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# THE INFLUENCE OF CORAL DEGRADATION ON TROPICAL FISH COMMUNITY STRUCTURE

**Thesis submitted by**

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James Cook University

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# ABSTRACT

Coral reefs harbour a spectacular diversity of fishes that derive food and shelter from the habitat provided by living corals. Unfortunately, both natural and anthropogenic disturbances are intensifying the global alteration and loss of live coral cover. The likely impacts of this loss on reef associated fish communities have yet to be fully assessed. The broad aim of this thesis was to examine the processes and mechanisms underlying the effects of live coral reductions on coral-associated reef fish communities. A combination of surveys and experimental manipulations were used to explore this relationship for both the fish community as a whole, and key components that represented species with differing associations with live coral.

To examine the role of coral disturbance in structuring diverse coral reef fish communities, I surveyed and compared assemblages associated with 2 coral species (*Seriatopora hystrix* and *Pocillopora damicornis*) in 3 health states (live, degraded and dead colonies with algal cover) (Chapter 2). This study showed that despite differences in the structure of assemblages associated with live and degraded colonies between coral species, there were similar patterns in reef fish community change with coral death. Assemblages associated with dead, algal-covered colonies of both coral species held virtually no coral obligates, while coral-specific differences in obligate abundance were apparent between live and degraded colonies. There was a shift in the diversity of reef fish communities between health states, within both coral species. Live and degraded colonies were numerically dominated by coral-associated fishes while dead, algal-covered colonies were numerically dominated by fishes closely

associated with non live-coral habitats. The total abundance of species was lowest in algal-covered colonies of both coral species, largely due to the low number of small size classes (new recruits and juveniles) associated with the habitat. Overall, this study has shown that coral health will play a substantial role in structuring reef associated fish assemblages, though the effects of coral loss on fish communities will be dependent on coral species and the taxonomic and functional composition of its associated fish assemblage

Within Chapter 2 I found that dead, algal-covered colonies held substantially lower abundances of fishes in small size classes (i.e. new settlers and recruits) than live or degraded colonies. Historically, disparity in coral reef fish community composition has been attributed to ecological factors affecting patterns of reef fish larval settlement. However, the mechanisms that determine how new settlers will respond to coral stress and the repercussions of coral loss in structuring reef fish communities are poorly understood. In Chapter 3, therefore, I examined the role of coral degradation in structuring patterns of coral reef fish settlement. Within aquaria choice experiments, reef associated damselfishes (both coral and non-coral associated) avoided dead, algal-covered colonies, preferentially settling into either live or partially degraded colonies. Using a habitat-limited recruitment model, such avoidance of algal-covered habitats at settlement was predicted to substantially alter patterns of reef fish settlement. I hypothesised that settlement of coral-associated fishes would become habitat-limited within degraded reef landscapes, with new settlers unable to find suitable settlement habitat. Consequently, an extensive field experiment showed that live coral colonies formed important settlement substratum for a range of reef associated fishes. *In situ* experimental live coral degradation on small coral colonies led to rapid reductions in the abundance of coral-associated fishes settling into the colonies (2 - 4 weeks after disturbance), replaced by extremely low abundances of species closely associated with the algal biomass. From these experiments, I argued that the abundance and diversity of new settlers apparent within coral habitats would reflect the health of the ecosystem; live coral alteration and loss leading to reduced new settler abundance and a phase shift in new settler diversity within the degraded habitat.

