corals are categorized by growth form (e.g. branching, tabular, massive) rather than taxon (e.g. Ault and Johnson 1998a; Wilson et al. 2008). This method inherently assumes that all branching or tabular corals provide equivalent microhabitat to fishes, although this is unlikely to be true given the significant variation in structure among coral species. The few studies that have examined fish-coral microhabitat associations in greater detail have revealed that abundance and distribution of specialized fishes is largely determined by the availability of their preferred microhabitats (Holbrook et al. 2000; Munday 2002). Further high resolution studies of the specific microhabitat requirements of reef fishes are urgently needed to understand their susceptibility to habitat change.

Observed population declines of coral specialists following habitat degradation underscore the importance of understanding patterns of microhabitat specialization in reef fishes.

Although most coral-associated species decline in abundance to some extent in response to habitat degradation, species that are highly specialized in their use of resources can suffer much greater population declines compared to species with more generalist patterns of resource use (Pratchett et al. 2008). For example, coral-dwelling gobies from the genus *Gobiodon* are known to be highly dependent on particular *Acropora* species as microhabitat (Munday 2000) and following extensive coral degradation in Kimbe Bay, Papua New Guinea the abundance of the *Gobiodon* spp. that used the widest range of coral species declined by ~50%, whereas the *Gobiodon* spp. that used the smallest range of corals went locally extinct (Munday 2004). Such localized extinctions may be stepping stones on the path to global extinction for species with very specialized microhabitat requirements.

The consequences of habitat degradation for coral-associated reef fishes

Coral bleaching is one of the primary causes of coral reef habitat degradation and it is well established that bleaching-induced habitat loss can cause declines in the abundance of coral-associated reef fishes (Booth and Beretta 2002; Jones et al. 2004; Bellwood et al. 2006). However we know very little about the underlying causes of these declines or how habitat bleaching itself influences basic demographic processes. Coral reef fish populations are replenished through the settlement of new individuals from the plankton, and it is possible that this habitat disturbance actually disrupts the recruitment process. Although laboratory choice experiments suggest that naïve larvae have the innate ability to distinguish between live and dead coral microhabitats and may avoid settling into dead corals (Öhman et al. 1998; Feary et al. 2007a), it is unknown whether settlers avoid bleached corals or how this type of habitat degradation influences early post-settlement persistence. If settlers do avoid colonizing corals that are degraded by coral bleaching or if they experience lower persistence in these degraded microhabitats, this could have serious implications for the replenishment of reef fish populations in disturbed environments.

As coral microhabitats become increasingly scarce due to chronic disturbances such as coral bleaching, competition is likely to play an increasingly important role in determining the local abundance and distribution of species. Newly-settled recruits face a high risk predation (Almany and Webster 2006) and certain coral microhabitats afford better protection from predators than others (Beukers and Jones 1997). Competition for shelter space in these high quality microhabitats may therefore lead to reductions in the abundance of inferior competitors. Although there is some evidence that competition for shelter space can influence the distribution and abundance of adult coral reef fishes (Munday et al. 2001; Holbrook and Schmitt 2002), its potential effects on recruit abundance and distribution have rarely been demonstrated (but see Schmitt and Holbrook 1999). Moreover, the outcome of competition may be influenced by the underlying microhabitat structure, with some species dominant in certain microhabitats but subordinate in others (Ebersole 1985). However, very few studies have investigated how microhabitat influences competitive interactions between coral reef fishes. Research into the effects of competition for shelter on early post-settlement survival and the influence of microhabitats in mediating competitive interactions is imperative if we are to understand how changes in habitat availability will affect reef fish communities.

Disturbances on coral reefs will eventually cause both habitat loss and increased fragmentation of the remaining coral habitat and numerous studies have documented declines in fish abundance following disturbances that reduce live coral cover (Wilson et al. 2006). However, it is unclear whether these declines in fish abundance occur due to a reduction in the amount of habitat available, increased habitat patchiness, or a combination of both these factors. The only study to separate the effects of habitat loss and fragmentation for coral reef organisms suggests that while coral loss causes rapid declines in abundance and species richness, coral fragmentation may not negatively impact coral-associated species (Caley et al. 2001). In fact, experimental fragmentation of host coral colonies significantly increased the abundance of trapezid crabs that could persist on a standard amount of habitat (Caley et al. 2001). The impacts of habitat fragmentation on coral reef fish abundance and diversity remain to be seen, however if effects are positive this could have important implications for the conservation and management of coral-associated reef fish communities on degraded coral reefs.

Research Aims and Thesis Structure

The overarching aim of this thesis is to provide new insights into the effects of habitat degradation on coral specialist reef fishes that will improve the conservation of these at-risk species in an era of increasing coral reef degradation. Although all data chapters are related in this common goal, each is written as a stand-alone publication. Damselfishes (Pomacentridae) were chosen as the focal family for this research because they are ubiquitous and abundant members of coral reef fish communities and have been identified as particularly vulnerable to coral degradation due to their widespread use of branching corals as habitat and settlement sites (Pratchett et al. 2008). It is estimated that more than half of the coral reef fish community is reliant on corals as settlement sites (Jones et al. 2004; Wilson et al. 2006). Insights gained from studying the effects of coral degradation on damselfish recruits are therefore likely to extend to the numerous other fish on coral reefs that rely on corals as recruitment microhabitat. The specific aims of this thesis are to:

1. *Describe patterns of coral microhabitat specialization among coral-associated damselfish recruits and examine the susceptibility of these microhabitats to degradation from coral bleaching.*

2. *Examine the effects of host coral bleaching on the settlement and early post-settlement persistence of coral specialist fishes.*
3. *Investigate the influence of intra- and interspecific competition for microhabitat space on early post-settlement survival.*
4. *Examine the independent and interactive effects of habitat loss and fragmentation on the survival, abundance and species richness of recruitment-stage coral-associated reef fishes.*

In Chapter 2, I use high taxonomic resolution surveys of the availability and use of coral microhabitats to document the degree of coral specialization among recruits of 10 damselfish species. In these surveys branching corals are identified to species-level, and therefore provide the first reports of species-level associations between damselfish recruits and corals. In addition, I also present the first information on relative bleaching susceptibility of 16 common species of branching coral that represent important recruitment microhabitats for coral reef fishes. Using this information, I am able to identify the species of damselfish and corals that are at greatest risk of population decline as a result of chronic coral bleaching. Recruits of three of these vulnerable species—*Chrysiptera parasema*, *Pomacentrus moluccensis* and *Dascyllus melanurus*—are then used as focal species in subsequent chapters to investigate the effects of coral degradation.

Chapter 3 describes an observational study in which I monitor host corals *in situ* over two months throughout a thermally-induced coral bleaching event to document the effects of host coral bleaching and mortality on the associated fish community. This bleaching event coincided with a settlement pulse for *P. moluccensis*, allowing me the unique opportunity to investigate whether coral bleaching disrupts the settlement of this coral specialist and also examine the effects of microhabitat bleaching and mortality on early post-settlement persistence. In addition, I compare the persistence of adult pairs of coral specialist gobies between healthy, bleached and dead colonies over seven weeks. As the first to take place during rather than after a natural bleaching event, this study provides novel insights into the immediate effects of coral bleaching on the coral-associated fish community.

Chapter 4 is a manipulative patch reef experiment which examines the influence of intra- and interspecific competition for shelter space on the survival of specialized *C. parasema* recruits. *Dascyllus melanurus* recruits are used as an interspecific competitor due to their similar coral microhabitat preferences. In this study, competitor density treatments are also cross-factored with two different coral species in order to investigate the influence of the underlying microhabitat on the outcome of competition. I hypothesize that differential mortality from predators is the cause of observed differences in the survival of recruits on reefs with different competitor and coral treatments and highlight the importance of early post-settlement interactions in determining patterns of microhabitat use.

The final chapter (Chapter 5) is based on an experiment designed to separate the effects of habitat loss and habitat fragmentation on the survival of juvenile *C. parasema*. This was carried out by manipulating the quantity and configuration of *Acropora subglabra* on large experimental patch reefs. This species of bottlebrush coral is a preferred microhabitat of *C. parasema* recruits and is also highly susceptible to severe bleaching and mortality (Chapter 1). I also monitor the abundance and species richness of other coral-associated species that recruit to the reefs during the 4-month study period. Consequently, this study enhances understanding of how changes to the amount and arrangement of coral microhabitats will influence the replenishment of coral-associated fish communities in disturbed reef environments.

CHAPTER 2: SPECIALIZATION BY CORAL-ASSOCIATED DAMSELFISHES ON THE GENUS *ACROPORA* AND THEIR VULNERABILITY TO BLEACHING

2.1 ABSTRACT

Coral reef habitats are increasingly being degraded and destroyed by a range of disturbances, most notably climate-induced coral bleaching. Habitat specialists, particularly those associated with susceptible coral species, are clearly among the most vulnerable to population decline or extinction. However, the degree of specialization on coral microhabitats is still unknown even for one of the most ubiquitous, abundant and well-studied of coral reef fish families - the damselfishes (Pomacentridae). Using high taxonomic resolution surveys of microhabitat use and availability, this study provides the first species-level description of patterns of coral microhabitat association and selectivity among recruits of 10 spp. of damselfish in order to determine their vulnerability to coral habitat degradation. In addition, surveys of the relative bleaching susceptibility of 16 common branching coral species revealed which recruitment microhabitats are at highest risk of decline as a result of chronic coral bleaching. Two of the damselfishes (*Pomacentrus nigromanus* and *Neopomacentrus asyzron*) were found to be microhabitat generalists and therefore considered most resistant to habitat degradation. Four other species (*Amblyglyphidodon leucogaster*, *A. curacao*, *Chromis ternatensis* and *Pomacentrus aurifrons*) were considered susceptible to declines in reef structural complexity due to their reliance on microhabitats with complex structure. Recruits of the remaining four species (*Chrysiptera parasema*, *Pomacentrus moluccensis*, *Dascyllus melanurus* and *Chromis retrofasciata*) were identified as highly vulnerable to live coral degradation due to their specialized associations with relatively few coral species. The bleaching surveys revealed that five species of *Acropora* were

highly susceptible to coral bleaching, with more than 50% of colonies either severely bleached or dead. Two of these highly susceptible coral species were the preferred recruitment microhabitats of specialized *C. parasema* recruits, placing this species at greatest risk of local extinction. Careful monitoring of populations of these specialized damselfishes and the coral microhabitats on which they depend are necessary for the conservation of these species as disturbance to coral reef habitats becomes more frequent.

2.2 INTRODUCTION

Habitat specialization, whereby species depend upon only a narrow range of habitats for their livelihood and survival, is an ecological strategy employed by a wide range of organisms (Pianca 1966; Rosenberg 1990; Svenning 1999; Matthews and Mazumder 2006). Through specialization, species in their preferred habitats benefit by having a higher survival or fitness, and competitive advantage over generalist species (Caley and Munday 2003). There are also inherent costs associated with being a habitat specialist. Specialization is believed to evolve during periods of long-term environmental stability (Futuyma and Moreno 1998; Kassen 2002), and the evolution of specific behaviors or physical traits that facilitate specialization inevitably make it impossible to switch to alternative habitats if the preferred habitat becomes scarce or unavailable (Futuyma and Moreno 1988). Consequently, in the current era when natural habitats are increasingly being degraded and destroyed, habitat specialization has become a key predictor of population decline and extinction risk (Julliard et al. 2004; Koh et al. 2004; Munday 2004; Safi and Kerth 2004). A full appreciation of this risk depends not only on an organism’s degree of habitat specialization, but also the degree to which specific habitats are under threat.

Degradation and loss of critical habitats is occurring at unprecedented rates in many ecosystems of the world and coral reefs are a prime example (Knowlton 2001; Wilkinson 2004). Healthy coral reefs offer a great diversity of microhabitats (e.g. coral species) and many coral-associated species have become specialized on a narrow range of coral microhabitats (Munday 2000; Gardiner and Jones 2005; Srinivasan 2006; Wilson et al. 2008). However corals are increasingly threatened by thermally-induced mass coral bleaching as a result of climate change (Carpenter et al. 2008) and variation in bleaching susceptibility among coral taxa is expected to cause significant changes in the composition of coral habitats. A shift away from communities dominated by branching corals to those dominated by massive and encrusting corals of less structural complexity has been predicted due to the higher susceptibility to bleaching among branching corals (Marshall and Baird 2000; Loya et al. 2001).

The loss of branching *Acropora* is of particular concern because these structurally-complex corals typically dominate coral assemblages (Wallace 1999) and are major habitat providers for coral reef fishes (Bellwood et al. 2004; Wilson et al. 2006). Although *Acropora* are more susceptible to mass bleaching than many other coral taxa (Marshall and Baird 2000; McClanahan et al. 2004), communities of these fast-growing corals are often able to recover relatively quickly (e.g. within 5 yrs) following disturbance (Baker et al. 2008). Despite this, the predicted increase in frequency and severity of mass bleaching events (Sheppard 2003; Donner et al. 2005; Hoegh-Guldberg et al. 2007) combined with the vulnerability of *Acropora* to other disturbances such as tropical storms, *Acanthaster planci* outbreaks and coral diseases, may jeopardize the ability of these communities to recover from chronic disturbance events. As a consequence of these multiple threats, ~50% of all *Acropora* species now have an elevated risk of extinction according to IUCN Red List criteria (Carpenter et al. 2008). Although little is known about the variation in response to thermal anomalies among *Acropora* species, certain growth forms appear to be more susceptible to bleaching than others (Marshall and Baird 2000).

Species-level information on the relative bleaching susceptibility of these important habitat providers would improve our ability to predict the effects of chronic bleaching on coral assemblages and also the reef fishes that depend on coral resources.

Declines in live coral cover and the loss of branching *Acropora* clearly pose a threat to reef fishes that depend on corals for food, habitat or settlement sites (Wilson et al. 2006). However the response to declines in coral cover may vary among coral-associated fishes, with species that use only a limited subset of available coral species suffering greater declines than those with a wider niche breadth. For example, following coral depletion caused by an *Acanthaster* outbreak on the Great Barrier Reef, butterflyfish species that fed on less than 20 coral taxa suffered greater declines in abundance than those that used more than 40 different corals (Pratchett et al. 2008). Similarly, in Kimbe Bay, Papua New Guinea, a 59% decline in *Acropora* abundance between 1997 and 2003 due to the combined impacts of coral bleaching and increased sedimentation caused declines in the abundance of coral-dwelling gobies that were contingent on the degree of *Acropora* specialization among these species (Munday 2004). The most generalist goby in its use of available *Acropora* species exhibited the smallest decrease in abundance, whereas the species that used the narrowest range of *Acropora* spp. became locally extinct (Munday 2004). This evidence suggests that species-level coral specialization and selectivity can be important predictors of the response to habitat change among coral-dependent reef fishes. Highly specialized and selective species are likely to be most sensitive to changes in the availability of their preferred corals, whereas less-selective species may be more resistant to changes in the coral assemblage because they can use alternative microhabitats. The extent of the threat to specialized fishes depends upon which coral species are preferred and which are most at risk.

On Indo-Pacific reefs, it is estimated that between 9-11% of species across 16 coral reef fish families are directly reliant on live corals for food, shelter or settlement sites (Jones et al.

2004; Munday et al. 2007; Pratchett et al. 2008). Among these coral-dependent reef fishes, the damselfishes (Pomacentridae) have been identified as particularly vulnerable to declines in coral cover due to the widespread use of branching corals as habitat and settlement sites within this family (Pratchett et al. 2008). Despite the enormous attention that has been given to damselfish ecology (see Sale 1991, 2002), the degree of species-level coral selectivity, and therefore potential susceptibility to population decline as a result of habitat loss, has yet to be examined. Perhaps because of the challenges associated with identifying corals in the field, previous studies have typically categorized corals by genus or growth form when describing patterns of microhabitat use among damselfishes (e.g. Ault and Johnson 1998a; Holbrook et al. 2000; Srinivasan 2006; Wilson et al. 2008). Although these studies are useful in identifying general patterns of microhabitat association, they lack the taxonomic resolution necessary to distinguish differences in species-level coral specialization among damselfish species or species-specific responses to coral loss.

The purpose of this study was to examine the relative susceptibility of damselfish species to habitat change, by documenting and relating (1) the species-level coral habitat preferences of coral-associated damselfishes, and (2) the bleaching susceptibility of branching coral species commonly used as microhabitat by reef fishes. Despite the potential for important insights into the effects of bleaching-induced habitat degradation on reef fish communities, this is one of the first studies to relate information on habitat preferences with the vulnerability of preferred habitats to bleaching (also see DeMartini et al. 2010). The present study focused on recently settled recruits because this life history phase is a known population bottleneck for coral reef fishes during which the risk of mortality is high (Doherty et al. 2004; Almany and Webster 2006). Habitat characteristics appear to be extremely critical for survival during this vulnerable life history stage (Jones et al. 2004) and the habitat requirements of juvenile damselfishes are also likely to be more specialized than those of adults (Wilson et al. 2008).

The 10 damselfish species examined—*Amblyglyphidodon curacao*, *A. leucogaster*, *Chromis retrofasciata*, *C. ternatensis*, *Chrysiptera parasema*, *Dascyllus melanurus*, *Neopomacentrus azysron*, *Pomacentrus aurifrons*, *P. moluccensis* and *P. nigromanus*—are all common species in Kimbe Bay (PNG) that associate with live coral throughout their lives, although the degree of reliance on coral microhabitats appears to vary between species. First, I described patterns of broad microhabitat use among recruits of these species to establish their dependence on live coral and ability to use alternative microhabitats. I then conducted high taxonomic resolution surveys of the availability and use of *Acropora* species to determine which coral species are selected or avoided as recruitment habitat. Finally, I present data on relative bleaching susceptibility among branching coral species and compare this information with the microhabitat preferences of recruits to improve predictions of the effects of bleaching-induced *Acropora* decline on coral-associated damselfishes.

2.3 METHODS

This study was conducted in Kimbe Bay, a large sheltered embayment on the northern coast of the island of New Britain in Papua New Guinea (5°30'S, 150°05'E). This bay is located within the Coral Triangle, the world's epicenter of marine biodiversity, and more than 70 species of *Acropora* have been identified at this location (Wallace 1999). The Museum of Tropical Queensland holds a collection of skeletal specimens and field photographs of *Acropora* species from Kimbe Bay, and this museum collection was used as a reference to verify identifications of *Acropora* species at the study site.

2.3.1 Microhabitat use and availability surveys

Surveys of microhabitat use and availability were conducted on both the exposed and sheltered side of six near-shore platform reefs. At each of the 12 survey sites, four 50 m transects were laid along the reef slope at 2, 6, and 10 m to demarcate a 200 m section of reef. Habitat availability was quantified by identifying the substratum under 100 randomly placed points along each transect. Substratum was classified as one of eight microhabitat categories: 1) *Acropora* spp. coral, 2) *Pocillopora* or *Seriatopora* spp. coral, 3) other branching or foliose coral, 4) massive or encrusting coral, 5) soft coral or gorgonian, 6) branching sponge, 7) other complex substrate, or 8) other flat substrate. When *Acropora*, *Seriatopora*, or *Pocillopora* spp. corals occurred under a point the colonies were further identified to species level and the growth form was also recorded for *Acropora* spp. (sensu Wallace 1999). The 200 m section of reef was then systematically searched for damselfish recruits by swimming in a zigzag pattern from the 10 m transect line up to the 2 m transect line. Recruits were only included in the survey if they were estimated to have settled within the previous three weeks based on their body size. When a recent settler was located, the microhabitat category and/or coral species it occupied was identified as described above. When a conspecific group of recruits was encountered, the microhabitat occupied by the group was recorded as a single data point to ensure independence of microhabitat use data.

2.3.2 Broad patterns of microhabitat association

Resource selection ratios (Manly et al. 2002) were calculated for each microhabitat category to determine if any were used more or less frequently than expected based on their availability using the formula:

$$\widehat{w_i} = \frac{o_i}{\pi_i}$$

where o_i is the proportion of recruits occupying microhabitat type i, and π_i is the proportion of microhabitat type i available. Data from the microhabitat use surveys were pooled across reefs to calculate proportional habitat use. Microhabitat availability data were pooled across depths and exposures to estimate percent cover for each reef and the mean of the six reefs was used in selection ratio calculations. To allow multiple comparisons between microhabitat types, a Bonferroni-corrected 95% confidence interval was calculated for each selection ratio using the formula:

$$Z_{\alpha/2I}\sqrt{\left\{\frac{o_i\,(1-o_i\,)}{u_+\pi_i^2}\right\}}$$

where $Z_{\alpha/2I}$ is the critical value of the standard normal distribution, $\alpha=0.05$, I=number of substratum categories, and u_+ is the total number of recruits for which microhabitat use was recorded. A 95% confidence interval spanning values less than 1 or containing the value 1 would indicate that the microhabitat was avoided or used in proportion to its availability, respectively. A 95% confidence interval spanning values greater than 1 would indicate selectivity for that microhabitat. In this study, the terms “selected” and “avoided” refer to the abundance of recruits on particular microhabitats and do not necessarily indicate direct selection or avoidance behavior (also see Discussion).

2.3.3 Selectivity and specialization on *Acropora* spp.

Smith’s measure of niche breadth (Smith 1982) was used to assess the relative degree of specialization on *Acropora* spp. among the 10 species of damselfish:

$$FT = \sum_{i=1}^{R}\sqrt{(p_i}q_i)$$

where, p_i is the proportion of recruits using coral species *i*, q_i is the proportion of coral species *i* available, and R is the total number of *Acropora* spp. This measure ranges in value from 0 (most specialized) to 1 (least specialized). It takes into account resource availability and has the advantage of being less sensitive to the use of highly rare or highly abundant resources compared to other common niche breadth measures (Krebs 1999). Resource selection ratios with Bonferroni-corrected 95% confidence intervals were then used to determine which *Acropora* spp. were selected or avoided by recruits. Although surveys documented a total of 32 *Acropora* species available for use as recruitment habitat, 12 of these coral species were excluded from analyses because they were extremely rare. *Acropora* spp. were excluded if they occurred under less than 15 points in total across all sites and reefs during habitat availability surveys, therefore covering less than 0.1% of the substratum. The data for the 20 most abundant *Acropora* spp. was pooled across transects, exposures and reefs to estimate proportional availability (π_i) and use (o_i) in selection ratio calculations.

2.3.4 Bleaching susceptibility among branching coral species

Surveys of bleaching susceptibility of different coral species were conducted during a natural coral bleaching event in Kimbe Bay in April 2008. The study took place at one of the six reefs that was used in microhabitat use and availability surveys. Bleaching surveys targeted 16 species of branching coral and included 10 of the *Acropora* spp. used in the selectivity analyses. All colonies of these target species larger than 10 cm in diameter were counted and bleaching severity assessed along six 50 x 1 m belt transects on both the reef crest (2m) and upper slope (6m). Bleaching severity was scored on a four-point scale similar to that used by Marshall and Baird (2000): (1) Unbleached = healthy colony with no visible loss of color, (2) Moderately Bleached = 1-50% of colony affected or entire colony pale, (3) Severely Bleached = 51-100% of colony with strong pigmentation loss (includes bleached colonies with partial mortality) and (4) Dead = recently killed colony covered by light algal overgrowth.

2.4 RESULTS

2.4.1 Broad patterns of microhabitat association

The microhabitats used by a total of 3118 damselfish recruits were recorded during the microhabitat use surveys. Recruits of all 10 damselfish species were selective for *Acropora*, although proportional use and selectivity for the other microhabitat categories varied considerably among species. Four species—*C. parasema*, *P. moluccensis*, *D. melanurus* and *C. retrofasciata*—were categorized as obligate coral-dwellers because they rarely used any other substratum except branching hard corals as recruitment habitat (Table 2.1). *Pomacentrus moluccensis* and *C. parasema* were particularly selective for *Acropora*, with more than 80% of recruits observed using this microhabitat, whereas *D. melanurus* and *C. retrofasciata* recruits also used branching *Pocillopora* and *Seriatopora* microhabitats in significant proportions.

In contrast to the obligate branching coral-dwellers, *C. ternatensis*, *P. aurifrons*, *A. curacao* and *A. leucogaster* recruits utilized a wider range of microhabitats and were selective for branching sponges and/or soft corals in addition to branching hard corals (Table 2.1). At least 75% of *C. ternatensis* and *P. aurifrons* recruits used branching hard corals, although they used other branching coral genera more often than *Acropora*, *Pocillopora* and *Seriatopora* (Table 2.1). In addition to using *Acropora*, 30% of *A. leucogaster* recruits used branching sponges and 20% of *A. curacao* used soft corals. However all four of these species avoided low complexity massive and encrusting coral microhabitats, and were therefore described as complex microhabitat dwellers (Table 2.1).

Table 2.1 Proportional use and selectivity for broad microhabitat categories among recruits of 10 species of coral-associated damselfish. Table values represent the percentage of recruits observed in each microhabitat category. Selection for a particular microhabitat is indicated by (+), avoidance by (A), and use in proportion to availability by (=) based on resource selection ratios and their Bonferroni-corrected 95% confidence intervals.

	n	*Acropora* corals	*Seriatopora* & *Pocillopora* corals	Other branching corals	Branching soft corals	Branching sponges	Massive & encrusting corals	Other complex	Other flat
Obligate branching coral-dwellers									
C. parasema	540	83.7^{+}	5.7^{+}	9.4^{A}	0	0.6^{A}	0	0.4^{A}	0.2^{A}
P. moluccensis	383	83.3^{+}	11.8^{+}	4.4^{A}	0	0	0	0.5^{A}	0
D. melanurus	177	62.7^{+}	34.5^{+}	2.2^{A}	0	0	0	0.6^{A}	0
C. retrofasciata	321	33.7^{+}	52.3^{+}	13.4$^{=}$	0	0.6^{A}	0	0	0
Complex microhabitat dwellers									
A. leucogaster	145	40.0^{+}	0.7$^{=}$	9.7$^{=}$	11.7^{+}	30.3^{+}	1.4^{A}	5.5$^{=}$	0.7^{A}
A. curacao	141	45.4^{+}	1.4$^{=}$	14.2$^{=}$	19.8^{+}	5.0$^{=}$	8.5^{A}	5.7$^{=}$	0
C. ternatensis	250	35.2^{+}	3.2$^{=}$	42.4^{+}	4.0$^{=}$	8.0^{+}	4.0^{A}	2.8^{A}	0.4^{A}
P. aurifrons	654	22.2^{+}	5.1^{+}	49.2^{+}	2.0$^{=}$	7.3^{+}	8.4^{A}	3.1^{A}	2.7^{A}
Microhabitat generalists									
P. nigromanus	263	26.6^{+}	3.8$^{=}$	16.4$^{=}$	8.4^{+}	17.9^{+}	17.1$^{=}$	5.3$^{=}$	4.5^{A}
N. azysron	244	15.6^{+}	1.6$^{=}$	38.5^{+}	3.7$^{=}$	4.5$^{=}$	22.6$^{=}$	5.7$^{=}$	7.8^{A}

Recruits of the remaining two damselfish species—*P. nigromanus* and *N. azysron*—exhibited the most generalist patterns of microhabitat use. These recruits used almost every microhabitat in proportion to or more than expected based on availability, including low complexity massive and encrusting coral growth forms (Table 2.1).

2.4.2 *Acropora* spp. selectivity and specialization

A total of 1178 coral-associated damselfish recruits were observed in the 20 most abundant *Acropora* species. Overall, patterns of *Acropora* use across the 10 damselfish species did not correspond closely to patterns of relative availability of *Acropora* microhabitats (Fig. 2.1). Although the two *Acropora* species used in highest proportions by damselfish recruits (i.e. *A. nasuta* and *A. kimbeensis*) were also two of the most abundant *Acropora* species, the coral species present in highest abundance (i.e. *A. muricata*) was rarely used (Fig. 2.1). Further, the much less abundant *A. caroliniana* and *A. paniculata* were used in much greater proportions than the more commonly available *A. brueggemanni* and *A. palifera* (Fig. 2.1).

The obligate coral-dwelling damselfishes were generally more specialized and selective in their use of *Acropora* compared to the complex microhabitat-dwellers and microhabitat generalists (Table 2.2). Two of the most specialized damselfishes, *C. parasema* and *P. moluccensis*, never used or avoided more than half of the commonly available *Acropora* spp., instead selecting only a few preferred coral species as recruitment habitat. *Chrysiptera parasema* recruits were selective for colonies of *A. kimbeensis* and *A. caroliniana*, as well as bottlebrush colonies of *A. longicyathus* and *A. subglabra* (Table 2.2) and 66% of recruits were observed on these four coral species alone (Fig. 2.2). *Pomacentrus moluccensis* were selective for completely different *Acropora* spp. than *C. parasema* recruits, and preferred colonies of *A. nasuta* and *A. microclados*, as well as large tabular colonies of *A. solitaryensis* (Table 2.2). Patterns of *Acropora* use were similar for *C. retrofasciata* and *D. melanurus*, with at least 60% of recruits of both species using colonies of *A. nasuta, A. valida,* *A. kimbeensis* and *A. caroliniana* (Fig. 2.2). The most specialized damselfish, in terms of its use of *Acropora,* was the complex microhabitat-dweller *A. leucogaster* (Table 2.2). Recruits of this species had an extremely narrow *Acropora* niche, with 82% found on only three coral species—large tabular colonies of *A. plumosa*, *A. paniculata*, and *A. valenciennesi* (Fig. 2.2). These corals were also important microhabitats for *C. ternatensis* and *A. curacao* recruits (Fig. 2.2), although these recruits were not particularly selective and instead used 15 of the 20 *Acropora* spp. in proportion to availability (Table 2.2). *Pomacentrus aurifrons*, *P. nigromanus* and *N. azysron* were the most generalist species in terms of their *Acropora* use (Table 2.2) and recruits tended to occur in similar proportions across the coral species that they used (Fig. 2.2).

2.4.4 Differential bleaching susceptibility of branching coral microhabitats

Incidence of bleaching was assessed for a total of 1439 coral colonies across 16 coral species and 74% of these colonies were affected to some degree by bleaching. The response varied between *Acropora* species, although growth form was not a clear predictor of bleaching susceptibility (Table 2.3). For example, tabular *A. hyacinthus* were severely susceptible, with 62% of colonies either severely bleached or dead, yet colonies of another tabular species, *A. solitaryensis*, were never severely bleached (Table 2.3). *Acropora nasuta* and *A. kimbeensis*, the two *Acropora* species used in highest proportions by recruits of the coral-associated damselfish community (Fig. 2.1b), had a lower incidence of severe bleaching and mortality than many of the other branching coral species examined (Table 2.3). However, significant proportions of these colonies were moderately affected and only 25% of *A. kimbeensis* colonies were unaffected by bleaching (Table 2.3). *Seriatopora* and *Pocillopora* corals, which are particularly important microhabitats for obligate coral-dwellers *D. melanurus* and *C. retrofasciata* (Table 2.1), exhibited differences in susceptibility—31% of *S. hystrix* colonies were severely bleached or dead, compared to only 6% of *P. verrucosa* colonies.

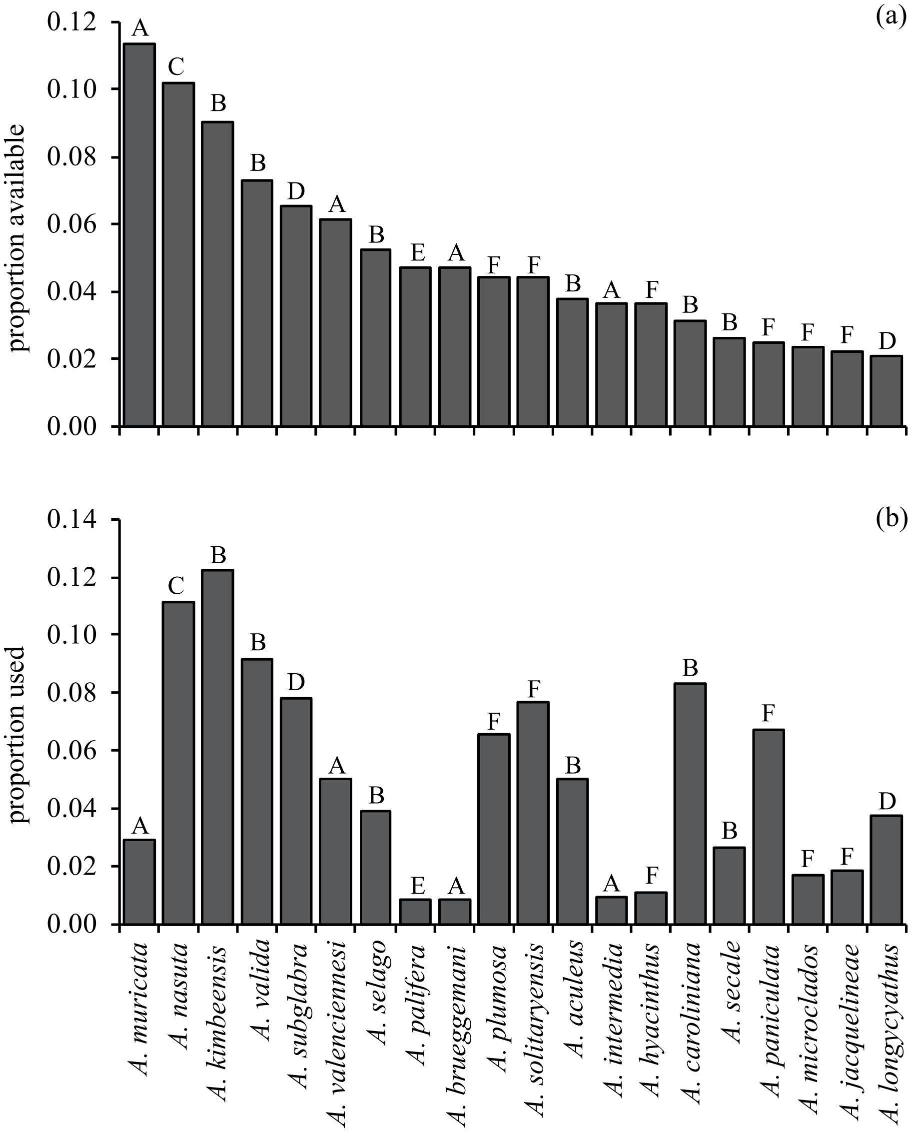

Figure 2.1 (a) The relative availability of the 20 most abundant *Acropora* species in Kimbe Bay and (b) the proportion of the total number of recruits (1178 individuals) across 10 coral-associated damselfish species observed using each *Acropora* species as settlement microhabitat. Letters above each bar indicate the typical growth form of that species. A = arborescent, B = bushy, C = corymbose, D = bottlebrush, E = club-like branches, F = tabular or plating.

Table 2.2 Selectivity and specialization by recruits of 10 species of coral-associated damselfish for 20 common *Acropora* spp. available as habitat in Kimbe Bay, Papua New Guinea. Selection for a coral species is indicated by (+), use in proportion to availability by (=), and avoidance by (A) based on resource selection ratios and their Bonferroni-corrected 95% confidence intervals. (0) indicates that coral species was never used.

	n	Niche breadth	*A. valenciennesi*	*A. intermedia*	*A. palifera*	*A. muricata*	*A. brueggemanni*	*A. plumosa*	*A. solitaryensis*	*A. secale*	*A. nasuta*	*A. valida*	*A. paniculata*	*A. kimbeensis*	*A. caroliniana*	*A. microclados*	*A. selago*	*A. longicyathus*	*A. aculeus*	*A. subglabra*	*A. hyacinthus*	*A. jacquelineae*	Total selected or used in proportion	Total avoided or never used
<u>Obligate branching coral-dwellers</u>																								
C. parasema	361	0.731	0	A	0	A	A	A	0	0	A	=	=	+	+	0	=	+	=	+	0	=	9	11
P. moluccensis	213	0.752	A	A	A	A	0	A	+	=	+	=	=	A	A	+	=	A	0	0	=	0	8	12
C. retrofasciata	88	0.789	0	0	0	A	0	=	=	=	=	=	=	=	+	0	=	=	=	=	0	=	13	7
D. melanurus	91	0.789	0	0	0	A	0	0	=	=	=	=	=	=	=	0	=	=	=	=	0	0	11	9
<u>Complex microhabitat dwellers</u>																								
A. leucogaster	57	0.570	=	=	0	=	=	+	0	=	0	0	+	0	0	0	0	0	=	=	=	=	11	9
A. curacao	59	0.835	=	=	=	=	=	=	=	=	=	=	=	0	0	0	=	0	=	0	=	=	15	5
C. ternatensis	84	0.840	=	=	0	=	=	=	=	=	A	=	=	=	=	0	A	=	=	=	=	0	15	5
P. aurifrons	130	0.879	=	A	0	A	=	=	=	=	=	=	=	=	=	0	=	=	=	=	0	0	14	6
<u>Microhabitat Generalists</u>																								
N. azysron	33	0.815	=	0	=	=	0	=	=	0	=	=	=	=	=	0	=	0	0	0	=	0	12	8
P. nigromanus	62	0.844	=	0	=	A	0	=	0	=	=	=	=	=	=	0	=	=	=	=	0	=	14	6

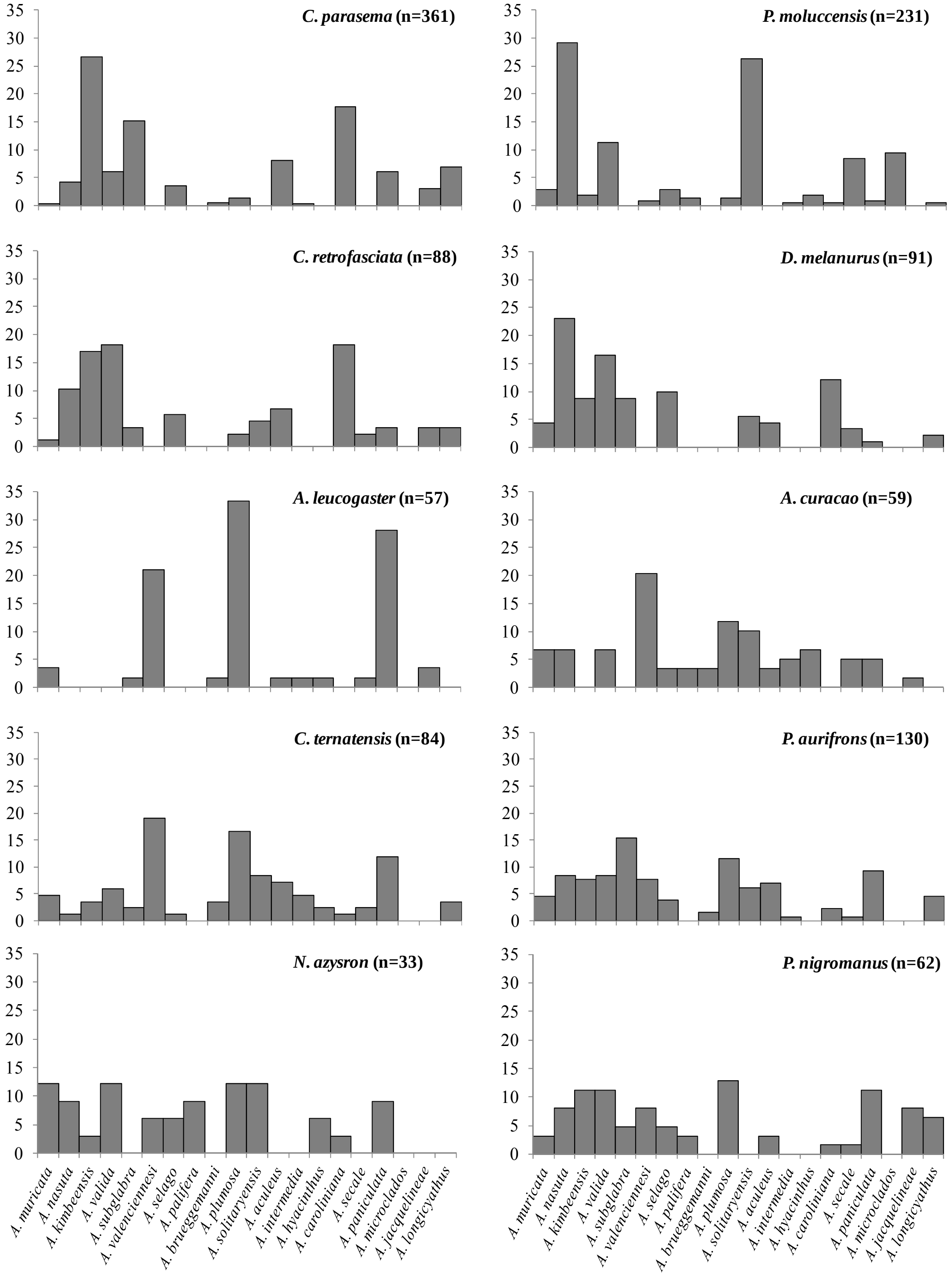

Figure 2.2 Percentage of recruits of each species of damselfish observed in the 20 most abundant *Acropora* species in Kimbe Bay, Papua New Guinea. Coral species on the x-axis are arranged based on their relative availability, from most abundant to least abundant.

Table 2.3 Variation in bleaching susceptibility among coral species commonly used as recruitment habitat by coral reef fishes in Kimbe Bay. Table values represent the percentage of colonies in each of four bleaching categories. Susceptibility categories were defined as: Severe = >15% dead, High = at least 50% of colonies severely bleached or dead, Moderate = <50% of colonies severely bleached or dead, Lowest = <10% of colonies severely bleached or dead.

Coral species	**Growth form**	**n**	**% Unbleached**	**% Moderate**	**% Severe**	**% Dead**	**Relative Susceptibility**
A. subglabra	bottlebrush	82	1	24	34	40	severe
A. hyacinthus	tabular	125	15	23	42	20	severe
A. brueggemanni	arborescent	29	0	38	62	0	high
A. aculeus	bushy	14	7	43	43	7	high
A. longicyathus	bottlebrush	8	13	38	50	0	high
A. microclados	tabular	70	24	43	26	7	moderate
S. hystrix	branching	230	10	59	29	2	moderate
A. millepora	corymbose	103	18	53	15	14	moderate
A. selago	bushy	85	33	44	18	6	moderate
A. echinata	bottlebrush	9	11	67	11	11	moderate
A. humilis	digitate	66	15	64	20	2	moderate
A. nasuta	corymbose	173	37	48	11	4	moderate
A. kimbeensis	bushy	68	25	62	10	3	moderate
A. sarmentosa	bushy	19	26	63	11	0	moderate
P. verrocosa	branching	350	46	48	5	1	lowest
A. solitaryensis	tabular	8	25	75	0	0	lowest

Five coral species—*A. subglabra*, *A. hyacinthus*, *A. brueggemanni*, *A. aculeus* and *A. longicyathus*—were identified as highly or severely susceptible, with at least 50% of colonies either severely bleached or dead (Table 2.3). These five coral species were important recruitment microhabitats for the coral specialist *C. parasema* and also the complex microhabitat dweller *P. aurifrons*, with approximately one-third of recruits of both species using these corals (Fig. 2.3). Moreover, two of these highly susceptible coral species, *A. subglabra* and *A. longicyathus*, were microhabitats preferred by highly specialized *C. parasema* recruits (Table 2.2). Given that only 1% of *A. subglabra* colonies were unaffected by bleaching and 74% were severely bleached or dead (Table 2.3), *C. parasema* is likely to experience significant loss of its preferred recruitment microhabitats due to coral bleaching. However, only 2% of recruits of the second most specialized damselfish, *P. moluccensis*, used the five most susceptible corals (Fig. 2.3), suggesting that the primary coral species that these recruits rely on for habitat tend to be more resistant to bleaching-induced habitat loss in Kimbe Bay.

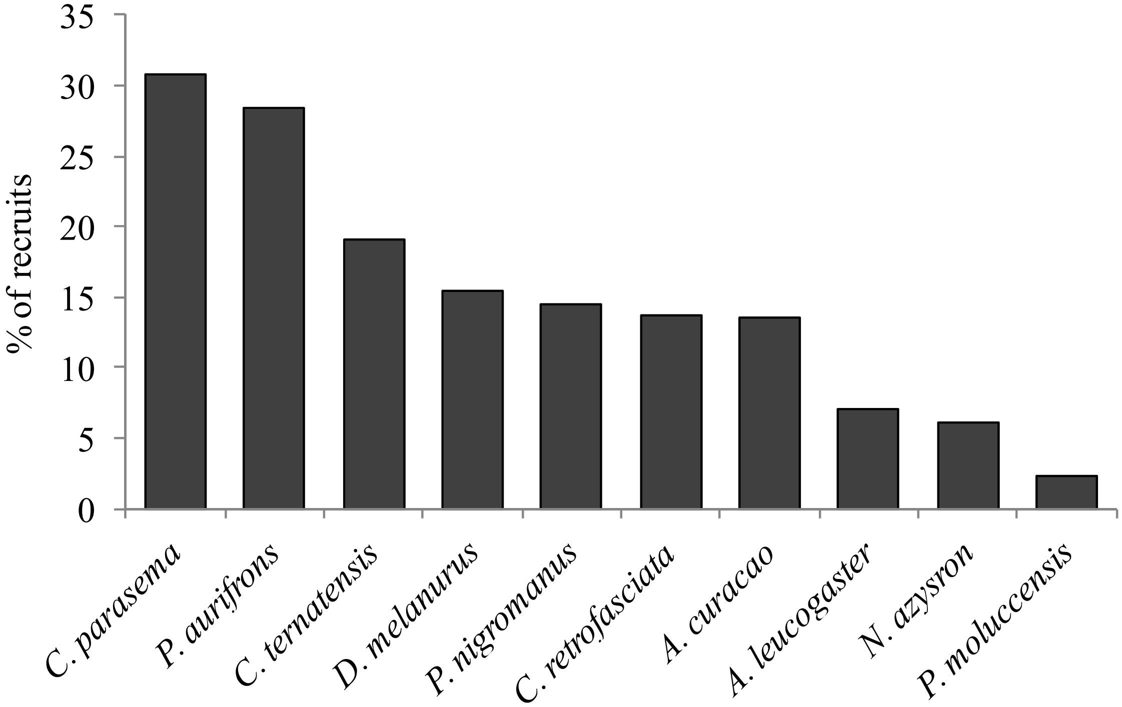

Figure 2.3 Percentage of recruits using the 5 coral species (i.e. *A. subglabra*, *A. hyacinthus*, *A. brueggemanni*, *A. aculeus* and *A. longicyathus*) that are most highly susceptible to severe bleaching and mortality in Kimbe Bay, Papua New Guinea.

2.5 DISCUSSION

This study is one of the first to document species-level *Acropora* preferences among coral-associated damselfishes as well as the bleaching susceptibility of coral species that represent important recruitment microhabitats for these fish (also see DeMartini et al. 2010). It clearly shows that the majority of coral-associated damselfishes are discriminating among different branching coral species, but with varying degrees of specialization. The species level data on both habitat use and coral bleaching has provided significant insights into the damselfish species at greatest risk of population decline and at least local extinction due to habitat loss.