The response of reef fish communities to coral degradation and algal overgrowth was species and functional group specific (Chapter 2). However, there were higher than expected levels of resistance to coral degradation within a range of coral-associated fishes (Chapter 2). Applying terrestrial-based theory, I hypothesised that such differences in resistance were potentially influenced by species habitat specialisation (Chapter 4). Habitat specialists were more likely to remain within degraded coral colonies than generalists, due to their lowered ability to successfully migrate between habitats. Within Chapter 4, I compared the resistance and migration ability of both habitat generalist and specialist coral-dwelling goby species (Gobiidae). At low levels of coral loss specialists exhibited a higher propensity to remain in colonies than generalists, though there was no difference in resistance at both medium and high levels of coral loss. Over the majority of distances examined, specialists also showed substantially lower levels of successful migration. These results suggest that specialists are more likely to become isolated in degraded habitats than generalists, increasing the probability of their decline with habitat degradation. I argue that if this pattern holds true for the array of coral-associated reef fish species, such disparity in response to live coral disturbance between specialists and generalists may result in disproportionate reductions in the population abundance of habitat specialists in degraded habitats.

Although species-specific differences in live coral dependence were likely to influence how fish assemblages responded to live coral loss, within Chapter 2 I showed that the abundance of a diverse range of coral-associated fishes were not substantially lower in degraded than live coral colonies. Recent evidence suggested that even with no observable change in abundance, however, reduced resource availability in degraded habitats may have negative effects on resident fishes physiological condition. Therefore, within Chapter 5, I compared the growth, condition and persistence of 2 planktivorous damselfish species (Pomacentridae) over 29 days, translocated onto coral colonies in 3 experimental treatments: live, partially and fully degraded colonies. This research showed that both species growth rates were directly related to live coral cover; populations associated with fully degraded colonies showed the lowest growth while those associated with live colonies the highest. There was no significant change in the condition or persistence of populations, between treatments. These results suggested that the short-term response of coral-associated reef fishes to low live coral were reductions in growth rather than condition or absolute abundance. I argued that such bottlenecks in the growth rate of fish species associated with degraded habitats may negatively influence their time to maturity, fitness and lifetime fecundity.

The results of this thesis have fundamental implications in understanding the response of coral reef fish communities to increasing levels of live coral degradation. Fluctuations in species replenishment, differences in the resistance of individuals dependent on their habitat specialisation, and reductions in the growth of individuals remaining in degraded habitats will significantly affect the structure of the reef associated fish community within degraded reef systems. Ultimately, the alteration and loss of the living coral tissue will play a substantial role in structuring tropical reef fish community structure.

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## STATEMENT OF SOURCES

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institutions of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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## STATEMENT OF CONTRIBUTION OF OTHERS

I declare that this thesis is my own work, and has been supported by the following organisations and people. The field budget was funded by the Australian Coral Reef Society, Great Barrier Reef Marine Park Authority, Mahonia Na Dari Research and Conservation Centre, Walindi Plantation Resort and The Nature Conservancy. Additional support for the project was provided by a James Cook University Merit Research Grant to Dr M.I. McCormick and an Australian Research Council Discovery grant to Professor G.P. Jones.

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## DECLARATION OF ETHICS

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

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# TABLES

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## FIGURES

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# CHAPTER 1: GENERAL INTRODUCTION

Understanding the relationship between organisms and their environment has been a fundamental endeavour in ecological research (Noss 1990; Dunning et al. 1992; Lawton 1999). An important feature of an organism's environment is the structure of the habitat, which provides critical resources such as food, shelter and living space. The characteristics of the habitat play a central role in determining ecological patterns, from interactions among individuals (White and Pickett 1985) to whole communities (Willson 1974; Wiens and Rotenberry 1981; Holmes et al. 1996). At the individual level, the movement of individuals within and between populations may be affected by the availability of suitable habitats (McPeek and Holt 1992; Hanski 1998), while the habitat structure may be critical in mediating important ecological interactions such as competition and predation between individuals (Persson and Eklov 1995; Rodenhouse et al. 1997). The distribution of populations may be closely associated with particular characteristics of the underlying habitat (Pagel et al. 1991; Pulliam et al. 1992; Kirkpatrick and Barton 1997) regulating patterns of birth and death (Rosenzweig 1991; Lawton 1999). While at the community level, the biological and physical complexity of habitats may play a significant role in promoting species diversity (Bell et al. 1991; Hanski 1998).