Two of the ten damselfish species examined, *N. azysron* and *P. nigromanus*, are not likely to be highly vulnerable to habitat change given their generalist patterns of microhabitat use, which included low-complexity substratum. In contrast, structural complexity is a necessary feature of the recruitment microhabitats of *A. leucogaster*, *A. curacao*, *C. ternatensis* and *P. aurifrons*. Although these four species often used branching corals, they were also able to use alternative microhabitats with complex structure, such as branching sponges and soft corals. Consequently, these species are likely to be most affected by the reductions in reef structural complexity that occur in the years following bleaching-induced coral loss. However, four of the damselfish species examined in this study are expected to be highly vulnerable to the declines in live coral cover that occur immediately following bleaching, as well as the changes in coral assemblage structure that may occur due to differential bleaching susceptibilities among coral species. *Chrysiptera parasema*, *P. moluccensis*, *C. retrofasciata*, and *D. melanurus* recruits were all restricted to branching hard corals as recruitment microhabitat and more than 85% of recruits used only three branching coral genera—*Acropora, Seriatopora* and *Pocillopora*. These obligate coral-dwelling recruits were also highly selective for certain coral species within these genera and typically associated with only 2-4 coral species. Information on the relative bleaching susceptibility among these coral species revealed that some of the preferred microhabitats of the specialized damselfish recruits were highly susceptible to severe bleaching and mortality (i.e. *A. subglabra*) whereas others were more often moderately rather than severely affected (i.e. *A. nasuta*, *A. kimbeensis*). Although bleaching susceptibility varied between preferred coral microhabitats, the three coral genera on which these damselfish recruits depend are more vulnerable to disturbances such as coral bleaching, *Acanthaster* outbreaks and coral disease than many other coral taxa (Marshall and Baird 2000; De'ath and Moran 1998; Willis et al. 2004), highlighting the general vulnerability of these coral microhabitat specialists to habitat loss and shifts in coral community composition.

Although previous studies have emphasized the vulnerability to habitat loss among coral reef fishes that depend on live corals as settlement habitat (Jones et al. 2004; Pratchett et al. 2008), the degree of specialization and selectivity for certain coral microhabitats among recruits was not well understood. The results of this study show that coral reef fish recruits can exhibit a high degree of specialization and selectivity for certain coral species as settlement microhabitat. More than 55% of *P. moluccensis* recruits used only two species of coral, 60% *C. parasema* recruits used only 3 coral species, and 50% of *C. retrofasciata* recruits used only *Seriatopora hystrix*. This dependence on only a few coral species among damselfish recruits is on par with the level of host coral specialization observed among coral-dwelling gobies (Munday 2000) and the selectivity for certain coral prey observed among corallivorous butterflyfishes (Pratchett 2007). Such a high level of specialization on coral resources has been shown to lead to population decline and even local extinction among coral-dependent fishes in response to disturbances affecting the coral community (Pratchett et al. 2008; Munday 2004). It is likely that recruits in many other coral reef fish families have specialized microhabitat requirements similar to those of the damselfishes identified in this study, and future research into the degree of coral selectivity among a wider range of species would facilitate more robust predictions about the likely effects of disturbance on coral reef fish communities (Wilson et al. 2010).

Why were certain coral species used by damselfish recruits so much more than others? One possibility is that larvae actively selected these preferred coral species at settlement. Although there is evidence to suggest that coral reef fish larvae are capable of distinguishing between live and dead coral microhabitats (Öhman et al. 1998; Feary et al. 2007a) whether different coral species provide unique cues to settlers is not well understood. However, because recruits up to 3 weeks post-settlement were included in surveys of microhabitat use, differential post-settlement mortality as a cause of observed patterns of "selectivity" cannot be ruled out. Indeed, there is substantial evidence that competitive and predatory interactions can alter patterns of habitat use established at settlement (e.g. Jones 1991; Schmitt and Holbrook 1999; Booth 2002), that these interactions are strongest within 48 hours of settlement (Almany and Webster 2006), and that post-settlement mortality of recruits can differ considerably between coral species (Beukers and Jones 1997; Bonin et al. 2009). For example, 85% of *C. parasema* recruits survived the early post-settlement period on the bottlebrush coral *Acropora elseyi* compared to only 25% on *Pocillopora verrucosa* (Bonin et al. 2009). Furthermore, available evidence suggests that the presence of conspecifics provides a stronger cue for settlers than does microhabitat (Booth 1992; Lecchini et al. 2005a,b). If more recruits typically survive the risky early post-settlement period in certain corals and larvae are cued to settle with conspecifics, this could potentially explain why recruits develop apparent preferences for certain coral species.

Information on the relative bleaching susceptibility among branching coral species provided an indication of which preferred recruitment microhabitats are most likely to become scarce due to chronic coral bleaching. Although colony growth form alone was not a clear indicator of bleaching susceptibility, fine-branching species with small inter-branch spaces (i.e. *A. subglabra*, *A. hyacinthus*) tended to be more susceptible than coral species with thicker branches (i.e. *P. verrucosa*, *A. solitaryensis*). Tissue thickness has been identified as an important factor influencing bleaching susceptibility between coral taxa (Loya et al. 2001; McClanahan et al. 2004) and this may explain the higher susceptibility to bleaching of fine-branching species observed in this study. Declines in the availability of fine-branching *Acropora* species as a result of frequent bleaching is likely to have negative impacts on all recruits that rely on the small inter-branch shelter spaces provided by these microhabitats to escape from predators. In particular, the severe susceptibility to bleaching of the fine-branching bottlebrush *A. subglabra* may seriously impact *C. parasema* populations because these recruits are highly selective for this microhabitat.

Although *P. moluccensis* recruits exhibit a similar degree of coral specialization as *C. parasema* recruits, the two species of coral *P. moluccensis* recruits used most frequently, *A. nasuta* and *A. solitaryensis*, were not as highly susceptible to severe bleaching and mortality. Consequently, *P. moluccensis* may not face quite as immediate a risk of population decline due to loss of preferred microhabitats compared to *C. parasema*.

Despite the apparently high degree of specialization for particular coral species observed among the obligate coral-dwellers, the true test of whether these species are fundamentally restricted in their microhabitat use will be their response to declines in the availability of preferred coral resources. For example, Pratchett (2001) reported that although both *C. baronessa* and *C. trifascialis* appeared to be highly specialized in their choice of coral prey, the two species responded very differently to declines in live coral cover following an *Acanthaster* outbreak on the Great Barrier Reef. *Chaetodon baronessa* expanded its diet to include a wider range of coral species when its preferred prey, *A. hyacinthus*, was unavailable, whereas *C. trifascialis* was driven to near local extinction (Pratchett 2001). Some specialized species may therefore be capable of using alternative resources if the ones they prefer become scarce, while others may not be capable of doing so. Although it seems highly unlikely that damselfish recruits would be incapable of using non-preferred coral species as settlement habitat, survival may be lower in these microhabitats (Beukers and Jones 1997; Bonin et al. 2009). Moreover, being forced to use alternative resources could have sub-lethal consequences that do not immediately impact abundance. Recent research has shown that the growth of juvenile *C. parasema* and *D. melanurus* is sensitive to the condition of host coral colonies (Feary et al. 2009) and it is possible that recruits experience variation in growth between healthy corals of different species. For example, growth of the coral-dwelling *Gobiodon histrio* is 3 times lower when living on healthy colonies of an alternative host coral, *A. loripes*, compared to healthy colonies of its preferred host, *A. nasuta* (Munday 2001). Future research into the effects of utilizing non-preferred coral species among these specialized damselfishes should therefore include impacts on growth and condition as well as persistence.

The degree to which coral-specific habitat specialization predicts the impact of habitat degradation on different fish species may ultimately depend on the magnitude of the disturbance event. In this study, the magnitude of the bleaching episode was such that there was considerable variation among coral species in the extent of habitat damage. However, previously in Kimbe Bay there was an extreme period of coral decline that led to the almost complete loss of branching coral species and in response the abundance of half the coral reef fish species in the community declined by at least 50% (Jones et al. 2004, Munday 2004). When the extent of habitat loss is this extreme, even species that are less specialized in their associations with corals are likely to experience significant population declines.

This study has shown that damselfish recruits can be highly specialized in their use of corals as recruitment microhabitat, and the specialists identified here generally choose fine-branching coral species. Unfortunately, these types of corals appear to be highly susceptible to bleaching and loss of these critical microhabitats may have significant consequences for the persistence of these specialized fish species. Moreover, many of the coral species which represent important recruitment microhabitats for reef fishes in Kimbe Bay (e.g. *Acropora kimbeensis*) exhibit a form of rarity that makes them vulnerable to local extirpation (Richards 2009). The conservation and management of coral-dependent reef fishes will therefore require monitoring of not only these specialized species, but populations of their preferred corals as well.

CHAPTER 3: RECRUITMENT AND PERSISTENCE OF CORAL-DWELLING FISHES IS RESISTANT TO BLEACHING BUT NOT TO MORTALITY OF HOST CORALS †

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† **Bonin MC**, Munday PL, McCormick MI, Srinivasan M, Jones GP (2009) Coral-dwelling fishes resistant to bleaching but not to mortality of host corals. *Marine Ecology-Progress Series* 394:215-222

3.1 ABSTRACT

Coral bleaching is becoming an increasingly common disturbance on coral reefs and although corals can remain bleached for months prior to recovery or death, little is known about how bleaching affects the associated fish community. This study reports on recruitment and persistence of coral-dwelling fishes during a natural coral bleaching event in Kimbe Bay, Papua New Guinea. Transect surveys revealed that up to 80% of branching coral habitats were affected by bleaching. Healthy (i.e. unbleached), severely bleached, and dying colonies of corymbose *Acropora* were tagged along the reef crest and resident fish communities were monitored over time. There was no difference in the number of *Pomacentrus moluccensis* that settled to healthy versus bleached corals. Furthermore, the mean number of *P. moluccensis* recruits remaining on healthy and bleached corals did not differ after four weeks. In contrast, the number of recruits remaining on dead colonies was lower after four weeks and the frequency of recruit retention was significantly lower on dead colonies compared to healthy or bleached colonies. Similarly, the abundance of coral-dwelling gobies living on healthy or bleached corals did not decrease significantly over eight weeks, but all gobies disappeared from corals that died from bleaching. These results suggest that *P. moluccensis* recruits do not avoid bleached corals at settlement and that subsequent survival and/or movement of both recruits and adult coral-dwelling gobies is not

negatively influenced, provided that the host coral remains alive. However it is clear that if corals die from bleaching coral-specialized fishes will quickly disappear, even prior to structural erosion of the habitat.

3.2 INTRODUCTION

Disturbance plays an important role in determining the structure and dynamics of ecological communities (Sousa 1984; Pickett and White 1985). Although moderate disturbances can promote species diversity by reducing the impact of competitive dominants, severe disturbances invariably have a negative impact on the majority of species. On coral reefs, both physical (e.g. storms) and biological (e.g. crown-of-thorns starfish, coral bleaching, coral disease) disturbances can dramatically impact on coral reef habitat and associated organisms (Karlson and Hurd 1993; Aronson and Precht 1995; Jones and Syms 1998; Jones et al. 2004; Wilson et al. 2006). Although physical disturbances that break down reef structure generally have the most severe impacts on the associated animal communities (Graham et al. 2006), biological disturbances that affect only living coral tissue can be equally detrimental for some groups of animals (Wilson et al. 2006). Species may be resistant to or recover from some disturbances, but the point at which disturbances become intolerable is not well understood.

Mass coral-bleaching events, caused primarily by elevated sea surface temperatures as a result of climate change, are one of the most critical disturbances that coral reef ecosystems currently face (Hoegh-Guldberg 1999; Wilkinson 2004). When corals are exposed to temperatures 1-2 degrees above their average maximum for several consecutive days they become stressed and expel their symbiotic dinoflagellates (their main source of energy and pigmentation). Heat-stressed corals can either recover or die from bleaching, although corals that recover may suffer from reduced growth, fitness, and physiological condition (Jokiel and Coles 1977; Baird and Marshall 2002). Differing susceptibilities to bleaching among corals can then lead to dramatic shifts in the structure of coral communities. In a recurring pattern, the branching corals that provide greatest habitat structure for other organisms are often replaced by less structurally complex massive and encrusting growth forms (Marshall and Baird 2000; Loya et al. 2001; McClanahan et al. 2007).

Coral decline due to bleaching can have far-reaching and detrimental consequences for organisms that rely on corals for food, shelter or living space (Pratchett et al. 2008, 2009). To date most studies have documented the impact of coral mortality caused by bleaching on associated animal communities (e.g. Lindahl et al. 2001; Booth and Beretta 2002; Spalding and Jarvis 2002; Garpe et al. 2006). Information about the effects of bleaching *per se* is very limited. Given that bleaching is becoming a chronic disturbance during which corals can remain bleached for months prior to recover or death (e.g. Baird and Marshall 2002) it is crucial to understand how bleaching itself influences basic demographic processes of coral-associated organisms.

Although sparse, the available evidence suggests that the effects of bleaching on animals that depend on live corals for food and shelter can be significant. Symbiotic coral crabs of the genus *Trapezia* suffer reduced abundance and physiological condition when living and feeding on bleached host corals compared to crabs living and feeding on healthy host colonies (Glynn et al. 1985; Iglesias-Prieto et al. 2003). Although very little is known about the influence of bleaching on animals that use corals primarily for shelter rather than nutrition, the significant declines in abundance of coral-dwelling species shortly after bleaching, and prior to habitat erosion, suggests that habitat bleaching may also have rapid effects on persistence (Lindahl et al. 2001; Bellwood et al. 2006). For example, in surveys conducted immediately after the 1998 bleaching event on the Great Barrier Reef, when some corals were still bleached, Bellwood et al. (2006) found that the abundance of coral-dwelling damselfishes and gobies had already declined significantly. However it is generally unclear if these declines in abundance occur as a result of bleaching itself or subsequent coral mortality. This information is critical to understand the level of resistance to and potential recovery from bleaching episodes of different intensity. For coral-dwelling fishes, healthy coral tissue often appears to be just as important a component of the habitat as structural complexity (Booth and Beretta 2002; Wilson et al. 2006; Feary et al. 2007b) and bleaching itself may prompt resident fishes to vacate affected host corals in search of undisturbed habitat.

The effects of bleaching may also extend beyond species with an obligate relationship to live coral by influencing settlement and early post-settlement survival of a wide range of species. Many reef fish species use live coral as settlement habitat (Jones et al. 2004; Garpe and Öhman 2007) and although it is clear that settlers can distinguish between live and dead coral (Öhman et al. 1998; Feary et al. 2007a) it is currently unknown if they avoid settling onto bleached corals. Reef fish use visual and chemical cues to recognize their settlement habitat (Booth 1992; Elliot et al. 1995) and the loss of pigmentation and physiological stress corals experience during bleaching could potentially disrupt these cues. If this is the case, bleaching could have significant and persistent effects on population replenishment, particularly in locations where seasonal recruitment peaks coincide with periods of increased risk of bleaching (e.g. Great Barrier Reef). Moreover, if recruits do settle onto bleached corals the pigment loss associated with bleaching could further increase their already high vulnerability to predation. Healthy live coral tissue is thought to help camouflage resident fishes (Wilson et al. 2006) and bleaching could make recruits more visually conspicuous to predators.

This study was conducted during a natural coral bleaching event in Kimbe Bay, Papua New Guinea and is the first to investigate the immediate effects of bleaching *per se* on coral reef fish recruitment and persistence. We began by documenting the extent of bleaching at the study site and then used *in situ* monitoring of fishes living on host colonies across a range of bleaching degradation categories to quantify the immediate effects of this biological disturbance on recruitment and persistence of coral-associated fishes. Like trapezid crabs, coral-dwelling gobies of the genus *Gobiodon* are live coral symbionts and their high degree of live coral dependence and site fidelity make them ideal candidates for *in situ* study. The two species monitored here, *Gobiodon histrio* and *Gobiodon quinquestrigatus*, occur in only a small suite of corymbose *Acropora* species in Kimbe Bay (Munday 2000). Once breeding pairs are established, *Gobiodon spp*. may spend their entire lives within the branches of their home coral colony (Wall and Herler 2008). Similarly, the lemon damselfish, *Pomacentrus moluccensis*, is well-suited to study the effects of bleaching on recruitment because it exhibits a strong preference for live coral at settlement (Öhman et al. 1998), recruits directly into adult habitat (Brunton and Booth 2003) and is highly site-attached, with tagging studies showing little movement on contiguous reef environments (Beukers et al. 1995). The specific questions we examined were: (1) How does host colony bleaching and mortality influence persistence of adult resident gobies? (2) Do settlement-stage *P. moluccensis* avoid settling onto bleached corals? and (3) How does host colony bleaching and mortality influence the post-settlement persistence of recruits?

3.3 METHODS

3.3.1 Study site

This study was conducted from April to June 2008 during a natural coral bleaching event in Kimbe Bay, Papua New Guinea. The first reports of bleaching in the area in 2008 were at the end of March (V. Messmer pers. comm.) so the study period encompassed the majority of the coral bleaching, recovery and mortality that occurred during the event. The study took place on the exposed side of Garbuna reef, a large platform reef approximately 1 km from shore.

3.3.2 Extent of bleaching to branching coral habitats

To determine the extent of bleaching to branching corals, four replicate 50 m line-intercept transects were deployed and benthic substratum was identified under 100 random points along each transect. Surveys were conducted along the reef flat, crest, upper slope and lower slope (0, 2, 6 and 10 m respectively) to document differences in the extent of bleaching across these depth-stratified habitats. Live corals were identified to genus and growth form and were categorized as either healthy (e.g. normal pigmentation) or affected by bleaching.

3.3.3 Effect of coral bleaching and mortality on adult goby persistence

To determine how host colony bleaching affected the persistence of coral-dwelling gobies, 25 healthy and 20 severely bleached colonies of *Acropora nasuta* that hosted breeding pairs of either *Gobiodon histrio* or *G. quinquestrigatus* were tagged and monitored for seven weeks. *Acropora nasuta* was chosen because it is a preferred host coral for both gobies (Munday 2000) and is abundant at the study site. In order to categorize host colony bleaching degradation we used a four-point scale similar to that developed by Marshall and Baird (2000): (1) Healthy = no visible loss of color, (2) Moderately Bleached = 1-50% of colony affected or entire colony pale, (3) Severely Bleached = 51-100% of colony with strong pigmentation loss (colony appears white), (4) Dead = 80-100% of colony covered by light algal overgrowth. Only host colonies that were categorized as Severely Bleached at the initial inspection were tagged for inclusion in the study. At each subsequent census, colony inter-branch spaces were searched using an underwater torch to identify and count remaining gobies. Bleaching severity of the host colony was then scored using the four-point scale and proportional mortality was estimated to the nearest 5% in order to monitor progress in the recovery or death of each colony over time.

3.3.4 Effect of coral bleaching on settlement of *Pomacentrus moluccensis*

Prior to the new moon settlement pulse in May 2008, 20 Healthy and 19 Severely Bleached colonies of corymbose *Acropora* were tagged along the reef crest. Because the presence of conspecifics is a known settlement cue for *Pomacentrus moluccensis* (Öhman et al. 1998), at least one older recruit was present on all of the tagged colonies. Colonies were then monitored weekly for five weeks to track changes in recruit abundance and coral health over time. At each census, the number of *P. moluccensis* recruits was counted, the degree of bleaching severity of the host coral was scored and proportional mortality estimated. Small body size and pale coloration of the new settlers allowed them to be clearly distinguishable from older recruits on the colonies.

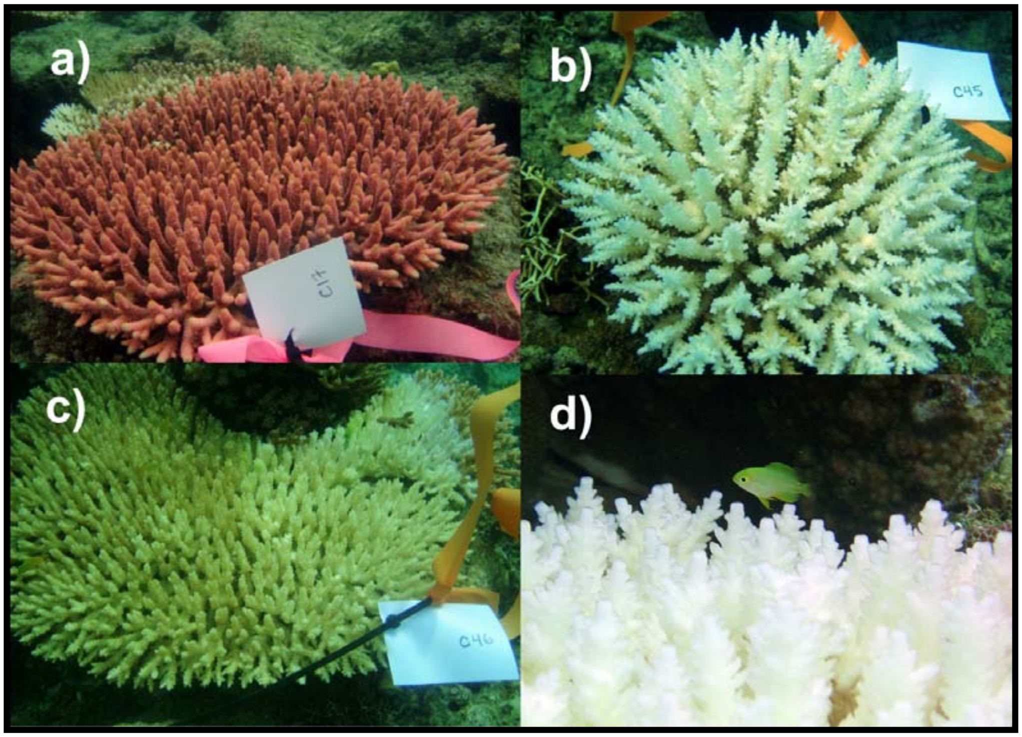

Figure 3.1 Colonies of corymbose *Acropora* were monitored over time to compare recruitment and persistence of coral-dwelling fishes on hosts that were (a) healthy, (b) severely bleached or (c) dead. (d) Living on bleached corals could make coral reef fish recruits more visually conspicuous to predators.

3.3.5 Effect of coral bleaching and mortality on post-settlement persistence of recruits

In the first few days following the settlement pulse, the reef crest was again searched for corymbose *Acropora* colonies in various stages of health that hosted newly settled *Pomacentrus moluccensis*. A total of 67 coral colonies were located and tagged—30 Healthy colonies, 22 Severely Bleached colonies and 15 Dead colonies. Colonies categorized as Severely Bleached at the initial census appeared very white with little to no pigmentation and colonies categorized as Dead had between 80-100% mortality at the time of tagging (Fig. 3.1). Weekly monitoring of each colony was then conducted to document the response of the colony to bleaching and associated changes in the number of *P. moluccensis* recruits remaining. Percent mortality of the host coral was also estimated to the nearest 5%.

3.4 RESULTS

3.4.1 Extent of bleaching to branching coral habitats

The branching coral community covered ~25% of the benthos and was dominated by corals from the genus *Acropora*. Mean cover of branching corals did not differ significantly between depths (ANOVA: $F_{3,12}$=0.179, p=0.909), although the proportion of these corals affected by bleaching decreased significantly with increasing depth (Fig. 3.2; ANOVA: $F_{3,12}$=6.977, p=0.006). On the reef flat approximately 80% of branching corals were bleached, compared to 23% on the lower reef slope.

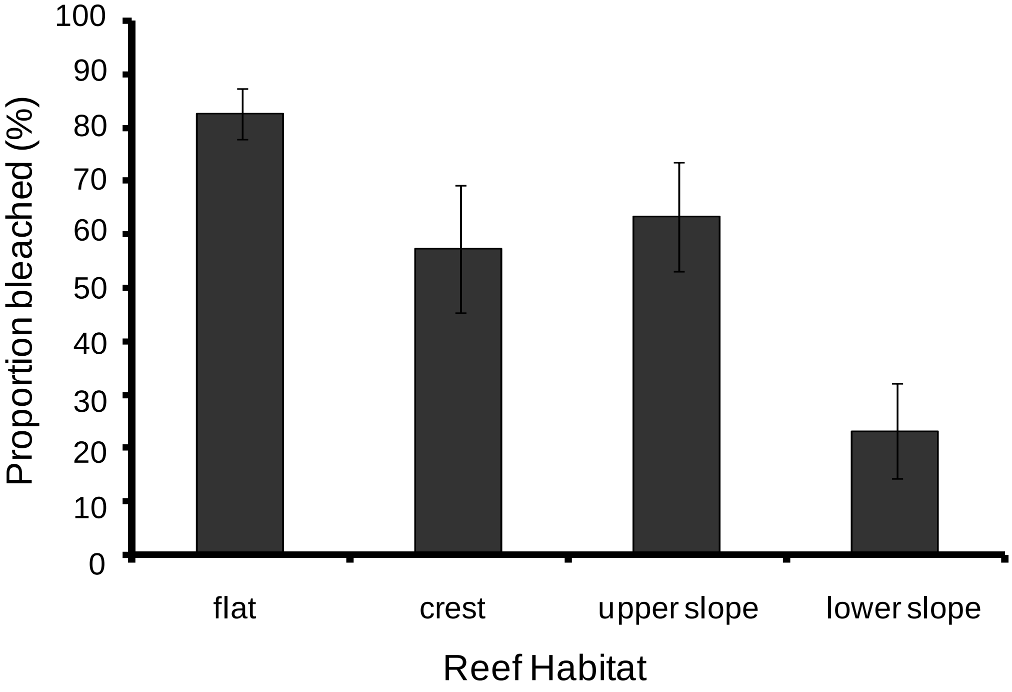

Figure 3.2 Mean proportion of branching corals affected by bleaching along a depth gradient. Error bars represent +/- SE.

3.4.2 Effect of coral bleaching and mortality on adult goby persistence

The 25 healthy colonies of *Acropora nasuta* that hosted coral gobies remained healthy with no bleaching or mortality during the seven week study, whereas the 20 severely bleached hosts either showed signs of recovery (n=16) or died (n=4). There were significant differences in the density of gobies remaining in healthy, bleached and dead host corals after seven weeks (ANOVA: $F_{2,42}$=16.702, p<0.001). Although mean density of gobies on bleached corals tended to be slightly lower than on healthy corals (Fig. 3.3) a Tukey's HSD test revealed that this difference was not significant. However, goby density was significantly lower on dead corals after seven weeks compared to both healthy and bleached corals. On healthy and bleached host colonies ~2 fish remained in each colony throughout the study whereas goby abundance on dying colonies declined moderately during the first month and then dropped sharply so that at the end of the study no gobies remained on colonies that died from bleaching (Fig. 3.3).

3.4.3 Effect of coral bleaching on settlement of *Pomacentrus moluccensis*

There was no difference in the number of *Pomacentrus moluccensis* settling to healthy and severely bleached coral colonies (ANOVA: $F_{1,37}$=0.350, p=0.558). During a settlement pulse both healthy and bleached host corals received an average of 4-5 settlers per coral and persistence of these settlers did not differ between healthy and bleached colonies over the next month (Fig. 3.4).

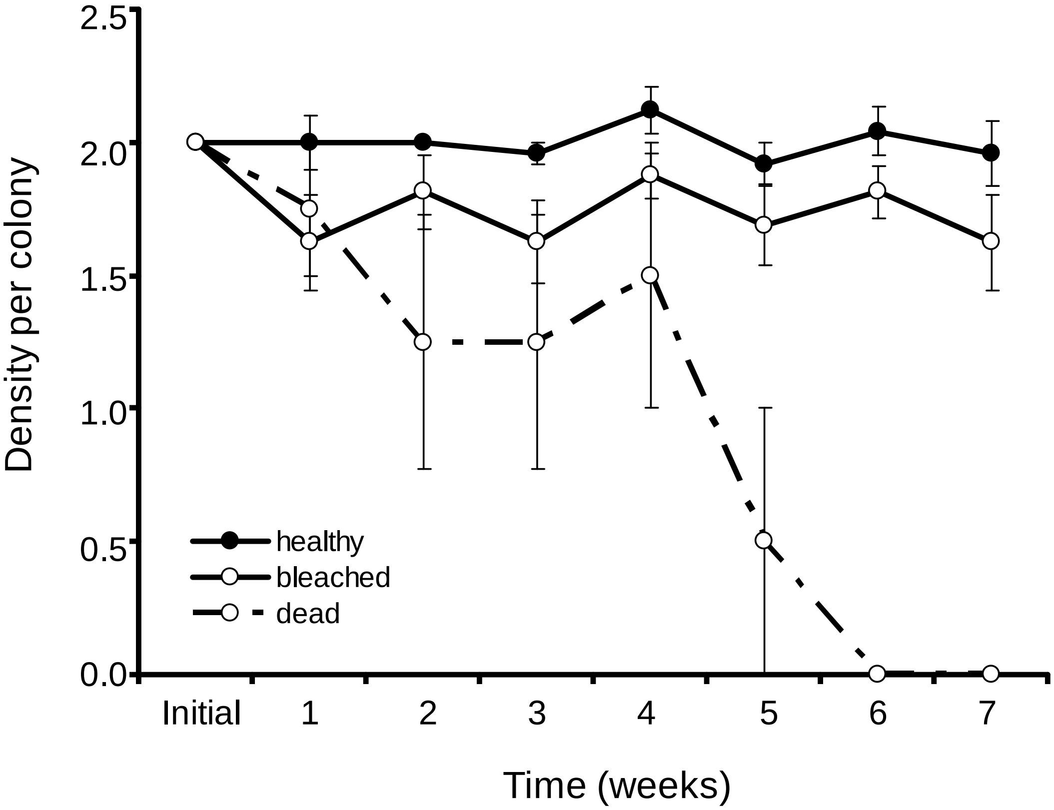

Figure 3.3 Persistence of coral-dwelling gobies living on healthy (n=25), severely bleached (n=16) or dead (n=4) colonies of *Acropora nasuta* over seven weeks. Colonies initially hosted pairs of either *Gobiodon histro* or *Gobiodon quinquestrigatus*. Error bars represent +/- SE.

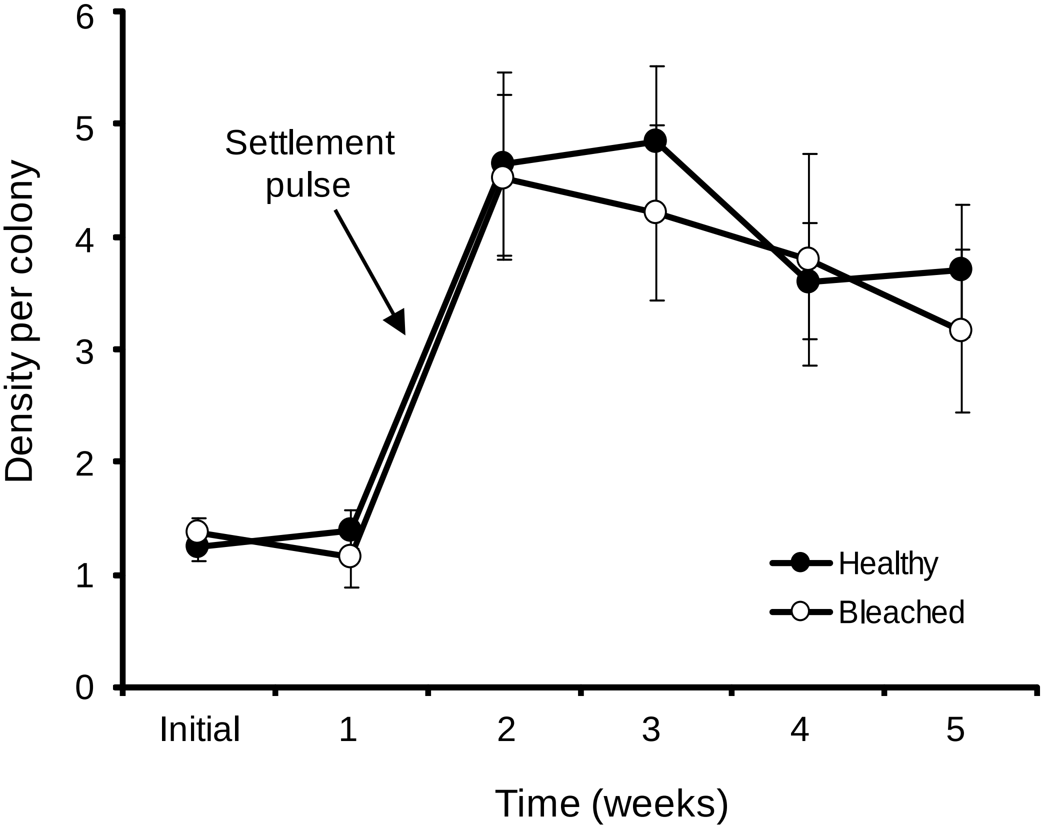

Figure 3.4 Settlement of *Pomacentrus moluccensis* to healthy (n=20) and severely bleached (n=19) colonies of corymbose *Acropora*. Error bars represent +/- SE.

3.4.4 Effect of coral bleaching and mortality on post-settlement persistence of recruits

All healthy colonies remained unbleached with no partial mortality throughout the four week study and all the colonies categorized as dead had lost 100% of their live tissue by the time of the second census. The bleached colonies remained bleached throughout the study although most showed signs of recovery by the end of the fourth week. These bleached host colonies had a low incidence of partial mortality, with only three colonies experiencing 15-30% tissue loss. The abundance of *Pomacentrus moluccensis* recruits declined steadily over time on host corals in all three degradation categories and consequently there was no significant difference in the mean density of recruits remaining on healthy, bleached or dead corals after four weeks (ANOVA:

$F_{3,64}$=2.25, p=0.113). However, significantly fewer dead colonies retained recruits compared to bleached (Fisher's exact: p=0.043) and healthy (Fisher's exact: p=0.024) colonies, although there was no difference in recruit retention between bleached and healthy colonies (Fisher's exact: p=0.423). Only 2 of the 15 dead colonies had recruits after 3 weeks and abundance on those two colonies continued to decline during the fourth week. In contrast, recruits persisted to the end of the study on approximately half of both bleached (n=22) and healthy (n=30) colonies and declines in abundance on these colonies appeared to stabilize by the third week (Fig. 3.5). Although recruits of other species did settle to some of the experimental corals during the study, the presence of these recruits was rare compared to the numerically dominant *Pomacentrus moluccensis* recruits, and therefore assumed not to strongly influence the persistence patterns observed.

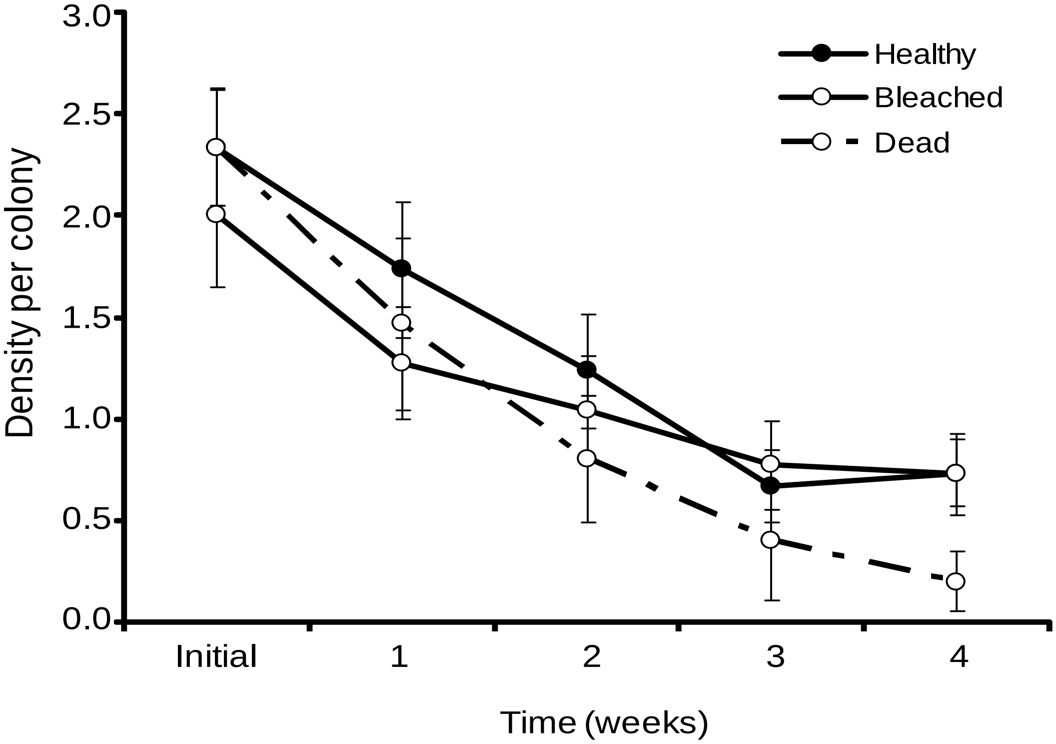

Figure 3.5 Persistence of *Pomacentrus moluccensis* recruits on healthy (n=30), bleached (n=22) and dead (n=15) host colonies of corymbose *Acropora* over four weeks. Error bars represent +/- SE.

3.5 DISCUSSION

Despite the increasing prevalence of coral bleaching on reefs worldwide, this study is one of the first to directly examine the effects of bleaching on the associated fish community. This was possible because we monitored fish settlement patterns and abundance during a natural bleaching event. Our results suggest that recruitment and persistence of specialized coral-dwelling fishes is resistant to this level of disturbance, provided it does not progress to coral death. Habitat bleaching in itself did not negatively affect settlement patterns or post-settlement survival of recruits and had minimal effects on persistence of adult resident fishes. In contrast, host colony mortality ultimately led to lower abundance of recruits and caused all adult fish to disappear from their host colonies.

Although several monitoring studies have documented significant declines in the abundance of coral-dwelling fishes shortly after bleaching (e.g. Lindahl et al. 2001; Bellwood et al. 2006), it was previously unclear at what stage between bleaching and coral mortality these effects occurred. The results of this study indicate that bleaching itself is not likely to be the cause of these declines and if corals bleach and recover it should have minimal effects on numerical processes (e.g. recruitment, mortality and movement) in the associated reef fish community. However, if corals suffer widespread mortality following bleaching the loss of live coral tissue will have rapid negative effects on persistence of both recruit and adult coral associated fishes. These effects of live tissue loss were evident well before the structural erosion of the habitat, providing further support for an emerging view that live coral tissue itself is an important resource for many coral-specialized reef fishes (Booth and Beretta 2002; Wilson et al 2006; Feary et al. 2007a; Holbrook et al. 2008).

The similarity in the number of *Pomacentrus moluccensis* settlers arriving to healthy and severely bleached corals indicates that bleaching does not disrupt settlement cues. Although

P. moluccensis demonstrate a strong preference for live coral as settlement habitat and avoid settling into dead, algal covered colonies (Öhman et al. 1998) settlers did not avoid corals that showed signs of stress due to bleaching. After settlement, declines in abundance of recruits on all colony types was expected because predation mortality at this life-history stage is exceptionally high (Almany and Webster 2006). Less expected was that the persistence trajectories of *P. moluccensis* recruits living on healthy and severely bleached colonies would be so similar. In order to explain why live coral tissue is such an important resource for reef fishes, Wilson et al. (2006) hypothesized that coral tissue may provide camouflage to fish living in close association to corals. If this is the case, bleaching would remove this attribute of the habitat and make recruits more conspicuous to predators. This study provided a first test of that prediction under natural conditions, and the very similar persistence of recruits on both healthy colorful host corals and those with bleached white tissue suggests that pigmentation of host corals does not affect overall survival of recruits, at least for *P. moluccensis*. However, there could be more subtle effects of this type of habitat change, such as changes to predator and recruit behavior in association with bleached corals, which warrant future study.

Settlement is a major population bottleneck in coral reef fish communities and the widespread reliance on live coral as settlement habitat makes these communities particularly vulnerable to disturbances that affect live coral (Jones et al. 2004; Wilson et al. 2008). However, the observation that settlement and early post-settlement survival is not negatively affected by habitat bleaching lends support to emerging evidence that replenishment of coral reef fish communities is resistant to at least the early stages of coral degradation. The species richness of fish colonizing experimental plots in Moorea was largely resistant to changes in coral cover and only declined sharply when the cover of live coral was <10% (Holbrook et al. 2008). Similarly, in laboratory choice experiments Feary et al. (2007a) found that many settlement-stage reef fish, including *P. moluccensis*, would settle into both healthy live corals and those degraded by up to

75% partial mortality. However, even fish that associate with dead habitats as adults avoided settling into totally dead, algal-covered colonies (Feary et al. 2007a). Furthermore, in this study significantly fewer dead colonies retained recruits compared with those that did not bleach, or bleached but did not die. Consequently, total colony mortality appears to be the tipping point at which the habitat becomes unfavourable to coral-associated fishes.

If dead corals are unsuitable as settlement habitat, why were we able to find some settlers living on dead host corals? It may be that when many corals in an area are bleached and dying, priority effects and competition for the few remaining healthy colonies forces inferior competitors to use degraded habitats. Competition for microhabitats among recent settlers can be intense (Bonin et al. 2009) and early post-settlement survival for *P. moluccensis* decreases with increasing group size on a colony (Brunton and Booth 2003). Using a less crowded, lower quality habitat is likely to be a short-term solution to avoid competition when high quality habitat is in short supply. However, this strategy does not seem to be effective in the long run given the ultimately lower persistence on dead colonies.

The response of adult resident fishes to host coral bleaching and mortality paralleled that of recruits. Goby persistence was largely resistant to habitat degradation from bleaching and partial mortality, with some pairs not vacating severely bleached colonies until 50-90% of the live coral tissue had died. Like recruits, small-bodied gobies face a high risk of predation when moving away from shelter so migration is only likely over relatively short distances. For both *Gobiodon histro* and *Gobiodon quinquestrigatus*, successful re-location depends upon suitable coral habitat being within 3 m of their original host colony (Feary 2007). The risk involved in re-location is further compounded by the fact that if preferred host corals are not available nearby, gobies will be forced to take up residence in alternative habitats where they can suffer substantial reductions in growth and survival (Munday 2001). This high degree of habitat specialization may help to explain the unwillingness of these live coral symbionts to vacate host corals even when they suffer substantial degradation. The lack of a bleaching effect on the abundance of coral-dwelling gobies contrasts the response to host coral bleaching in another live coral symbiont, the trapezid crab. These crabs feed primarily on the mucus produced by their host corals, and bleaching to the coral on which they feed will significantly reduce their body condition (Glynn et al. 1985). Perhaps as a result of this strong dependence on coral mucus as a food source, Iglesias-Prieto et al. (2003) observed a decline in the density of *Trapezia ferruginea* living in bleached corals compared to healthy, unaffected corals during the 1997-1998 ENSO event in the southern Gulf of California. Although the diet of *Gobiodon* spp. does include coral tissue, they also feed on zooplankton (Patton 1994) and this greater flexibility in diet may allow gobies to persist on bleached host corals when crabs cannot. However, there may be sub-lethal consequences for fishes that inhabit and feed on degraded host colonies and this is an important area for future research (see Feary et al. 2009).

Although reef fish communities do appear to be resistant to considerable degradation to live coral, the fact that fish will settle into or use degraded patches of suitable habitat should not be taken as a safeguard against predicted changes to coral habitats as a result of climate change. Corals with branching growth forms are highly susceptible to bleaching and coral communities that suffer recurrent bleaching may lose the structural complexity necessary to support diverse reef fish communities. For species with a strong dependence on live branching coral, adaptation to habitat degradation is unlikely (Munday et al. 2008) and there are already indications that the risk of extinction from habitat loss is real (Munday 2004). Finally, although habitat bleaching does not appear to affect the immediate survival of coral-dwelling fishes, future research is required to determine if there are sub-lethal effects of living in degraded habitats.

CHAPTER 4: INTERACTIVE EFFECTS OF INTERSPECIFIC COMPETITION AND MICROHABITAT ON EARLY POST-SETTLEMENT SURVIVAL IN A CORAL REEF FISH †

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† **Bonin MC**, Srinivasan M, Almany GR, Jones GP (2009) Interactive effects of interspecific competition and microhabitat on early post-settlement survival in a coral reef fish. *Coral Reefs* 28:265-274

4.1 ABSTRACT

Microhabitat type and the competition for microhabitats can each influence patterns of abundance and mortality in coral reef fish communities, however the effect of microhabitat on the intensity and outcome of competition is not well understood. In Kimbe Bay, Papua New Guinea, surveys were used to quantify microhabitat use and selectivity in two live-coral specialist damselfishes (Pomacentridae), *Chrysiptera parasema* and *Dascyllus melanurus*. A patch reef experiment was then conducted to test how intra- and interspecific competition interacts with two types of microhabitat to influence survival of recently settled *C. parasema*. Surveys demonstrated that *C. parasema* and *D. melanurus* recruits utilize similar coral microhabitats; 72% of *C. parasema* and 85% of *D. melanurus* used corymbose and bottlebrush growth forms of *Acropora*. One microhabitat type, *Pocillopora* sp. coral, was commonly used by *D. melanurus* but rarely used by *C. parasema*. The patch reef experiment revealed that both microhabitat and interspecific competition influence abundance of recently settled *C. parasema*. Microhabitat had the strongest influence on survival of *C. parasema*. In the absence of interspecific competitors, approximately 85% of *C. parasema* survived for 5 days after transplantation to high complexity bottlebrush *Acropora* reefs compared to only 25% survival on *Pocillopora* reefs. In both microhabitats, interspecific competition with *D. melanurus*, but not intraspecific competition, significantly

decreased survival of *C. parasema*. Taken together, these results suggest that the observed distribution of *C. parasema* results from specialized microhabitat requirements and competition for space in those microhabitats. This study demonstrates that interspecific competition and microhabitat type can interact to influence early post-settlement survival in coral reef fishes, though whether and how these factors influence survival will depend on the behavioral attributes and strength of habitat associations among potential competitors.

4.2 INTRODUCTION

Patterns of habitat use often vary among organisms in response to a range of interacting processes, including habitat selection, competition and predation (Futuyma and Moreno 1988; Rosenzweig 1991; Gurevitch et al. 1992; Morris 2003). Observations on the range of habitats occupied by a species or the degree of apparent habitat specialization are typically insufficient to reveal the underlying mechanisms (Futuyma and Moreno 1988; McNally 1995). A species may use a narrow range of suitable habitats for several reasons, including strong habitat preferences, or because it has been eliminated by competitors or predators in other habitats. Habitat specific differences in survival or reproduction may result from intrinsic differences in habitat quality, or because the effects of competition or predation vary among habitats. An understanding of the potentially complex relationships between apparent specialization and biological interactions among species is vital to predict how communities will respond to changes in habitat availability.

The intensity of competition both within and among species can exhibit a strong interaction with patterns of habitat preference and availability (Rosenzweig 1991). For example, the density of competitors may influence the range of habitats used by a species, with individuals using only preferred habitats at low densities, but increasing use of marginal habitats with increasing competition (Pimm and Rosenzweig 1981; Abramsky et al. 1990). In addition, asymmetric competition between species often leads to the exclusion of subordinate competitors from mutually preferred habitats (Connell 1983; Schoener 1983; Thompson and Fox 1993; Young 2004). Subordinate competitors are therefore expected to survive better when dominant competitors are removed or their densities reduced (Colwell and Fuentes 1975; Price 1978). Consequently, the density of both intra- and interspecific competitors may influence patterns of habitat use and apparent specialization.

Coral reef fishes are associated with a complex and diverse environment that includes a wide range of microhabitats (Jones 1991; Jones and Syms 1998). Perhaps because of the high diversity characteristic of these communities, habitat specialization appears to be common (e.g. Munday et al. 1997; Munday and Jones 1998; Bean et al. 2002; Gardiner and Jones 2005; Wilson et al. 2008). Many coral reef fish select particular microhabitats at settlement and can remain associated with them throughout adult life (Tolimieri 1995; Danilowicz 1996; Öhman et al. 1998; Leis and Carson-Ewart 2002). However, patterns of habitat use established through habitat selection are likely to be altered by post-settlement interactions and there is growing evidence that competition plays an important role in determining microhabitat associations (Ebersole 1985; Robertson and Gaines 1986; Jones 1991; Robertson 1996; Bay et al. 2001; Jones and McCormick 2002). In particular, competition for shelter from predators can directly influence patterns of distribution and abundance within and among microhabitats (Srinivasan et al. 1999; Schmitt and Holbrook 1999; Munday et al. 2001; Holbrook and Schmitt 2002). Dominant competitors can exclude subordinates from occupying mutually preferred microhabitats (Munday et al. 2001) and can reduce the abundance of subordinates by increasing their exposure to predators (Holbrook and Schmitt 2002). However, evidence for interspecific competition among recently settled fish is rare (but see Schmitt and Holbrook 1999) despite the importance of this life-history phase in determining adult abundance and distribution.