The global modification and loss of habitats, and their associated communities, has brought new significance and urgency to the investigation of organism-habitat relationships (Tilman et al. 1994; Turner 1996; Tilman 1999). Reductions in population size (Vitousek et al. 1997), the loss of biodiversity (Brooks et al. 2002) and the disruption of ecosystem goods and services (McCarty 2001;

Malcolm et al. 2006) have been recorded in many terrestrial ecosystems. Habitat modification or loss following disturbance has been caused by a number of mechanisms, including over-hunting of key herbivores and predators (Lyons et al. 2004), the transformation of landscapes for cultivation or development (Vitousek et al. 1997), introduction of pest species (Hooper et al. 2005) and in recent times, climate change (Walther et al. 2002; Thomas et al. 2004).

Coastal marine habitats are exposed to a wide range of natural disturbances (e.g., storms, temperature fluctuations, rainfall and terrestrial run-off) (Farrell 1991; Warwick 1993; Connell et al. 1997). Variations in the intensity and scale of natural disturbance have played a major role in maintaining the biodiversity and spatial complexity of marine habitats (Brenchley 1981; Knowlton 1992; Hall 1994). There is increasing evidence, however, of the global modification and loss of a range of habitats in shallow marine environments with increasing natural and more recently, anthropogenic, disturbance events (e.g., Short and Wyllie-Echeverria 1996; Jackson et al. 2001; Duarte 2002). The risk of species extinction from the loss of marine habitats is increasing as the scale of habitat loss expands (Dulvy et al. 2003; Munday 2004b; Kappel 2005).

Coral reefs appear to be particularly vulnerable to a range of both natural (e.g., crown-of-thorns starfish predation episodes, coral disease and coral bleaching) and anthropogenic disturbances (e.g., over-fishing, sedimentation, pollution) that have reduced coral cover on a global scale (Hughes et al. 2003; Pandolfi et al. 2005; Pandolfi and Jackson 2006). It is estimated that a reduction of 40% to 60% of the world's coral reefs will occur over the next 50 years (Wilkinson 2004). The direct effects of disturbance on coral physiology and demography have been exhaustively studied (Brown 1997; Lesser and Farrell 2004; McClanahan 2004; Strychar et al. 2004) and have been the focus of a large number of scientific reviews (Glynn and D'Croz 1990; Hoegh-Guldberg 1999; Wilkinson 1999; McClanahan 2002). This work has shown that shifts in coral reef community composition, from coral dominated to other alternate states (i.e., algal dominated assemblages), are occurring at a much higher rate than apparent throughout their geologic history (Pandolfi and Jackson 2006; Pandolfi et al. 2006). This has led to widespread concern over the increasing decline in coral reef ecosystem health and integrity and concomitant losses in their biodiversity and social, cultural and economic value (Nystrom et al. 2000; Bellwood et al. 2004; Hughes et al. 2005).

The effects of disturbance are clearly significant in structuring benthic tropical communities (Hughes et al. 2003; Pandolfi et al. 2005; Pandolfi and Jackson 2006). Recent work, however, also indicates that the associated reef fish fauna may exhibit dramatic changes in structure and loss of biodiversity in relation to declining coral cover (Jones and Syms 1998; Halford et al. 2004; Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006). The magnitude of changes in coral reef fish communities in response to live coral loss (Jones et al. 2004; Garpe et al. 2006; Graham et al. 2006) suggests a widespread reliance on the underlying reef habitat. However, the effects of coral disturbance on the associated reef fish fauna have been the subject of relatively few experimental studies (Jones and Syms 1998).

## Coral disturbance and the structure of coral-associated fish communities

Tropical reef fish communities are composed of species comprising the full spectrum of coral dependency, from extreme coral specialists (Munday et al. 1997) to those with highly flexible resource requirements (Guzman and Robertson 1989). Although we understand how different groups may be affected by coral loss, species-specific responses may still occur and will affect which demographic factors become important (Jones and Syms 1998; Wilson et al. 2006). A loss of species that have obligate associations with coral at any stage in their life cycle is expected to occur in habitats with reduced live coral cover (Bell and Galzin 1984; Williams 1986; Pratchett et al. 2006b; Pratchett et al. 2006a). Concomitant with this loss may be an increase in species that do not have strong associations with coral, but rather exploit other habitats that may become more common within the benthic community as a result of the disturbance (e.g. rubble, soft corals) (Syms and Jones 2000; Wilson et al. 2006). Within disturbed habitats rapid growth of algae may ensue (Hughes 1994; McClanahan et al. 2002b; McManus and Polsenberg 2004), increasing benthic organic production and leading to an elevated abundance of herbivores, detritivores and invertivores within the fish assemblage, (Jones et al. 2004; Bellwood et al. 2006) (but see Hart et al. 1996; Garpe and Ohman 2003). However, despite the potential for both declines and increases in fish abundance, responses to the degradation and/or death of corals are poorly understood for the majority of tropical reef fish communities (Jones and Syms 1998; Wilson et al. 2006).

Historically, variation in the composition of fish communities has largely been attributed to factors affecting settlement of reef fish larvae (Victor 1986; Caley et al. 1996; Booth and Wellington 1998). However, the mechanisms that determine how fish settlers respond to different stages of coral stress and the extent of coral loss on fish settlement are poorly understood (Jones and McCormick 2002; Wilson et al. 2006). Regardless of their associations with coral in later life, upwards of 65% of coral reef fish species will associate with live coral habitat at settlement, or as juveniles (Jones et al. 2004). The loss of live coral within reefs following a disturbance event may lead to reductions in the abundance or diversity of many of these fish species (Booth and Beretta 2002) due to a reliance on live coral for settlement (Bouchon-Navaro et al. 1985; Booth and Wellington 1998; Öhman et al. 1998). Habitat-limited recruitment (sensu Schmitt and Holbrook 2000) may become an important process by which changes in the composition of the fish community are manifested within degraded habitats. For a number of species, especially those closely associated with live coral, the abundance of adults will slowly decline in degraded habitats as suitable resources decrease and the replenishment of species declines (Jones et al. 2004). Understanding the level of association that reef fish have with live coral at settlement and the subsequent effects on both their abundance and diversity with declining coral cover will be important in understanding how fish community structure will change within degraded habitats (Wilson et al. 2006).

One of the central conservation issues highlighted by reductions in live coral cover on tropical reefs has been to identify the ecological characteristics that render species prone to decline (Jones et al. 2004; Berumen and Pratchett 2006; Pratchett et al. 2006b). Although a range of ecological factors may affect species response to disturbance (Bellwood et al. 2006), terrestrial-based theory has suggested that levels of habitat dependency may affect species persistence in degraded habitats (McKinney 1997; Hughes et al. 2000; Kotze and O'Hara 2003). Generalists are expected to utilise a range of habitats throughout the degraded landscape, whereas specialists, in similar landscapes, will be restricted to a small number of preferred habitats, due to their inability to emigrate successfully between habitats (Mabry and Barrett 2002). With increased habitat disturbance, generalists may move more freely within the landscape than specialists, using unfamiliar environments to reach preferred habitats (McKinney 1997; Mabry and Barrett 2002). Ultimately, specialists may be less able to cope with complete loss of preferred habitats, increasing their susceptibility to population loss and extinction (Kotze and O'Hara 2003; Fitzgerald et al. 2004). If this holds true for the array of coral associated reef fish species, increased reductions in a range of habitat specialised reef fish species may occur in disturbed coral systems (Jones et al. 2004; Munday 2004b).