While there is emerging evidence that both intra- and interspecific competition for preferred microhabitats may have important effects on the local distribution and abundance of coral reef fishes, the influence of using different microhabitats on the outcomes of ecological interactions among species is not well understood. The effects of these interactions are likely to vary among microhabitats that differ in complexity or the provision of resources. One possibility is that the effects of interactions, such as competition and predation, will be mitigated by habitat complexity. Empirical support for this prediction exists for predator-prey interactions on coral reefs—predator-induced mortality is lower in more complex microhabitats (Almany 2004a, b) because microhabitats of high structural complexity interfere with predator search and capture capabilities (Beukers and Jones 1997). However, the degree to which different microhabitats impact on the outcome of competitive interactions is largely unknown. In one of the only studies to examine the interaction between microhabitat structure and competition, Ebersole (1985) found that competitive dominance varied with microhabitat complexity for two congeneric species of damselfish. On structurally complex microhabitat, *Eupomacentrus planifrons* was dominant and could exclude *E. leucosticus*, but on less complex microhabitat *E. leucosticus* was the dominant competitor. Whether a reversal of competitive dominance in different microhabitats is a common phenomenon has yet to be determined and in general little is known about how the effects of competition vary among microhabitats in coral reef fish communities.

This study examined the influence of microhabitat type, competition and their interaction on early post-settlement survival of two live-coral dwelling damselfishes, *Chrysiptera parasema* and *Dascyllus melanurus*, in Kimbe Bay, Papua New Guinea. Although these two species occupy similar microhabitats, the effects of competitive interactions between them have not been investigated. In order to better understand how competition for space influences the abundance and distribution of these species shortly after settlement, quantitative surveys of habitat use and availability were first conducted to describe the overlap in microhabitat use and depth distributions of new recruits. Then a patch reef experiment was conducted in which three factors potentially affecting the survival of *C. parasema* were tested: (1) Intraspecific density; (2) The presence and absence of interspecific competitor *D. melanurus*; and (3) Two types of branching coral microhabitat that differ in structural complexity.

4.3 METHODS

4.3.1 Study site and species

The study was conducted on fringing reefs at the western side of Kimbe Bay, a large sheltered bay on the northern coast of the island of New Britain, Papua New Guinea (5°30’S, 150°05’E). The planktivorous damselfishes *C. parasema* and *D. melanurus* are common inhabitants of coral reefs in the study area. Both species settle directly into live coral and appear to depend on a similar subset of branching corals for shelter. In addition, both species are gregarious and commonly occupy coral patches in conspecific groups; juvenile *C. parasema* often aggregate on sprawling coral thickets in groups of 10-50 individuals whereas juvenile *D. melanurus* tend to occupy smaller coral patches in groups of 5-10 individuals (Limbourn et al. 2007).

4.3.2 Surveys of microhabitat availability, microhabitat use and depth distributions of *C. parasema* and *D. melanurus* recruits

Microhabitat availability, microhabitat use and depth distributions of *C. parasema* and *D. melanurus* recruits were estimated using visual surveys conducted from December 1998 to April 2001. Microhabitat use was surveyed 20 times during this period at two areas of fringing reef and four inshore platform reefs approximately 0.2-1 km from shore. Only recruits that were estimated to have settled within the previous 1-2 weeks were counted and surveys were conducted at least 4-6 weeks apart to ensure that no individuals from a previous survey were re-counted. Post-settlement age was determined based on body size, which was established by regularly monitoring size-at-recruitment and growth on a series of experimental patch reefs as part of another study (e.g. Srinivasan 2003). The two fringing reef sites were each a 250 m long section of reef that ran parallel to the shoreline and had a reef slope extending from the reef flat to 8-10 m. The four platform reefs rose steeply from deep water (80-100 m) and had steep reef slopes or walls extending to depths of 40-60 m on the windward side and reef slopes extending to 30-40 m on the leeward side. Surveys of microhabitat use were conducted at 0, 2 and 6 m at each of the fringing reef sites, and at 0, 2, 6 and 10 m on the windward sides, and 2 m on the leeward sides of each of the four platform reefs. At each site and depth, four 50 x 2 m belt transects were surveyed by laying out 50 m measuring tapes and swimming one pass of each tape, recording the microhabitat type occupied by each *C. parasema* or *D. melanurus* recruit within 1 m of either side of the transect line. Coral microhabitats were identified to genus level and distinguished between growth forms when appropriate.

Depth distribution surveys for *C. parasema* and *D. melanurus* were conducted in June 1999. Distributions of recruits of each species across depths were estimated by conducting surveys on the leeward slopes of two of the platform reefs at depths of 3, 6, 10, 15 and 20 m. As with surveys of microhabitat use, recruits of both species were counted along four 50 m x 2 m belt transects at each depth. Data was then averaged across the four transects at each depth to attain an estimate of mean density for each species.

To estimate the availability of the microhabitats used by recruits, surveys of benthic substrata were conducted along the same transects as the surveys of microhabitat use in November 1999. At each site and depth four 50 m line-intercept transects were used to estimate the percent cover of benthic substrata. The type of substratum under each of 100 random points along each transect was recorded and the number of points for each substratum type was then summed to obtain the percentage cover estimate.

4.3.3 Microhabitat selectivity of *C. parasema* and *D. melanurus* recruits

As microhabitat availability differed among depths, reef zones and reef types (fringing or platform), resource selection ratios were based on microhabitat use and availability data from the depth(s) at which each species was most abundant. For *C. parasema*, data from 10 m on the windward side of the platform reefs were used, and for *D. melanurus*, data was pooled from 2 m on the leeward side of the platform reefs and from 2 and 6 m on the fringing reefs. Substratum types were grouped into 13 microhabitat categories for analysis, and resource selection ratios (Manly et al. 2002) were used to determine whether *C. parasema* and *D. melanurus* recruits used certain microhabitats more or less frequently than expected based on their availability. For each species, the forage ratio ($\hat{w}_i$) was calculated for each of the 13 microhabitat types using the formula $\hat{w}_i = o_i/\pi_i$, where o_i is the proportion of recruits occupying microhabitat type i, and π_i is the proportion of microhabitat type i available (percent cover/100). Microhabitat use data was pooled across survey periods and transects to estimate proportional use for each microhabitat category. Microhabitat availability data was pooled across transects to calculate the mean percent cover of each microhabitat. For each selection ratio, a Bonferroni-corrected 95% confidence interval was calculated using the formula $z_{\alpha/2I}\sqrt{\{ o_i(1- o_i)/(u_+\pi_i^2)\}}$, where $z_{\alpha/2I}$ is the critical value of the standard normal distribution, $\alpha=0.05$, I=number of substratum types, and u_+ is the total number of recruits for which microhabitat use was recorded (Manly et al. 2002). A 95% confidence interval containing the value 1 indicates that a microhabitat type is used in proportion to its availability. A 95% confidence interval that spans values greater or less than 1, but that does not include 1, indicates that a substratum type is used more or less frequently, respectively, than expected based on its availability (Manly et al. 2002).

4.3.4 Influence of competition and microhabitat on survival of recently settled *C. parasema* and *D. melanurus*

A patch reef experiment was conducted in March-April 2006 in the lagoon system near Schumann Island, a small island approximately 1 km from shore in Kimbe Bay. An array of 24 live-coral patch reefs was constructed on a large, open sand flat off the western side of the island at a depth of 3-5 m. Each reef measured was constructed with a rubble base and then topped with 3-4 live coral colonies so that the circumference of each reef measured approximately 0.5 m^2. Half of the reefs were randomly assigned to each of two coral types: *Pocillopora verrucosa*, which has a branching growth form and *Acropora elseyi*, which has a more complex bottlebrush growth form. These two microhabitats were chosen because they are both common settlement microhabitat for many coral reef fish in Kimbe Bay (pers. obs.) and are branching corals that clearly differ in the structural complexity offered to newly recruited fish. Furthermore, because the microhabitat use surveys revealed that *C. parasema* are more common than *D. melanurus* on bottlebrush *Acropora*, and *D. melanurus* are more common than *C. parasema* on *Pocillopora*, the potential existed for a reversal of competitive dominance in these microhabitats. To minimize immigration and emigration of fishes from experimental reefs, each reef was isolated from the nearest natural reef by at least 20 m and from other experimental reefs by 15 m.

The effects of competition and microhabitat type on survival of recently settled *C. parasema* were tested by factorially manipulating the density of intra- and interspecific competitors on the 24 patch reefs (Table 4.1). In habitat patches where *C. parasema* occur, the average natural density per 0.5 m^2 is 6-8 recruits (pers. obs.). Therefore the lowest density treatment (4 *C. parasema*) represented the control density, at which competition was assumed to be minimal. Subsequent density treatments doubled and quadrupled the control density to test for effects of intraspecific competition (Table 4.1). Interspecific effects of competition with *D. melanurus* were tested by comparing survival of *C. parasema* in control treatments to treatments with a control density of *C. parasema* plus an equal density or 3x the density of *D. melanurus* (Table 4.1). This design allowed us to determine whether the effect of *D.melanurus* was independent of density through comparison of *C. parasema* survival between intra- and interspecific treatments at each density. Although our focus in the experiment was *C. parasema*, this design also allowed us to examine the effects of increased conspecific density and microhabitat on survival of *D. melanurus*.

Treatments were randomly assigned within each microhabitat type and were replicated in both space and time over a 14 day period. Recently settled *C. parasema* and *D. melanurus* were captured from the reefs surrounding Schumann Island and transplanted to experimental reefs on the day of collection (Fig. 4.1). The slightly larger body size of the stocked fish (e.g. approximately 2-3 weeks post-settlement) allowed them to be easily distinguished from any new recruits that might settle onto the patch reefs.

Once treatments were established, reefs were surveyed daily for five days to document losses and monitor potential movement of transplanted fish between patch reefs. The edges of the nearest natural reefs were also searched for any migrants from the patch reefs. Because no *C. parasema* or *D. melanurus* recruits occurred naturally along the edges of the natural reef nearest to the patch reefs, there were no non-experimental individuals nearby that could move onto the patch reefs. Therefore any individuals that were found along the natural reef edge could be assumed to be migrants from the patch reefs. At the end of the five day experiment all fish were cleared from patch reefs, treatments were randomly re-assigned and reefs were re-stocked with newly collected *C. parasema* and *D. melanurus*. The experiment was run twice during the

Table 4.1 Experimental design used to test for effects of competition and microhabitat on the survival of *Chrysiptera parasema* (C). Effects of intra- and interspecific competition with *Dascyllus melanurus* (D) were tested in two coral microhabitats, *Acropora elseyi* and *Pocillopora verrucosa*. CD = control density.

Acropora	**CD**	**CD x 2**	**CD x 4**
Intraspecific	4C	8C	16C
Interspecific		4C + 4D	4C + 12D
Pocillopora	**CD**	**CD x 2**	**CD x 4**
Intraspecific	4C	8C	16C
Interspecific		4C + 4D	4C + 12D

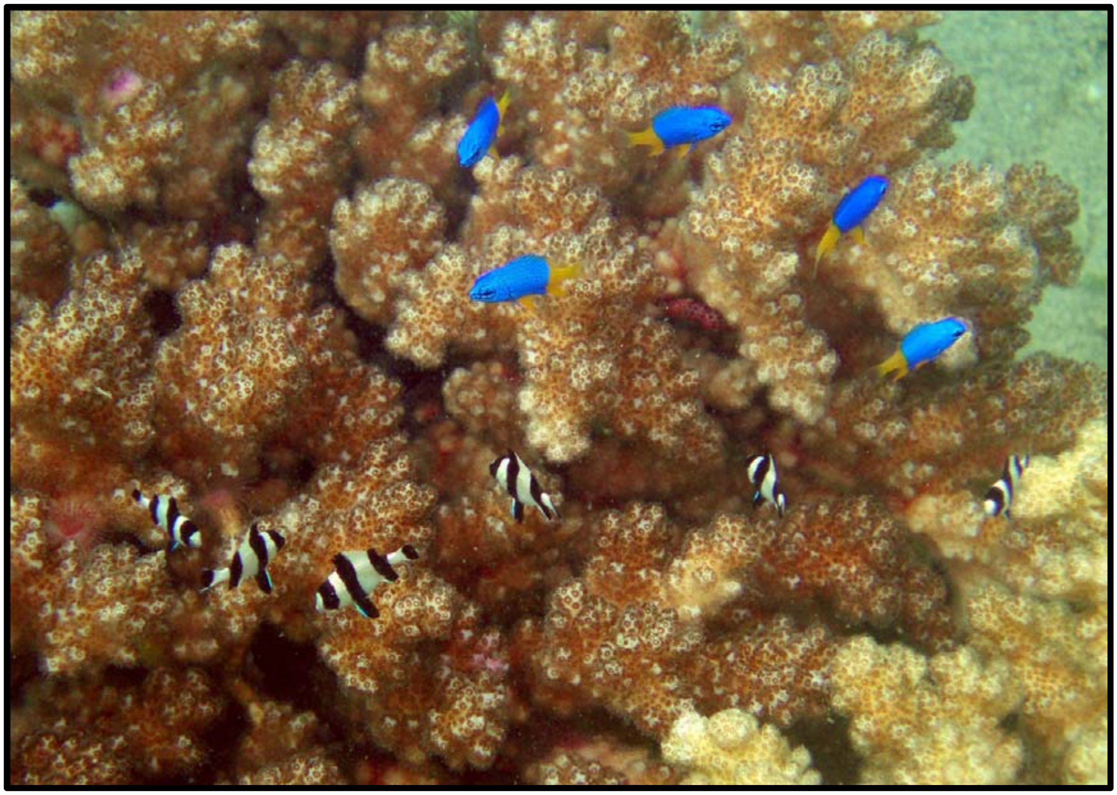

Figure 4.1 Interspecific competitors *Dascyllus melanurus* (stripes) and *Chrysiptera parasema* on a *Pocillopora* patch reef.

14 day period and in each trial there were two replicate reefs for each competition treatment and four replicate reefs for the control treatment.

Because no increase in abundance of *C. parasema* or *D. melanurus* was ever observed on experimental reefs during daily monitoring and migrants were not found on the edges of the nearest natural reefs, loss of fish from experimental reefs has been attributed to mortality rather than movement. Although it is possible that stocked fish moved across at least 20 m of open sand, this seems unlikely due to the small size of the recruits and the reliance of both species on live branching coral as habitat. In support of mortality as the primary source of losses, piscivores such as jacks (e.g. *Caranx melampygus*), coral breams (e.g. *Pentapodus trivittatus*), juvenile snappers (Lutjanidae), lizardfishes (e.g. *Synodus dermatogenys*), and flounders (e.g. *Bothus mancus*) were frequently observed near experimental reefs during daily censuses.

4.3.5 Statistical analyses

To test the effects of competitor density and microhabitat on survival of *C. parasema* and *D. melanurus*, the mean proportion of *C. parasema* or *D. melanurus* remaining in each treatment on the last day of the experiment was compared. This response variable was used for several reasons: (1) the survival trajectories in the experiment were consistent through time and (2) by the end of each experiment survival trajectories had stabilized (Figs. 4.4 and 4.5, Results). Data from the two trials conducted within the 14 day period were pooled for the analysis.

The effects of intra- and interspecific competition and microhabitat on survival of *C. parasema* were analysed using a protocol described by Underwood (1997, pp. 409-414). The factorial model included three factors: Density (fixed effect, two levels), Species Added (fixed effect, two levels), and Microhabitat (fixed effect, two levels). The partitioning of degrees of freedom required to separate the effects of increased density, interspecific competition, and microhabitat are complex and are detailed in Table 4.2. A significant effect of ‘Density’ would indicate that increasing the density of competitors on patch reefs had an effect on survival of *C. parasema* and a significant effect of ‘Species Added’ would indicate that survival of *C. parasema* differed between treatments where *D. melanurus* was added as the competitor compared to treatments where *C. parasema* was added as the competitor.

The effects of intraspecific density and microhabitat on survival of *D. melanurus* were analysed using a factorial design with two factors: Microhabitat (fixed effect, two levels) and Intraspecific Density (fixed effect, two levels). Proportional survival data for *D. melanurus* were arcsine transformed to conform to the ANOVA assumption of homogeneity of variances.

Table 4.2 Partitioning of df for three factor ANOVA testing for effects of Microhabitat and Competition on survival of *Chrysiptera parasema* (residual df = 38, total df = 47).

Source of Variation		df		
All treatments	9			
Microhabitat		1		
Competition		4		
Control vs. others			1	
Density			1	(including control, df = 2)
Species Added			1	
Density x Species Added			1	
Microhabitat x Competition		4		
Microhabitat x Control vs. others			1	
Microhabitat x Density			1	(including control, df = 2)
Microhabitat x Species Added			1	
Microhabitat x Density x Species Added			1	

4.4 RESULTS

4.4.1 Microhabitat use, microhabitat selectivity, and depth distributions of *C. parasema* and *D. melanurus*

C. parasema and *D. melanurus* recruits had highly overlapping microhabitat preferences, although *D. melanurus* used a smaller range of microhabitats compared to *C. parasema* (Fig. 4.2). Of 548 *D. melanurus* recruits surveyed, 97% used only three microhabitats—*Acropora* corals of corymbose and bottlebrush growth forms, and *Pocillopora* corals—and each of these microhabitat types was used more often than expected based on its availability (Fig. 4.2). *Chrysiptera parasema* recruits also used corymbose and bottlebrush *Acropora* corals in greater proportion than expected based on their availability, with 72% of the 1,588 *C. parasema* recruits surveyed occupying these two microhabitats. *C. parasema* recruits also used *Seriatopora* corals and 3 other growth forms of *Acropora* more often than expected. *Chrysiptera parasema* rarely occurred on *Pocillopora* corals (only one recruit was observed in this microhabitat at a depth of 6 m) although this microhabitat was commonly occupied by *D. melanurus* recruits. Finally, the depth distributions of these species were distinct, but overlapping, with *D. melanurus* recruits most abundant in the shallows from 3-6 m, and *C. parasema* recruits most abundant between 6-10 m (Fig. 4.3).

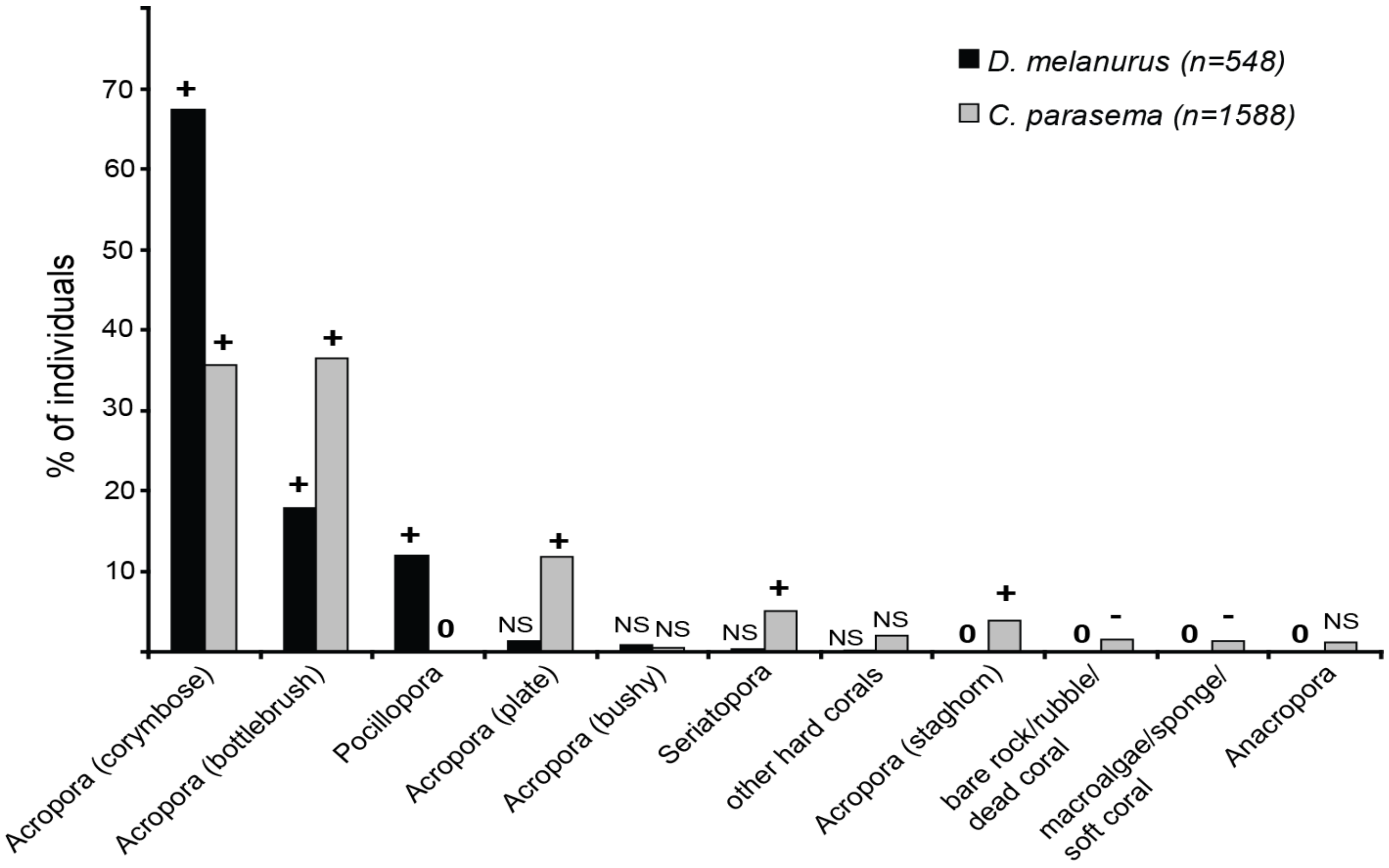

Figure 4.2 Microhabitats used by *Chrysiptera parasema* and *Dascyllus melanurus* recruits. Selectivity indices were calculated at the depth at which each species was most abundant. (+) indicates that the microhabitat was utilized more often than expected based on its availability, (-) indicates that the microhabitat was utilized less often than expected based on its availability, (NS) indicates that a microhabitat was used in proportion to its availability, and (0) indicates that a microhabitat was never used. Two growth forms of *Acropora* were used by less than 1% of both species and were not included in this figure.