A significant proportion of the coral reef fish fauna is closely associated with live coral. Many small fish species may live their entire life in the confines of an individual coral colony (Munday 2000, 2001), a number of planktivorous and herbivorous damselfishes are almost always found with live branching corals (Booth and Beretta 1994; Booth et al. 2000), while most corallivorous species are closely associated with corals as a food source (Reese 1981; Berumen et al. 2005; Pratchett 2005). Although reductions in live coral cover within colonies harbouring coral associated reef fish species may result in their emigration or mortality (Munday et al. 1997; Munday 2004b), reductions in live coral may not cause immediate changes in the absolute abundance of the associated fish assemblages (Cheal et al. 2002). Sublethal changes in the condition of reef fish associated with degraded habitats may manifest themselves weeks to months after live coral reductions (e.g., Munday 2001). Despite this, few authors have investigated the change in physiological condition of reef fish subject to disturbance events (but see Pratchett et al. 2004). Reductions in the availability of suitable resources for assemblages within disturbed habitats may have flow-on effects to the condition and fitness of individuals (Booth 1995). It follows therefore, that testing the condition of fish within these assemblages may prove to be a pertinent tool for understanding the potential stresses caused by disturbances (Jones and McCormick 2002). For example, we can predict that several species of coral reef fish may be flexible in their exploitation of habitats (i.e. habitat generalists), and will be able to exploit marginal habitats, however, will these species perform as well in these habitats?

## Thesis outline

### *Research methodology*

The majority of field work for this thesis is conducted in Kimbe Bay, West New Britain province, Papua New Guinea. The coral reefs of Kimbe Bay are globally significant in terms of biodiversity, with over 800 fish species and 400 coral species recorded. The bay holds an extensive array of shallow inshore patch reefs that are readily accessible (0.2 – 1 km from shore) and are separated by expanses of deep water (up to 300m deep, S. Seeto pers comm). Within the bay, reef fish recruitment into these inshore reefs does not show a strong seasonal pattern, with the majority of reef associated fishes recruiting onto coral reef habitats throughout the year (Srinivasan and Jones 2006). Such consistent patterns in reef fish recruitment allow me to examine the role of live coral loss in structuring both the spatial (i.e., between reefs) and temporal (i.e., between weeks and months) patterns of recruitment within an exceedingly diverse reef fish community (Chapter 3). In addition, an increasing degree of anthropogenic (i.e., sedimentation) and natural disturbances (i.e., bleaching and crown-of-thorn starfish predation) have contributed to significant declines in benthic community structure throughout the inshore reefs (Jones et al. 2004). This pattern of benthic degradation has led to extensive degraded coral reef landscapes interspersed with isolated live coral colonies. Remnant live colonies are similar in size, benthic structure and degree of isolation (pers obs). The reef fish communities associated with these colonies may be thought of as independent replicates, due to their high degree of spacing and the low ability of resident fishes (mainly comprising small bodied damselfishes [Pomacentridae] and wrasses [Labridae]) to emigrate between habitats (Booth 2002). These remnant coral colonies and their associated fish communities are utilised in the majority of field experiments undertaken for this thesis (Chapters 3, 4 and 5).

Although an increasing number of studies have examined the structure of reef fish communities after disturbance events, the majority of research has occurred at extremely large spatial scales (i.e., encompassing fish communities over 100’s to 1000’s of metres) (Halford et al. 2004; Jones et al. 2004; Graham et al. 2006). However, a large proportion of coral reef fishes live their entire benthic life at much smaller spatial scales, remaining within the confines of small patch reefs or coral outcrops (Sale 1991b). Therefore, the present research is based at small, local scales, from several metres to 10’s of metres. At small spatial scales, coral disturbances may have substantial effects on the health of colonies and the associated fish fauna just days to weeks following disturbance (Munday et al. 1997). However, the majority of research examining the role of coral loss in structuring coral associated fish communities has been conducted long after disturbances occur, up to years after coral loss (Halford et al. 2004; Jones et al. 2004; Graham et al. 2006). The present research focuses on the response of reef fish communities to live coral loss at short temporal scales: days, weeks and months after coral loss. Lastly, the available research is largely based on opportunistic surveys of reef fish communities after coral disturbance (Jones and Syms 1998). This study is based on a systematic combination of surveys and experimental manipulations designed to investigate the response of reef fishes to live coral loss and the demographic mechanisms important in structuring assemblages in degraded habitats.

### *Research aims and objectives*

Although a large body of theory exists on the processes that influence the dynamics of coral reef fish communities (Sale 1991b, 2002), little is known about the processes that underlie changes in fish communities due to coral degradation (Jones and Syms 1998). This thesis explores the repercussions of live coral degradation on the demographic mechanisms structuring tropical reef fish communities. Specifically, I examine 4 issues:

1. The role of coral degradation in influencing the structure of coral associated reef fish communities.
2. The influence of coral degradation in structuring recruitment patterns for a range of common Indo Pacific reef fishes.
3. The role of habitat dependency in influencing species emigration ability between degraded and live coral colonies.
4. Whether there is a sublethal response to low live coral in coral-associated reef fish populations.

This thesis is constructed as a series of stand-alone, but conceptually interconnected publications. **Chapter 2** examines fish assemblages associated with 2 coral species, *Pocillopora damicornis* and *Seriatopora hystrix*, among 3 coral health states: (1) live, (2) degraded and (3) dead colonies with recent algal growth. I hypothesise that the nature and strength of association between individual species and live coral will determine how fish assemblages differ between coral health states. The results of this research then allow me to propose 3 models to predict which demographic processes may become important in structuring reef fish communities with live coral loss: a habitat-limited recruitment model (**Chapter 3**), a movement model (**Chapter 4**) and a condition model (**Chapter 5**) (Fig. 1.1).

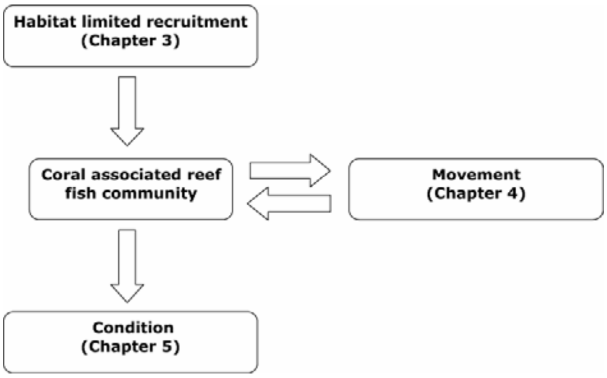

Fig. 1. 1. Diagram of 3 models examined in this thesis to predict which demographic processes would become important in structuring reef fish communities with live coral loss

**Chapter 3** examines whether habitat-limited recruitment is an important process by which changes in the composition of the fish community manifest within degraded habitats. I hypothesise that the nature and strength of association between newly-settled fishes and healthy coral will determine how they respond to habitat degradation. Utilising a two part experimental design, I examine whether reef fish larvae select between microhabitats in different health states in aquaria. Then using *in situ* coral colonies, I examine whether broad scale patterns in reef fish larval settlement are influenced by the health of benthic microhabitats.

**Chapter 4** examines whether movement between degraded and live coral habitats are influenced by species-specific habitat dependency. I hypothesise that habitat specialists are more likely to remain within degraded coral colonies than generalists, due to a lower ability to emigrate from degraded to live habitats. Experimentally inducing an *in situ* disturbance event, I compare the resistance of habitat specialists and a generalist to differing levels of coral loss and examine whether species migration ability varies with habitat dependency.

**Chapter 5** examines the short-term response of coral associated fish populations to low live coral. I hypothesise that reductions in individual species condition and/ or growth rather than persistence occur with live coral loss and that lower live coral leads to lower fish condition and/ or growth. Using replicate experimental coral colonies, I compare the condition, growth (somatic and otolith) and persistence of 2 coral associated fish species utilising colonies in 3 coral loss treatments, over a 29 day period.