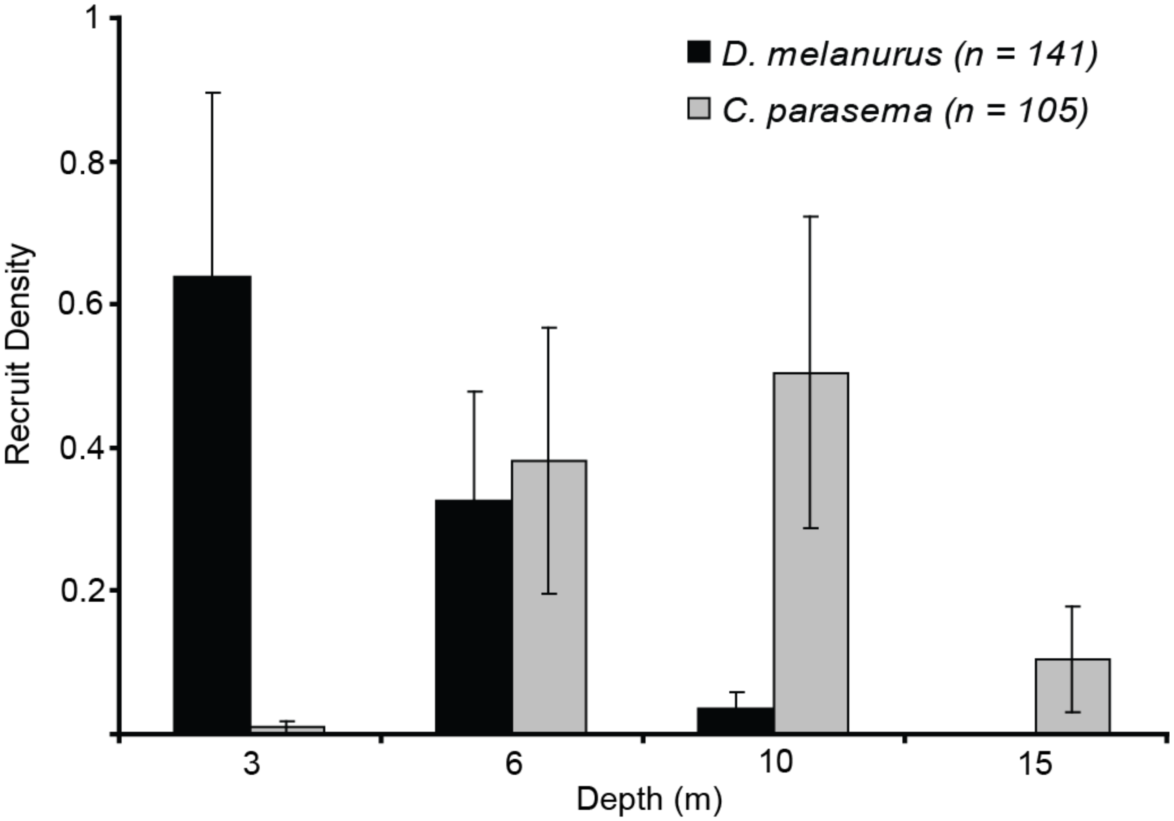

Figure 4.3 Mean density of *Chrysiptera parasema* and *Dascyllus melanurus* recruits per 100 m^2 transect observed at four depths. Error bars indicate ± 1SE.

4.4.2 Influence of microhabitat and competition on survival of *C. parasema* and *D. melanurus*

Survival of recently settled *C. parasema* was strongly influenced by microhabitat type and interspecific competition with *D. melanurus*, but not by intraspecific competition (Table 4.3). Despite increasing the density of conspecifics to 2x and 4x the control density of four fish, intraspecific density did not significantly decrease survival of *C. parasema* in either of the two microhabitats (Table 4.3, Fig. 4.4 a-b). Although the difference was not significant, survival of *C. parasema* on *Acropora* patch reefs appeared to increase slightly with increased density (Fig. 4.4a).

Microhabitat had the strongest effect on survival of *C. parasema*, with a 60% difference in survival between the two microhabitats (Table 4.3, Fig. 4.4 a-b). On *Acropora* reefs without *D. melanurus*, approximately 85% of *C. parasema* survived through the five day experiment, whereas on *Pocillopora* reefs only 25% of the initial cohort remained at the end of the experiment (Fig. 4.4 a-b).

Interspecific competition with *D. melanurus* had a significant negative effect on *C. parasema* survival and this effect did not differ significantly between microhabitats (Table 4.3). The presence of *D. melanurus* decreased survival of *C. parasema* recruits by approximately 34% on *Acropora* reefs and at least 19% on *Pocillopora* reefs (Fig. 4.4 c-d). On *Pocillopora* reefs, the combined effects of the microhabitat and interspecific competitor caused *C. parasema* recruits to be completely eliminated on seven of the eight reefs where *D. melanurus* were present. However on all eight reefs with the more complex bottlebrush *Acropora* microhabitat, *C. parasema* recruits were able to persist in the presence of competitor *D. melanurus*.

Table 4.3 ANOVA testing effects of Microhabitat type (M), Density (D), and the Species Added (S; either *Chrysiptera parasema* or *Dascyllus melanurus*) on survival of *C. parasema*.

Effect	df	MS	F	P
Microhabitat (M)	**1**	**4.4181**	**99.3155**	**<0.0001**
Density (D)	2	0.1373	3.0862	0.0573
Species Added (S)	**1**	**0.5157**	**11.5937**	**0.0016**
D x M	2	0.0006	0.0129	0.9872
D x S	1	0.0031	0.0687	0.7948
M x S	1	0.1671	3.7566	0.0601
M x S x D	1	0.0099	0.2221	0.6401
Residual	38	0.0445		
Total	47			

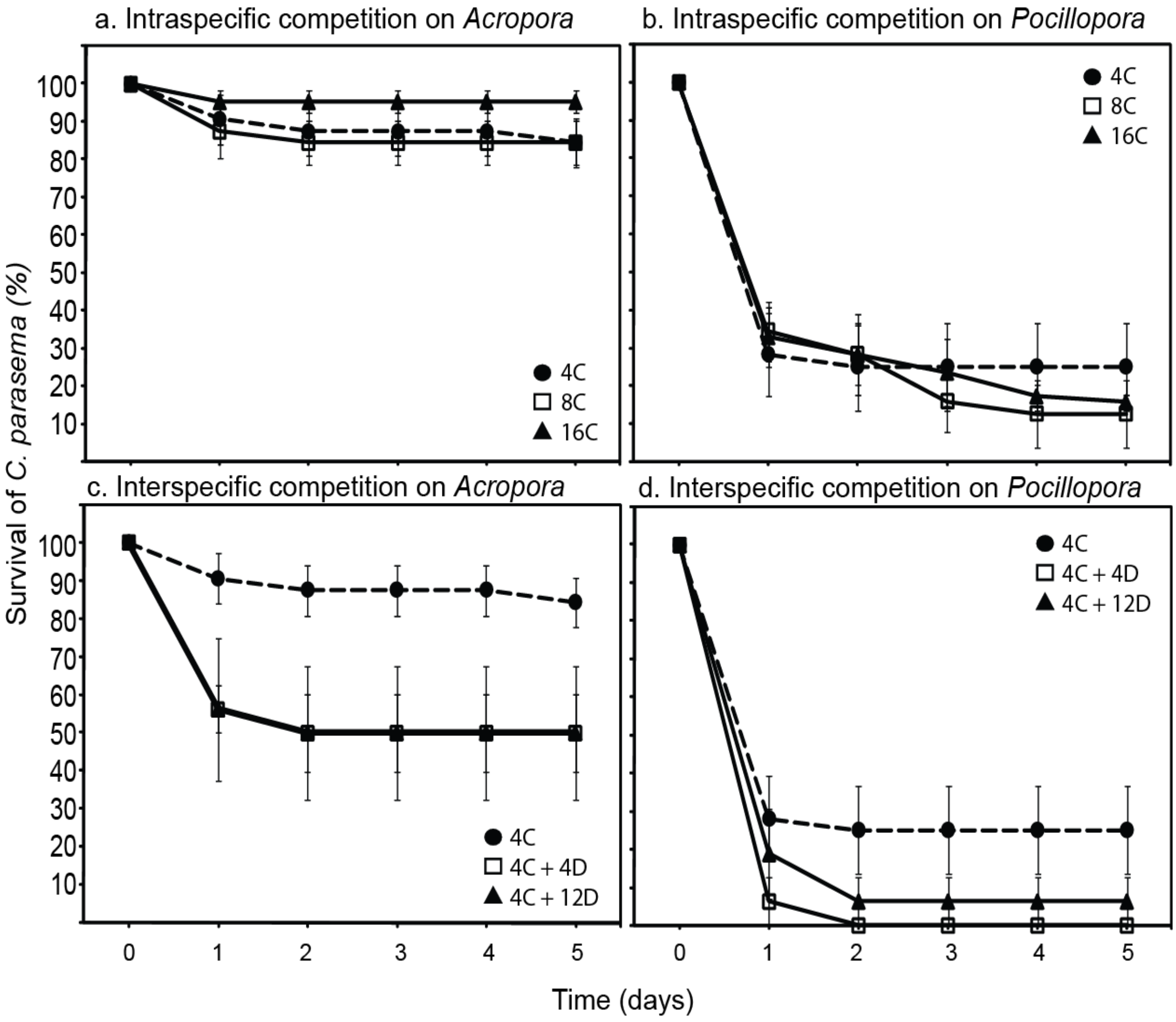

Figure 4.4 Comparison of the effects of intraspecific (a, b) and interspecific (c, d) competitor density on survival of recently settled *Chrysiptera parasema* in two microhabitats. In a-d total density for each treatment is 4 (circles, dashed line), 8 (squares), or 16 (triangles) individuals. Interspecific competition treatments in *Acropora* (c) and *Pocillopora* (d) consisted of 4 *C. parasema* with no interspecific competitors, or 4 *C. parasema* plus 4 or 12 *Dascyllus melanurus*. Error bars indicate ± 1SE.

In contrast to *C. parasema*, recently settled *D. melanurus* were negatively affected by conspecific density and there was no significant effect of microhabitat on survival (Table 4.4). At low densities (e.g. 4 individuals) *D. melanurus* survival remained at 100%, but a threefold increase in conspecific density caused a significant decrease in survival in both microhabitats (Fig. 4.5).

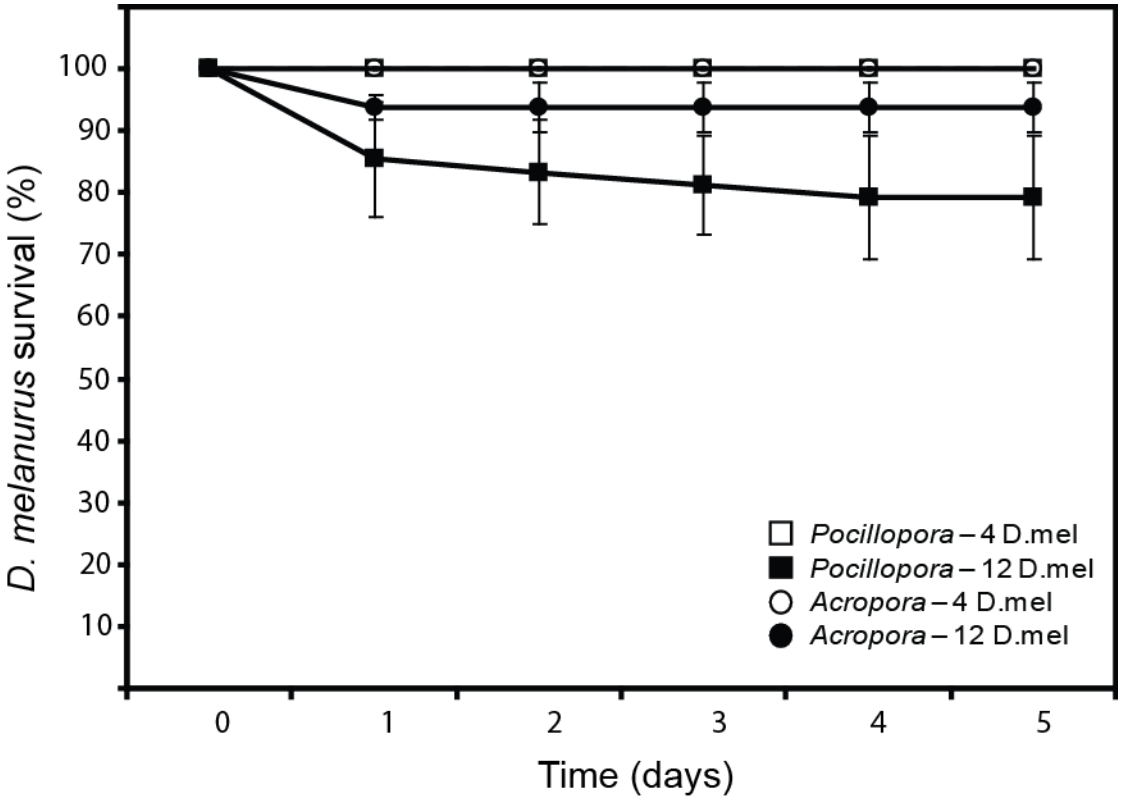

Figure 4.5 Effect of intraspecific density on survival of recently settled *Dascyllus melanurus* on *Acropora* (circles) and *Pocillopora* (squares) reefs. Open symbols represent treatments with a density of 4 *D. melanurus* and solid symbols represent treatments with a density of 12 *D. melanurus*. Error bars indicate ± 1SE.

Table 4.4 Two-way ANOVA testing for effects of intraspecific density (D) and microhabitat type (M) on survival of *Dascyllus melanurus*.

Effect	df	MS	F	P
Intraspecific Density (D)	**1**	**0.745**	**16.723**	**0.0015**
Microhabitat (M)	1	0.133	2.985	0.1097
D x M	1	0.133	2.985	0.1097
Residual	12	0.045		

4.5 DISCUSSION

This study confirmed that microhabitat and interspecific competition both influence the abundance and distribution of coral-dwelling fishes shortly after settlement. The two focal species, *Chrysiptera parasema* and *Dascyllus melanurus* selected and competed for similar coral microhabitats where their depth ranges overlapped. While *C. parasema* exhibited much better survival in its preferred microhabitat, its survival was substantially reduced by the presence of *D. melanurus* in this habitat and was not significantly influenced by conspecific densities. In contrast, survival of *D. melanurus* was independent of microhabitat type but was negatively affected by an increase in conspecific density.

We hypothesize that there is a significant asymmetry in the ability of recently settled *Chrysiptera parasema* and *Dascyllus melanurus* to compete for the shelter provided by live coral microhabitats. Hence, the presence of the dominant *D. melanurus* results in a higher predator-induced mortality on the inferior competitor, *C. parasema*. In support of this hypothesis, behavioral observations of interactions between recruits on the patch reefs consistently demonstrated *D. melanurus* to be the more aggressive species, instigating chases much more frequently than *C. parasema*. Previous studies have shown that dominant competitors can force subordinates to use suboptimal shelter sites within microhabitats (Holbrook and Schmitt 2002) or that they can restrict subordinates from accessing microhabitats altogether (Munday et al. 2001). Interactions with more aggressive competitors may also distract subordinate competitors, leading to reduced vigilance and increased conspicuousness to predators (Carr et al. 2002; Almany 2003). For the damselfish *Dascyllus flavicaudus*, intraspecific competition for refuge space in branching corals results in density-dependent predator-induced mortality that is evident within four days (Holbrook and Schmitt 2002). In addition to strong competition with the species, recently settled *Dascyllus flavicaudus* can also significantly reduce the abundance of subordinate competitor *Dascyllus aruanus* (Schmitt and Holbrook 1999). In this study a similar effect of interspecific competition between recently settled coral reef fish was observed, and the effect occurred quickly—the dominant *D. melanurus* reduced survival of *C. parasema* by more than 30% in only five days. These are the first studies to demonstrate interspecific competition between recently settled coral reef fish, and they suggest that asymmetric competition between settlers for microhabitat space has a strong influence on early post-settlement distribution and abundance in coral reef fish communities. The rapidity in which the competitive effect was detected in this study suggests that observed patterns of habitat use among recruits likely result from a combination of microhabitat selection and interspecific competition for shelter space.

The lack of a significant effect of intraspecific density on survival of recently settled *C. parasema* may indicate that the densities used in the patch reef experiment were not high enough to detect density dependence for this species. Indeed, *C. parasema* recruits are often observed aggregating in large groups of up to 50 individuals and survival on bottlebrush *Acropora* reefs tended to increase as group size increased. This result suggests that *C. parasema* may in fact benefit from group size at the densities tested, perhaps due to increased vigilance or an increase in the confusion effect as has been found for other schooling coral reef fish (Booth 1995; Sandin and Pacala 2005; Almany et al. 2007). In contrast, *D. melanurus* naturally occurs in smaller groups of up to 10 individuals (Limbourn et al. 2007) and this study showed that survival of *D. melanurus* decreased with increasing conspecific density suggesting that this species competes strongly for predator refuge within microhabitats. Considering the contrasting behavioral strategies of these two species, it is not surprising that the pugnacious *D. melanurus* had such a pronounced effect on the survival of *C. parasema*. These results highlight the importance of differences in behavioral ecology in determining the outcome of competition.

In addition to influencing patterns of microhabitat use, competitive asymmetries have also been shown to cause depth segregation between competing fish species in some temperate reef environments (Larson 1980; Hixon 1980). In Kimbe Bay we observed depth segregation in *D. melanurus* and *C. parasema*, with the dominant *D. melanurus* occupying the shallows from 3-6 m, and the subordinate *C. parasema* residing slightly deeper at 6-10 m. While not explicitly tested in the present study, several lines of evidence suggest that interspecific competition between *D. melanurus* and *C. parasema* restricts the depth distribution of *C. parasema*. Firstly, our study shows that *C. parasema* and *D. melanurus* prefer similar microhabitats, competition with *D. melanurus* can negatively affect the survival of *C. parasema*, and survival of *C. parasema* is poor in alternative microhabitats. Secondly, in the absence of interspecific competitors, growth and survival of *C. parasema* does not differ among deep and shallow reefs, whereas in contrast, *D. melanurus* recruits experience higher mortality and decreased growth at depths greater than 3 m (Srinivasan 2003). Finally, Srinivasan (2003) also showed that *C. parasema* expands its depth range when unoccupied patch reefs with a preferred microhabitat (e.g. bottlebrush *Acropora*) are provided. Thus, the apparent restriction of *C. parasema* to deeper reefs is not due to increased predator-induced mortality in the shallows or physiological limitations. It is also critical for *D. melanurus* to secure living space in the shallows. These lines of evidence suggest that the distribution of *C. parasema* is primarily determined by the availability of its preferred microhabitat, and that competition with the dominant *D. melanurus* excludes *C. parasema* from occupying this microhabitat in shallow water.

Despite the high diversity of microhabitats that coral reef fish encounter, this is one of the first studies to examine the influence of microhabitat on the intensity and outcome of competitive interactions in these communities. Microhabitat complexity may influence competitive dominance relationships (Ebersole 1985) and higher complexity microhabitats are typically expected to mitigate the negative effects of competition (Almany 2004a, b). In this study, the intensity of competition did not vary significantly between microhabitats and no reversal of competitive dominance was observed. Instead, *D. melanurus* was strongly dominant over *C. parasema* on both *Pocillopora* and higher complexity bottlebrush *Acropora* microhabitats. Although habitat complexity did not reduce the effect of competition between the asymmetric competitors in this study, any mitigating effect of habitat complexity is likely to be more pronounced when species have similar competitive abilities. Future studies investigating the influence of habitat complexity on the intensity of competition should consider the relative competitive abilities of experimental organisms.

Although habitat complexity did not have a strong influence on interspecific competition, differences in habitat complexity are likely to explain the differential survival of *C. parasema* between the two microhabitat types. Predation mortality of the planktivorous damselfish *Pomacentrus moluccensis* is higher in the open branching coral *Acropora nobilis* compared to the more complex branching coral *Pocillopora verrucosa* (Beukers and Jones 1997). In the present study survival of *C. parasema* on *P. verrucosa* and the more intricately-structured bottlebrush coral *Acropora elseyi* was compared and, like Beukers and Jones (1997), greater survival was documented in the more complex microhabitat. Taken together with the greater selectivity for corals with complex structures observed in the microhabitat use surveys, the significantly lower survival of *C. parasema* on a lower complexity microhabitat suggest that this species specializes on high complexity microhabitats. Although studies in other systems have also documented higher survival in more structurally complex habitats (Steele 1999; Arthur et al. 2005; Scharf et al. 2006), greater habitat complexity may also decrease survival for some species by making visual detection of predators more difficult (Rilov et al. 2007). Consequently, the effect of habitat complexity on survival will depend on the sensory and behavioral tactics used by prey and predators to detect one another.

In conclusion, this study suggests that observed patterns of habitat use and survival in coral reef fishes can be explained by a complex interaction between habitat preferences, competition and predation pressure. This study provides compelling evidence that interspecific competition for microhabitat space among recruits is an important structuring force in these communities. Furthermore, in light of the strong influence of microhabitat on survival of some coral-associated species, degradation to coral reef habitats is likely to have a considerable impact on the structure of coral reef fish communities.

CHAPTER 5: CONTRASTING EFFECTS OF HABITAT LOSS AND FRAGMENTATION ON CORAL-ASSOCIATED REEF FISHES †

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† **Bonin MC**, Almany GR, Jones GP (in press) Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* [doi:10.1890/10-0627.1]

5.1 ABSTRACT

Disturbance can result in the fragmentation and/or loss of suitable habitat, both of which can have important consequences for survival, species interactions and resulting patterns of local diversity. However, effects of habitat loss and fragmentation are typically confounded during disturbance events and previous attempts to determine their relative significance have proven ineffective. Here we experimentally manipulated live coral habitats to examine the potential independent and interactive effects of habitat loss and fragmentation on survival, abundance, and species richness of recruitment-stage, coral-associated reef fishes. Loss of 75% of live coral from experimental reefs resulted in low survival of a coral-associated damselfish, and low abundance and richness of other recruits 16 weeks after habitat manipulations. In contrast, fragmentation had positive effects on damselfish survival and resulted in greater abundance and species richness of other recruits. We hypothesize that spacing of habitat through fragmentation weakens competition within and among species. Comparison of effect sizes over the course of the study period revealed that in the first six weeks following habitat manipulations the positive effects of fragmentation were at least four times stronger than the effects of habitat loss. This initial positive effect of fragmentation attenuated considerably after 16 weeks, whereas the negative effects of habitat loss increased in strength over time. There was little indication that the amount of habitat influenced the magnitude of the effect of habitat fragmentation. Numerous studies have reported dramatic declines in coral reef fish abundance and diversity in response to

disturbances that cause the loss and fragmentation of coral habitats. Our results suggest that these declines occur as a result of habitat loss not habitat fragmentation. Positive fragmentation effects may actually buffer against the negative effects of habitat loss and contribute to the resistance of reef fish populations to declines in coral cover.

5.2 INTRODUCTION

Habitat loss and habitat fragmentation have both been identified as key drivers of population declines and biodiversity loss in marine and terrestrial ecosystems (Wilcox and Murphy 1985; Gray 1997; Brooks et al. 2002). However the independent effects of each process are typically confounded because disturbances often cause both the loss and fragmentation (i.e. the subdivision or breaking apart) of habitat. Effective management requires an understanding of both the independent and interactive effects of each process because mitigation strategies may differ depending on which factor is the primary cause of declines (Lindenmayer and Fischer 2007). An increasing number of observational (e.g. McGarigal and McComb 1995; Trzcinski et al. 1999; Villard et al. 1999) and experimental (e.g. Collins and Barrett 1997; Wolff et al. 1997; Caley et al. 2001; Hovel and Lipcius 2001) studies have addressed this problem by examining the effects of fragmentation independent of habitat loss (reviewed in Fahrig 2003). These studies suggest that the effects of habitat loss on measures of biodiversity (e.g. species richness, abundance) are consistently negative, although the effects of fragmentation are actually often positive, contrary to predictions from theory (e.g. Wilcox and Murphy 1985). These positive effects may arise as a result of increased immigration (Grez et al. 2004), reduced competition for resources (Collins and Barrett 1997; Wolff et al. 1997; Caley et al. 2001), or reduced predator abundance (Hovel and Lipcius 2001) in fragmented habitats, although further insight into the mechanisms that give rise to fragmentation effects is greatly needed (McGarigal and Cushman 2002).

An equally important question concerns the potential contrasting effects of habitat loss and fragmentation, and how these effects change with time after a disturbance. For example, if fragmentation effects are positive, the negative effects of habitat loss are likely underestimated by those studies unable to separate their effects. Most previous attempts to address this issue come from observational studies of forest bird communities that employ statistical methods to disentangle effects of fragmentation and loss (e.g. McGarigal and McComb 1995; Trzcinski et al. 1999; Villard et al. 1999). Although these studies collectively suggest that effects of fragmentation are weak compared to loss, recent work suggests that the statistical methods used to arrive at this conclusion are biased (Koper et al. 2007). Furthermore, few empirical studies have examined the potential interaction between loss and fragmentation. Theory suggests that fragmentation may only have negative effects when ≥70-80% of habitat is lost (Fahrig 1998; Flather and Bevers 2002), but this hypothesis has not yet been adequately tested (Fahrig 2003). Finally, very little is known about how the relative effects of loss and fragmentation change over time, although examination of this question could improve cross-study comparisons by providing insight into how relative effects may differ depending on the timescale of each study.

Previous work on the influence of habitat loss and fragmentation has largely focused on terrestrial ecosystems, and thus the impacts of these processes in the marine environment are not well understood. Coral reefs harbor a large proportion of marine biodiversity, are naturally patchy environments both at the landscape and local scale, and are likely to experience increased rates of habitat loss and fragmentation resulting from more frequent and intense disturbances. At the local scale, live coral loss resulting from spatially patchy disturbances (e.g. storms, coral bleaching, predation by crown-of-thorns starfish, coral disease) often creates fragments of surviving coral surrounded by reef pavement and coral rubble. Numerous studies have documented declines in the abundance and diversity of reef fishes with reductions in live coral cover (Jones et al. 2004; Garpe et al. 2006; Wilson et al. 2006; Pratchett et al. 2008; Holbrook et al. 2008), but it is unclear whether these changes occur primarily as a result of habitat loss, fragmentation or an interaction between the two. Effects of habitat fragmentation on reef fish communities have typically been inferred from studies that have used rarefaction curves to compare continuous reefs (i.e. a single large patch) to patch reef habitats while holding total reef area constant (Ault and Johnson 1998b; Acosta and Robertson 2002), and suggest that species richness in patchy habitats is equivalent to or greater than that of continuous reefs. However, whether similar patterns extend to recently fragmented habitats, or how patterns of abundance and diversity change over time after such a disturbance are currently unknown.

Although rarely undertaken, manipulative field experiments in which the amount and configuration of the habitat are experimentally controlled provide the most rigorous approach to evaluating the effects of habitat loss and fragmentation (McGarigal and Cushman 2002). In this study we experimentally separated the effects of habitat fragmentation and loss and examined the independent and interactive effects of these processes on survival, abundance and species richness of recruitment-stage, coral-associated fishes. Recruitment is the process by which reef fish communities are replenished following disturbance, so examining how recruitment responds to habitat loss and fragmentation is critical to predicting the impacts of disturbance on fish communities. Specifically, we addressed the following questions: (1) how does habitat fragmentation and habitat loss independently and interactively influence the survival, abundance and species richness of recruits; (2) what are the relative effects of habitat fragmentation and habitat loss, and how does this change with time after disturbance; and (3) does the total amount of habitat available alter the effect of fragmentation? We predicted that habitat fragmentation would have a positive effect on recruit survival, abundance and species richness, but that the effect of fragmentation would be weak relative to that of habitat loss.

5.3 METHODS

5.3.1 Study species

Bottlebrush corals of the genus *Acropora* are ideally suited to studying the separate influence of habitat fragmentation and habitat loss on coral reef fishes. At the study location, Kimbe Bay, Papua New Guinea (5°17´S, 150°17´E), bottlebrush *Acropora* are common on reef slopes and often occur in large monospecific thickets that cover more than 10 m^2 of the substrate (pers. obs.). Fragmentation is a common method of asexual reproduction for corals with this growth form (Wallace 1999), and storms can break apart these large thickets causing smaller fragments to settle on the reef slope below the original colony, a disturbance analogous to fragmentation without habitat loss. Fine branching corals like bottlebrush *Acropora* are also among those most susceptible to coral bleaching (Marshall and Baird 2000), which can create small patches of live coral embedded within the larger, otherwise dead colony (pers. obs), a process analogous to habitat loss and fragmentation occurring together.

The coral-associated fishes examined in this study specialize on *Acropora* habitats as recruits (Srinivasan 2006), and bottlebrush corals are frequently used as recruitment habitat by a wide variety of species (M.C. Bonin, unpublished data). The focal species used to measure how recruit survival responds to habitat loss and fragmentation, *Chrysiptera parasema*, is particularly dependent on bottlebrush *Acropora* (Chapter 2) and is a relatively weak competitor for habitat space (Chapter 4, Bonin et al. 2009). These ecological traits suggest that this species may be particularly vulnerable to the effects of habitat loss and fragmentation (Henle et al. 2004; Cushman 2006).

5.3.2 Experimental design

An array of 30 experimental reefs was arranged on a large, isolated sand flat at a depth of 5-10 m. Reefs were separated from each other by 15 m to inhibit the movement of recruits between reefs. Each reef consisted of a foundation of dead coral rubble surmounted by live colonies of the common bottlebrush *Acropora subglabra* attached with monofilament. Initially, each reef was standardized to an overall circumference of 3.5 m with 1 m^2 of live coral. Each reef was cleared of any existing fishes and then stocked with 20 newly-settled *C. parasema* collected from live corals using clove oil (an anesthetic) and hand nets. Transplanted fish were approximately 1-2 weeks post-settlement. A random sample of 10 fish from each group of 20 was measured and mean (SD) size was 8.91 (0.59) mm standard length (SL). There was no significant difference in the group mean size of fishes among treatments (One-way ANOVA: $F_{3,23} = 0.37$, $p = 0.778$). The reefs were stocked over several days and transplanted fish were allowed to acclimate for one week prior to habitat manipulations.

Reefs were randomly assigned to one of five habitat manipulation treatments (Fig. 5.1) with six replicates per treatment: (1) *control* (left undisturbed throughout the study); (2) *disturbance control* (habitat removed, shaken by divers for 2 min, and replaced); (3) *fragmentation* (reef divided into three equal-sized fragments arranged in a triangular pattern with fragments separated from each other by 1 m); (4) *75% loss* (live coral area reduced from 1 m^2 to 0.25 m^2), and (5) *75% loss + fragmentation* (live coral area reduced from 1 m^2 to 0.25 m^2 and reef divided into three equal-sized fragments arranged in a triangular pattern with fragments separated from each other by 1 m). Note that the 75% habitat loss in treatments 4 and 5 corresponds to theoretical prediction at which fragmentation is likely to have negative effects on population size (Fahrig 1998; Flather and Bevers 2002).

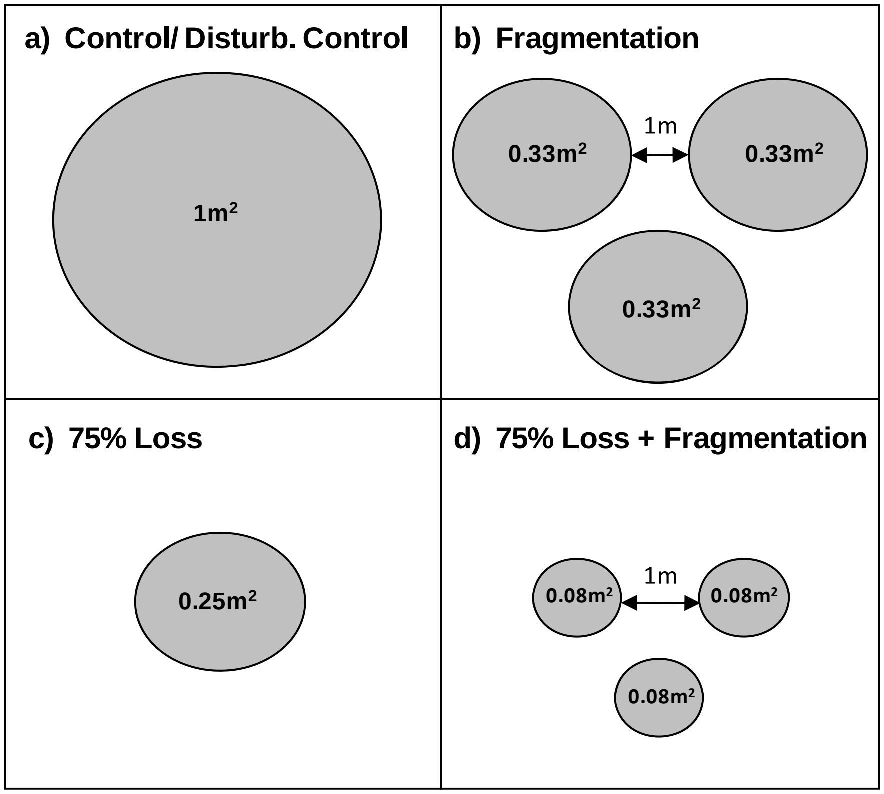

Figure 5.1 Experimental design. Shaded areas represent the amount and spatial configuration of live coral (*Acropora subglabra*) in each of the experimental habitat treatments: a) control and disturbance control, b) fragmentation, c) 75% loss and d) 75% loss + fragmentation.

Habitat manipulations were conducted over several days and after the one week acclimation period, reefs were censused once per week for the first 6 weeks, at 8 weeks and at 16 weeks to both monitor the abundance of transplanted fish and remove any naturally settled *C. parasema*. Twenty-six *C. parasema* settlers were removed from the reefs over the study period, and were easily distinguished from transplanted recruits due to their smaller body size and pale coloration. Other species of coral-associated fish were allowed to settle naturally to experimental reefs and the abundance and species richness of these settlers were censused at 2, 6 and 16 weeks following habitat manipulations. Because damselfish recruits are known to be highly site-attached and dependent on shelter for protection from predators, we considered movement between experimental reefs across 15 m of featureless sand unlikely (Doherty 1982). Therefore the disappearance of a transplanted *C. parasema* recruit between censuses was attributed to mortality rather than emigration. In support of this assumption, we never observed increases in the abundance of transplanted recruits on any reef, which would indicate movement between reefs.

5.3.3 Analyses

Two-way factorial ANOVAs were used to examine effects of habitat loss and fragmentation on *C. parasema* recruit survival and on the abundance and species richness of other recruits at 16 weeks. In addition, we used one-way ANOVAs to test whether there were differences among treatments at week 16 in the abundance of piscivores that had naturally colonized reefs during the study period. For reefs in the two fragmentation treatments (3 and 5) data were pooled across the three fragments to provide a response for that reef. Because there was no difference between *control* and *disturbance control* on the survival of *C. parasema* (One-way ANOVA: $F_{1,8}=0.064$, $p=0.807$), or abundance (One-way ANOVA: $F_{1,8}=0.010$, $p=0.923$) and species richness of other recruits (One-way ANOVA: $F_{1,8}=0.110$, $p=0.748$) two weeks after habitat manipulations, these two treatments were combined into a single control treatment for all analyses. Live coral on two control reefs (treatment 1) and one fragmentation reef (treatment 3) died during the study period due to infestation by corallivorous *Drupella* sp. snails. These reefs were omitted from analyses and Type III Sums of Squares was used to account for unequal sample size between treatments. Normal probability plots and Levene's test results were examined prior to each analysis to ensure that data met underlying assumptions of normality and homogeneity of variance. Abundance data for *C. parasema* was log transformed to improve homoscedasticity.

The relative magnitude of the effects of habitat fragmentation and loss were assessed by calculating the standardized difference between means, also known as the *d*-index (Cohen 1988). Therefore the effect size was equivalent to the difference between the mean of the treatment and the control, divided by the pooled within-group standard deviation (see Gurevitch et al. 1992 for an ecological example that includes equation details). Although numerous metrics are available for calculating effect size (see Osenberg et al. 1999), this metric was chosen because interpretation of the sign and magnitude of *d* was straightforward and it produced similar conclusions as other ecological metrics. The sign of *d* indicates the effect of the treatment on the response variable. In this study, a positive sign indicates an increase in abundance or species richness whereas a negative sign indicates a decline in abundance or species richness. Cohen (1988) suggests that d=0.2 would indicate a relatively weak effect, d=0.5 an intermediate effect, and d=0.8 a relatively strong effect of habitat fragmentation or loss. All statistical analyses were conducted using STATISTICA 9.0 (Statsoft Inc. 2009).

5.4 RESULTS

5.4.1 Recruit survival

One week after stocking each reef with 20 individuals, mean (SD) *C. parasema* recruit abundance was 18.2 (1.50) and was similar between treatments (Fig. 5.2). Following habitat manipulations, abundance declined on all treatments, treatments began to diverge after 8 weeks, and after 16 weeks abundance was lowest on reefs where 75% of live coral habitat had been removed (Fig. 5.2). There was a significant interactive effect of habitat loss and fragmentation on *C. parasema* abundance at 16 weeks (Table 5.1a); on reefs without habitat loss fragmentation did not affect survival, whereas on reefs where 75% of live coral was removed, fragmentation increased survival (Fig. 5.3a).

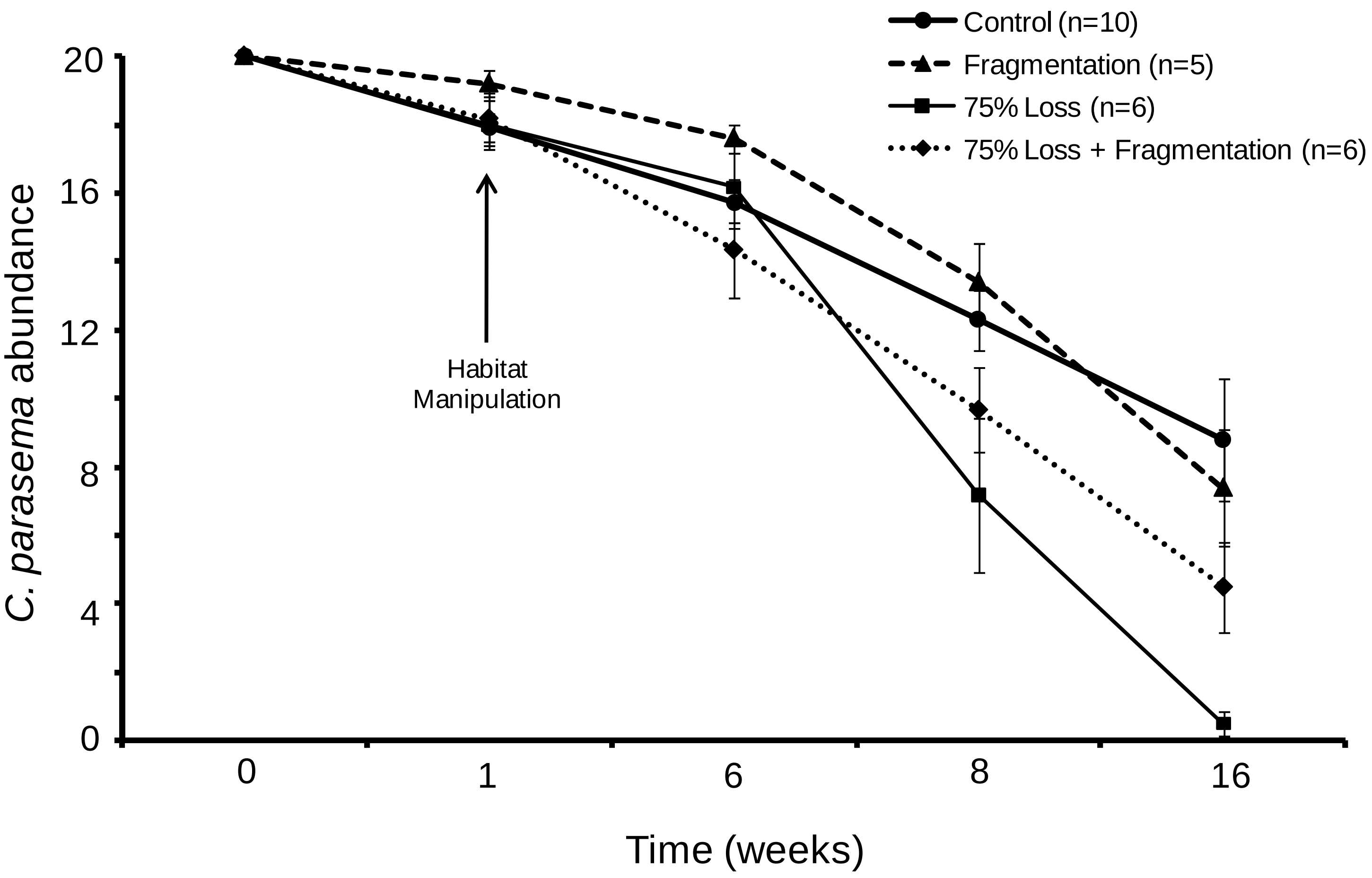

Figure 5.2 Relationship between mean abundance (±SE) of transplanted *C. parasema* recruits and habitat treatments over 16 weeks. Each reef was initially stocked with 20 *C. parasema* recruits and habitat manipulations took place after a one week acclimation period.

Table 5.1 Results of two-way ANOVAs testing effects of habitat treatments on (a) survival of stocked *C. parasema* recruits and the (b) abundance and (c) species richness of other coral-associated recruits that settled naturally during the experiment. Asterisks denote a significant effect ($P < 0.05$).

Source of Variation	df	MS	F	*P*
(a) Abundance of *C. parasema*				
Habitat Loss	1	1.528406	18.95155	0.000233**
Habitat Fragmentation	1	0.441057	5.468916	0.028414**
Interaction	1	0.47482	5.887551	0.023495**
Error	23	0.080648		
(b) Abundance of other recruits				
Habitat loss	1	4.5632	1.58300	0.220953
Habitat Fragmentation	1	26.5421	9.20767	0.005894**
Interaction	1	1.2789	0.44368	0.511979
Error	23	2.8826		
(c) Species richness of other recruits				
Habitat loss	1	5.70000	7.16393	0.013476**
Habitat Fragmentation	1	8.35263	10.49784	0.003615**
Interaction	1	0.14211	0.17860	0.676502
Error	23	0.79565		

Table 5.2 Relative magnitude of the effects of habitat loss and habitat fragmentation on survival of transplanted *C. parasema*, and abundance and species richness of coral-associated recruits at 6 weeks and 16 weeks following habitat manipulations. Effect sizes calculated using the *d*-index (See Methods). An effect size of 0.2 indicates a relatively weak effect and an effect of 0.8 or greater indicates a relatively strong effect of the habitat treatment. The sign of the effect indicates whether the treatment caused an increase or decrease in the response variable.

Time after habitat manipulations	Effect	*C. parasema* abundance	Abundance	Species richness
6 weeks	Fragmentation	0.90	3.02	2.04
	Loss	0.20	-0.21	-0.20
16 weeks	Fragmentation	-0.26	0.90	1.21
	Loss	-1.73	-0.82	-0.72

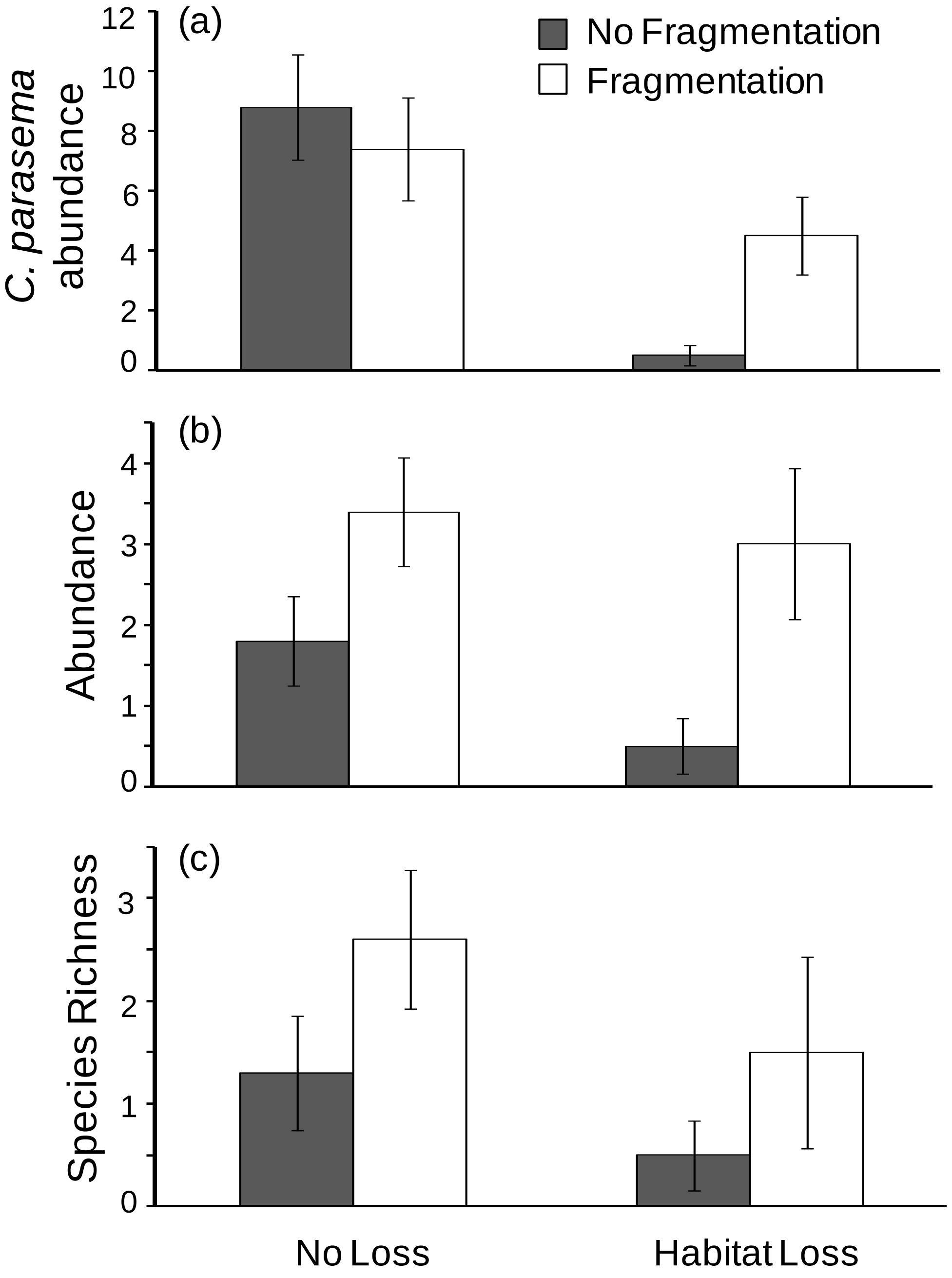

Figure 5.3 Interactive effects of habitat loss and fragmentation on (a) abundance of transplanted *C. parasema* recruits and (b) total abundance and (c) species richness of other coral-associated recruits that settled naturally to experimental reefs 16 weeks after habitat manipulations. Error bar ± 1 SE.

The relative magnitude of the effects of habitat loss and fragmentation changed over time (Table 5.2). In the short-term (at 6 weeks), fragmentation had a positive effect on *C. parasema* survival that was 4.5 times stronger than the comparatively weak effect of habitat loss. However, after 16 weeks the positive effect of fragmentation had diminished and the negative effect of habitat loss had increased; at 16 weeks the effect of habitat loss was 6.6 times stronger than the relatively weak effect of habitat fragmentation.

5.4.2 Recruit abundance and species richness

A total of 147 individuals of nine species of coral-associated fishes recruited naturally to experimental reefs during the study period; the butterflyfishes (Chaetodontidae) *Chaetodon octofasicatus* (n=68) and *C. lunulatus* (n=11), and the damselfishes (Pomacentridae) *Dascyllus melanurus* (n=22), *Pomacentrus aurifrons* (n=21), *D. trimaculatus* (n=14), *P. nigromanus* (n=6), *D. reticulatus* (n=3), *Chromis retrofasciata* (n=1) and *C. ternatensis* (n=1). Fragmentation influenced total recruit abundance and species richness at 16 weeks, whereas habitat loss only affected species richness (Table 5.1 b-c). Two weeks after habitat manipulations experimental reefs had similar abundance and species richness, but at 6 weeks abundance and richness were 4 times and 3 times greater, respectively, on fragmented reefs relative to control reefs (Fig. 5.4 a-b). Although both abundance and richness declined on fragmented reefs between 6 and 16 weeks, the positive effect of fragmentation persisted (Table 5.1 b-c). At 16 weeks recruit abundance and species richness were both greater on fragmented reefs compared to non-fragmented reefs regardless of the amount of available habitat (Fig. 5.3 b-c), and the interaction between loss and fragmentation was not significant (Table 5.1 b-c).

Contrary to expectations, and similar to the results for *C. parasema*, the positive effects of fragmentation were much stronger than the negative effects of habitat loss 6 weeks following

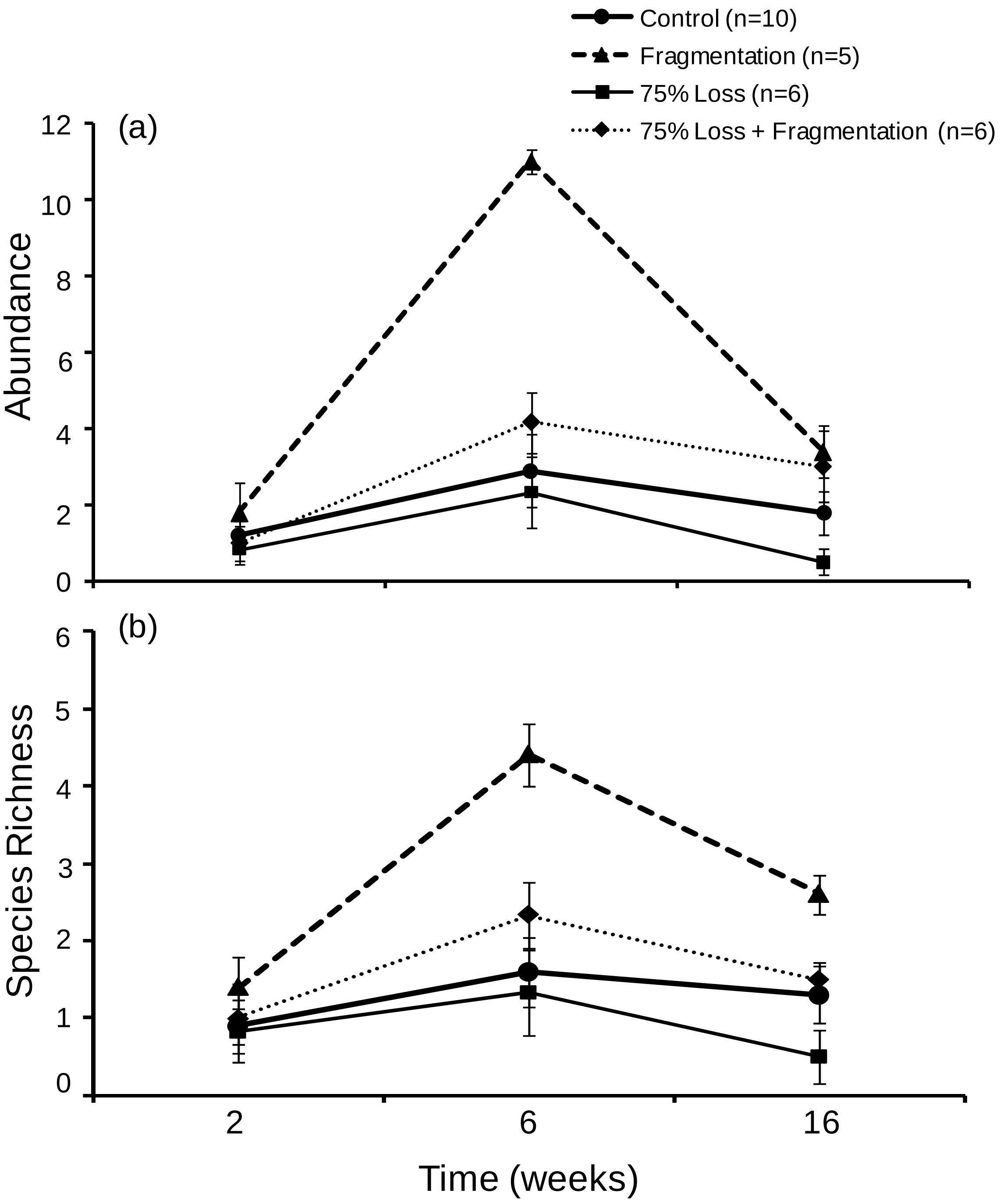

Figure 5.4 Effects of habitat treatments on (a) abundance and (b) species richness of coral-associated fishes that settled naturally to experimental reefs at 2 weeks, 6 weeks and 16 weeks after habitat manipulations. Error bar ± 1 SE.

habitat manipulations. Comparison of effect sizes at 6 weeks indicates that fragmentation effects on recruit abundance and species richness were 14 times and 10 times greater, respectively, than the relatively weak effects of habitat loss (Table 5.2). Over time, the negative effects of habitat loss increased, whereas the magnitude of the positive effect of fragmentation declined. After 16 weeks, habitat fragmentation and loss both had strong effects on recruit abundance and diversity that were relatively equivalent in magnitude but opposite in direction (Table 5.2).

5.4.3 Predator abundance

Abundance of potential predators of recruits at 16 weeks did not differ significantly among treatments. Schools of juvenile snappers (Lutjanidae) were present on all but two reefs, but their abundance did not differ significantly among treatments (One-way ANOVA: $F_{3,23}=1.82$, p=0.172). Larger piscivorous fishes – the snappers *Lutjanus timorensis* and *L. vitta*, the sea basses (Serranidae) *Cephalopholis boenak* and *Epinephelus areolatus*, and the scorpionfish (Scorpaenidae) *Pterois volitans*) – also colonized experimental reefs, although again, their collective abundance did not differ among treatments (One-way ANOVA: $F_{3,23}=0.50$, p=0.686).

5.5 DISCUSSION

Disturbance mediated habitat loss and fragmentation is a major conservation and management concern given that the rate and intensity of disturbance is predicted to increase due to climate change (Hughes et al. 2003; Hoegh-Guldberg et al. 2007). Management strategies designed to counter the negative effects of disturbance on populations and communities can differ depending on whether habitat loss or fragmentation is the dominant threat. For example, where habitat fragmentation poses the greatest threat, facilitating dispersal and protecting connectivity may be a priority, whereas if habitat loss poses the greatest risk, a focus on protecting larger areas of habitat may be justified (Lindenmayer and Fischer 2007). Disentangling the effects of habitat loss and fragmentation have proven difficult, but available evidence suggests that fragmentation may often have positive effects that counter the typically negative effects of habitat loss (reviewed in Fahrig 2003). A greater understanding of the independent and interactive effects of loss and fragmentation will therefore be useful in predicting the impacts of disturbance in natural systems and developing appropriate mitigation strategies.

In the present study, habitat loss alone had a strong negative effect on survival of transplanted damselfish (*C. parasema*) recruits, whereas fragmentation alone had little effect on survival four months after habitat disturbance. However, fragmentation had a positive effect on survival when 75% of the habitat was removed. One of the most important resources habitat provides is shelter from predators, and this is especially true for vulnerable coral reef fish recruits. During this life-history stage, recruits typically suffer high rates of mortality from predators (Hixon and Webster 2002; Almany and Webster 2006) and previous studies indicate that competition for shelter is often intense and can significantly reduce recruit survival (Schmitt and Holbrook 1999; Bonin et al. 2009). In the present study, the loss of 75% of the habitat likely intensified competition for space, which could explain the lower survival observed on habitat loss treatments. However, where habitat was reduced by 75%, fragmentation of the remaining habitat resulted in better survival relative to the habitat loss treatment without fragmentation. This result contrasts with studies that have reported reduced survival in fragmented habitats due to greater exposure to predators at habitat edges, the amount of which increases in fragmented habitats (e.g. Brittingham and Temple 1983; Andrén and Angelstam 1988).

What could have caused this positive effect of fragmentation on survival in this study? We hypothesize that reduced interference competition for shelter in fragmented habitats led to greater *C. parasema* survival. Agonistic interactions among recruits can make them more vulnerable to opportunistic predators (Holbrook and Schmitt 2002). Where recruits occurred on a single patch, they likely experienced more frequent agonistic interactions and suffered greater predator-induced mortality. Increasing the distance between habitat patches has been shown to significantly reduce the frequency of these agonistic interactions (Levin et al. 2000), so the separation of recruits onto discrete habitat fragments may have increased survival by decreasing the frequency of agonistic interactions and predation. This benefit of fragmentation is unlikely on reefs where space is not limiting, which may explain why fragmentation effects were minimal on reefs with no habitat loss.

Caley et al. (2001) reported similar positive effects of habitat fragmentation on the abundance of the commensal coral crab *Trapezia cymodoce*, which are highly territorial and actively expel any conspecifics that attempt to colonize their home coral colony. By partitioning corals into separate, smaller fragments, more territorial individuals were able to colonize and inhabit the same total amount of habitat. Given that several other studies have also reported positive fragmentation effects as a result of reduced competition (i.e. Collins and Barrett 1997; Wolff et al. 1997), this appears to be a common mechanism underlying positive fragmentation effects.

In addition to increasing survival of *C. parasema* recruits, habitat fragmentation also enhanced recruitment of other fish species. The abundance and species richness of coral-associated recruits that settled to experimental reefs was higher on fragmented habitat during the study, results similar to those from observational studies comparing patchy and continuous reef habitats (e.g. Acosta and Robertson 2002). Much ecological theory suggests habitat patchiness can increase species coexistence (reviewed by Hanski 1995). For example, subdivision of habitat can allow inferior competitors to find refuge on habitat patches that are not occupied by competitively superior species (Slatkin 1974; Atkinson and Shorrocks 1981; Hanski 1983). In our study, fragmentation of reefs created more discrete patches that could be colonized by settling recruits and likely increased the probability that settlers would find habitat not already occupied by a competitive superior. Because post-settlement survival increases greatly after a few days on the reef (Hixon and Webster 2002; Almany and Webster 2006), initial occupation of patches with less competition could be an important mechanism for surviving this early post-settlement period. Field observations of the distribution of species on fragmented and non-fragmented reefs support this hypothesis. For example, three congeneric, highly territorial and aggressive damselfish (*Dascyllus* spp.) that settled during the study never co-occurred on non-fragmented habitat, but on some fragmented reefs several species were distributed across the three patches. Whatever the mechanism, these results emphasize the need to separate the effects of habitat fragmentation from habitat loss and support the growing body of evidence that fragmentation effects are often positive and therefore unlikely to be the primary cause of biodiversity loss (e.g. Fahrig 2003; Yaacobi et al. 2007).

An alternative explanation for the effects on survival and recruitment could be differences in predator distributions between fragmented and non-fragmented reefs. For example, Hovel and Lipcius (2001) documented higher survival of juvenile blue crabs in fragmented seagrass habitat because the crab's primary predator was less abundant in this habitat. However, in the present study there was no difference in predator abundance between fragmented and non-fragmented reefs.

Statistical approaches to assessing the relative effects of habitat loss and fragmentation have prevailed in the literature, whereas comparatively few studies have examined this question experimentally (but see Wolff et al. 1997; Caley et al. 2001). Although the collective implications of studies using the statistical approach suggest that effects of fragmentation are weak relative to those of habitat loss, significant biases associated with this methodology have renewed the need to examine this issue (Koper et al. 2007). We quantified the relative effects of loss and fragmentation by comparing response data at two time periods following habitat manipulations. We found that in the early sampling period the positive effects of habitat fragmentation on survival of *C. parasema*, and on abundance and species richness of recruits, were much stronger than the effects of habitat loss. Over time, the negative effects of habitat loss increased in magnitude whereas the positive effects of fragmentation declined. After 16 weeks the negative effect of habitat loss on *C. parasema* survival was considerably stronger than that of fragmentation, whereas for abundance and richness of other recruits, the effects of the two factors were similar in magnitude but opposite in sign. Whether such strong, short-term effects of habitat fragmentation are common is unknown because many studies reporting weak or no fragmentation effects are based on surveys of habitats in which many years have elapsed since disturbance (e.g. McGarigal and McComb 1995; Trzcinski et al. 1999; Villard et al. 1999). Future studies should consider that the relative magnitude of habitat loss and fragmentation effects may depend on how much time has elapsed since the disturbance.

Why did fragmentation effects decline over time on experimental reefs? In the initial weeks following habitat manipulations recruits were small and site attached, and thus unlikely to interact frequently with individuals on other fragments. However in the longer-term, the positive effect of fragmentation likely gained through separation of competitors may have declined as recruits grew into juveniles and expanded their range of movement to include other habitat fragments. In support of this hypothesis, we observed no movement of recruits between fragments during the early sampling period, but after 16 weeks the older and larger juveniles were often observed moving between fragments and interacting with one another. Thus as recruits grew larger, their space requirements likely increased, causing greater competition. Greater spacing between habitat fragments to inhibit inter-fragment movement may have prevented the positive effect of fragmentation from declining over time, and future experiments varying inter-fragment distance could be used to test this hypothesis.

This is one of the few studies to experimentally test for interactive effects of habitat loss and fragmentation. Theory suggests that fragmentation may only have negative effects when ≥70-80% of habitat is lost (Fahrig 1998; Flather and Bevers 2002). However, in the present study we found a significant interaction between habitat loss and fragmentation for only one of the three measured response variables; fragmentation influenced *C. parasema* survival only when habitat cover was reduced by 75%, but contrary to theory, this effect was positive, not negative. Based on this result, empirical support for the threshold theory is limited.

Coral reefs are subject to numerous disturbances which result in the loss and fragmentation of coral habitats and the detrimental effects of these disturbances on coral reef fish communities are well documented (Jones et al. 2004; Garpe et al. 2006; Wilson et al. 2006; Pratchett et al. 2008). However it was previously unclear if declines in reef fish abundance and diversity occur as a result of habitat loss, fragmentation or an interaction between the two. Our results suggest that habitat loss, not habitat fragmentation, is the primary cause of these declines and are therefore consistent with the view that preventing habitat loss is a critical priority for conservation of biodiversity. More often than not, habitat loss and fragmentation will occur together and our study suggests that positive fragmentation effects may actually buffer against the negative effects of habitat loss and contribute to the resistance of reef fish populations to declines in coral cover. Although not a landscape-scale study, patch-scale studies such as ours can aid in understanding the mechanisms underlying fragmentation effects (McGarigal and Cushman 2002). Whether the patch-scale patterns documented here apply to the larger reefscape is currently unknown, but should be emphasized in future research given the increasing degradation of coral reef habitats worldwide.

CHAPTER 6: GENERAL DISCUSSION

The current extent of the degradation of coral reefs and the predicted global losses due to climate change jeopardize the future of reef fishes, particularly those that are dependent on corals for essential habitat. This thesis has provided significant insights into the consequences of coral habitat degradation for some of the most vulnerable members of the reef fish community - the coral specialists. The four different thesis chapters employed a diversity of observational and experimental approaches to help understand the complex relationships between these specialists and their underlying habitat. While many of the expected ecological costs of specialization in degrading environments were confirmed, an unexpected level of resistance to some levels of disturbance, and even some benefits to disturbance, were documented.

Chapter 2 provided the first coral species-specific view of habitat associations in coral-associated damselfishes and identified four species that are most at risk due to their obligate dependence on branching coral as recruitment microhabitat and the degree to which they are specialized on a narrow range of coral species. In the first study to examine the immediate response of coral reef fishes to habitat bleaching *in situ*, Chapter 3 revealed that the settlement of coral specialists is not disrupted by bleaching, although their early post-settlement persistence is adversely affected by habitat degradation. Given the apparent importance of post-settlement processes in driving declines in coral reef fish abundance following disturbance, Chapter 4 explored the effects of competitive interactions on early post-settlement survival and is the second study to demonstrate that interspecific competition for space can significantly reduce survival of inferior competitors. Finally, Chapter 5 provided the first experimental separation of the effects of habitat loss and fragmentation on coral reef fishes and revealed that the loss of coral habitats has significant negative consequences for recruit persistence and diversity, whereas fragmentation effects were actually positive. The implications of these findings for understanding the effects of continued habitat degradation on reef fish communities are discussed below.

How specialized are reef fishes?

The high degree of specialization on particular coral species as recruitment microhabitat revealed in Chapter 2 provides further support for the emerging realization (e.g. Munday et al. 1997; Holbrook et al. 2000) that microhabitat use among reef fishes is likely to be much more specialized than is currently appreciated. Fish almost certainly perceive of differences among microhabitats at a much finer scale than our survey techniques typically account for and greater effort at quantifying microhabitat use at a higher resolution is likely to be rewarded with significant advancement in our understanding of the microhabitat requirements of reef fishes. The results presented in this thesis suggest that the common practice of grouping corals into growth forms may prevent us from accurately monitoring changes in the availability of suitable habitats because fish may associate with only a few coral species within a growth form and largely avoid the rest. In addition to the species of coral, the size of the colony and the surrounding substrate may further limit the suitability of the microhabitat (Sale 1972; Elliot et al. 1995; Holbrook et al. 2000). The availability of high quality microhabitats is therefore likely to be greatly overestimated using current survey techniques. As coral reefs are degraded further it will become increasingly important to accurately monitor the availability of microhabitats that are critical to species persistence, yet this can only be achieved through improved understanding of their fundamental microhabitat requirements.

The ecological cost of specialization

If coral bleaching becomes a frequent disturbance on corals reefs, as has been widely predicted (Donner et al. 2005; Hoegh-Guldberg et al. 2007), it will begin to regularly coincide with the settlement events that typically serve to replenish reef fish populations. The results of several laboratory studies suggest that settlers avoid degraded microhabitats (Öhman et al. 1998; Feary et al. 2007a) and this behavior could potentially lead to recruitment failure during bleaching. However, Chapter 3 revealed that in a natural reef environment even the coral specialist *P. moluccensis* will settle to coral microhabitats that are degraded by severe bleaching. Moreover, the early post-settlement persistence of these recruits is not negatively affected if the bleached coral they settle to recovers. These insights suggest that when bleaching events coincide with settlement pulses it is unlikely to disrupt population replenishment provided that bleaching does not result in widespread coral mortality. However, recent settlers quickly vacate corals that die from bleaching (Chapter 3), presumably in search of suitable live coral microhabitat. Because these recent settlers are unlikely to successfully re-locate due to intense competition over microhabitat space (Chapter 4) and high risk of predation (Almany and Webster 2006), severe bleaching events that cause extensive coral mortality may significantly reduce population replenishment due to high rates of early post-settlement mortality.

In this era of extensive coral reef degradation, high quality recruitment microhabitats will become increasingly limited resources and the loss of these critical resources will have the greatest consequences for coral specialists. The particular corals on which recruits specialize are often those that afford the best protection from predators (Chapter 4) and this increased survival may represent a significant benefit of specialization. However species that adopt a strategy of habitat specialization are likely to benefit by a lower risk of predation, but at a cost of increased competition over habitat space (Jones and McCormick 2002). This competition for space can significantly reduce the survival of inferior competitors (Chapter 4) and is likely to become even more intense as the availability of critical recruitment microhabitat declines. The continued degradation of coral reef habitats may tip the balance so that the cost of microhabitat specialization (i.e. competition for space) outweighs the benefits (i.e. protection from predators).

Specialized species that are not strong competitors for space are unlikely to persist in areas where their preferred microhabitats are scarce. The results presented in this thesis suggest that *C. parasema* is one such species. Recruits of this damselfish are the most specialized of the coral-associated damselfish community in their use of corals as recruitment microhabitat (Chapter 1) and they experience a high cost of 60% greater predation mortality if they occupy non-preferred coral species (Chapter 4). They are also poor competitors for space in their preferred corals, with the presence of interspecific competitor *D. melanurus* reducing survival of *C. parasema* recruits by up to 34% (Chapter 4).

The finding that specialists can be poor competitors apparently contradicts theory that suggests specialists should have a competitive edge over generalists when using their preferred resource (McNally 1995). Other researchers have also presented evidence against this theory for reef fishes (i.e. Berumen and Pratchett 2008) and in general there is little empirical support for the notion that specialists outperform generalists on their preferred resources (Futuyma and Moreno 1988; but see Caley and Munday 2003 for only known example). However a species' ecological versatility is determined by multiple niche axes and it is possible that although *C. parasema* is highly specialized in its microhabitat use, it is a generalist along other niche axes and this flexibility has allowed it to co-exist despite its poor competitive abilities. Indeed, Srinivasan (2003) demonstrated that *C. parasema* recruits are generalists when it comes to their depth distributions on coral reefs, whereas *D. melanurus* are restricted only to the shallows. Habitat specialized *C. parasema* recruits may therefore have a depth refuge from superior space competitors such as *D. melanurus*. Although this depth refuge may reduce the negative effects of increased competition for *C. parasema*, its' high degree of microhabitat specialization and poor capacity for survival on alternative microhabitats still place this species at significant risk of population decline as result of coral reef degradation.

Habitat loss versus fragmentation

Declines in the abundance of coral-associated reef fishes following disturbances that reduce live coral cover have been widely documented (reviewed by Wilson et al. 2006) and this thesis has identified that habitat loss, but not habitat fragmentation, is responsible for these declines (Chapter 5). Loss of 75% of the coral habitat reduced the survival of *C. parasema* recruits by 95% and also decreased the total abundance and species richness of settlers to the habitat patch. Disturbances to coral reefs (e.g. storms, coral bleaching) often result in 50-90% reductions in coral cover (Wilson et al. 2006) so this degree of habitat loss is well within the range typically experienced by coral reef fishes following disturbance. Declines in the abundance of coral-associated species may therefore manifest due to reduced survival of the recruits that would typically replenish their populations.

The discovery that habitat fragmentation significantly improved recruit persistence and diversity when habitat space was limited (Chapter 5) has several important implications for the monitoring and conservation of coral reef fish communities in degraded environments. First, this finding may provide insight into observations that fish communities are resistant to significant reductions in coral cover (e.g. Holbrook et al. 2008). Rather than species actually being unaffected by significant loss of habitat, the positive effects of habitat fragmentation may just mask the negative effects of habitat loss. Consequently, it is important to recognize that we may often under-estimate the negative effects of habitat loss when monitoring the response of fish communities to disturbances that also result in increased habitat patchiness. Furthermore, although we may prefer to dive on reefs that have large continuous stands of live coral, such habitat continuity does not appear necessary to maintain highly abundant and diverse reef fish communities. Future projects that aim to restore coral and fish communities on degraded reefs may therefore benefit from patchy placement of coral transplants.

Future research and conclusions

The insights arising from this thesis suggest several key areas for future research. First, the finding that damselfish recruits can be highly selective in their use of certain coral species as microhabitat emphasizes the critical gap that exists in our knowledge of the dependence on corals as recruitment microhabitat in the reef fish community (Wilson et al. 2010). It has been suggested that up to 65% of the fish species on coral reefs require corals as recruitment microhabitat (Jones et al. 2004) and this estimate needs to be tested through more research into the settlement microhabitats used by a wider range of coral reef fish families and species. Second, the observation that coral-associated species will recruit to severely bleached corals and are resistant to vacating these microhabitats despite substantial degradation highlights the importance of understanding the sub-lethal effects of living in degraded habitats. To my knowledge only two studies to date have examined this issue; one found that inhabiting a bleached coral had no significant effect on growth and body condition of coral reef fish recruits (McCormick et al. 2010) whereas another found significantly lower growth, but not body condition, of recruits that persisted on dead corals (Feary et al. 2009). Clearly more research into sub-lethal effects (e.g. growth, condition, reproduction) are required to improve our understanding of the long-term consequences of inhabiting degraded coral reef environments. Finally, as this was the very first study to examine the effects of habitat fragmentation on reef fish abundance and diversity, fragmentation effects require further investigation. The positive effects of fragmentation revealed here are likely to be dependent on both the degree of isolation of habitat fragments and the extent of habitat loss. At some point, the negative effects of extensive habitat loss will likely override any positive benefits of habitat patchiness and determining where this threshold level lies is becoming increasingly important as coral reef habitats continue to be degraded.

Although the wide geographic ranges typical of many reef fish are expected to protect them from global extinction, many of disturbances that degrade coral reef habitats are now occurring on a global scale. No tropical or subtropical reefs in the world are safe from the degradation caused by mass coral bleaching; these events can affect entire ocean basins and the 1998 bleaching event caused significant habitat loss on reefs worldwide (Baker et al. 2008). This thesis has demonstrated that at a local scale, this habitat loss and degradation can significantly reduce population replenishment and intensify competition over limited resources. These processes are likely to cause significant population declines and even localized extinctions for the coral specialized species that are most vulnerable to changes in habitat availability. The future of increasingly fragmented coral reef fish populations is in jeopardy and we may be on the verge of a dramatic increase in extinctions of coral reef fishes. Without continued efforts to understand the complex relationships between reef fishes and their fragile habitat, our tools for responding to this global ecological crisis will be limited.

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