# CHAPTER 2: CORAL DEGRADATION AND THE STRUCTURE OF TROPICAL FISH COMMUNITIES

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Feary, D.A., Almany, G.R., Jones, G.P., McCormick, M.I. (2007) Coral degradation and the structure of tropical reef fish communities. *Marine Ecology Progress Series* 333: 243-248

## Abstract

Coral reefs can be degraded by a variety of perturbations, including bleaching and predation by crown-of-thorns starfish. The combination of these disturbances has contributed to a global decline of live coral cover on reefs. While the effects of bleaching and starfish predation on corals are relatively well known, their consequences for fish communities are less understood. I compared fish assemblages associated with 2 coral species, *Pocillopora damicornis* and *Seriatopora hystrix*, among 3 coral health categories: (1) live, (2) degraded and (3) dead colonies with recent algal growth. Categories 2 and 3 occur sequentially during the first few weeks following bleaching or crown-of-thorns starfish predation. The abundance of species with an obligate association with live coral differed among coral health categories. Average total abundance of all fish species was lowest in algal-covered colonies of both coral species and these assemblages were dominated by species that are not closely associated with live coral. Lower fish abundance on algal-covered colonies was largely due to the low number of small size classes (new recruits and juveniles). This study suggests that habitat health may play an important role in structuring coral-associated fish assemblages.

## Introduction

Coral reefs support a spectacular diversity of fishes by providing food, shelter and living space. A variety of natural (e.g. coral bleaching, predation by crown-of-thorns starfish) and anthropogenic (e.g. overfishing, sedimentation, pollution) disturbances are contributing to a worldwide decline in hard corals (Pandolfi et al. 2003). There is increasing evidence that these disturbances can have a substantial effect on the structure of fish assemblages associated with coral reefs (Jones et al. 2004; Munday 2004b). However, our knowledge about the susceptibility to disturbance for the majority of common reef fish species and the diverse communities they form is far from complete (Jones and Syms 1998).

Coral reef fish species vary in the degree to which they are reliant on characteristics of the underlying substratum (Syms and Jones 2000). Coral-associated fish communities comprise a variety of species, representing the full spectrum of coral dependency, from extreme habitat specialists (Munday 2001) to species with highly flexible habitat requirements (Guzman and Robertson 1989). Species-specific differences in live coral dependence are likely to influence how fish assemblages respond to live coral loss (Munday 2004b). Fish species with a strong preference for or an obligate association with live coral are likely to decline in both abundance and diversity in response to increased mortality of their host corals (Shibuno et al. 1999). Degradation of live coral may also influence both the movement and recruitment of species that utilise non-living coral substrata, such as dead corals or rubble (Jones and Syms 1998). Furthermore, seaweeds typically colonise recently disturbed habitats (Hughes 1994) thereby increasing the availability of benthic algal resources. An increase in algal resources generally results in an increase in both the abundance and diversity of herbivores, detritivores and mobile invertebrate feeding fishes (McClanahan et al. 2002a). Despite the potential for both declines and increases in fish abundance, responses to the degradation and/or death of corals are poorly understood.

Understanding the life history traits of coral-associated fishes is integral to predicting the effects of live coral loss on fish assemblages (Jones and McCormick 2002). Fishes that can move easily among habitat patches and are either not closely associated with corals or are able to utilise a variety of habitats may be less susceptible to localised degradation or coral loss (Guzman and Robertson 1989; Pratchett et al. 2004). However, during early life history stages a large proportion of coral reef fish species are associated with live coral (Jones et al. 2004) through their use of live colonies as a settlement cue (Öhman et al. 1998), food source (Harmelin-Vivien 1989) or shelter (Webster 2002). Consequently, reductions in live coral may exert a negative influence on both settlement and recruitment in a range of coral reef fishes (Booth and Beretta 2002). Habitat-limited settlement and recruitment may therefore be an important process by which fish assemblages respond to habitat degradation (Jones et al. 2004).

In this study we examined whether there were differences in the fish assemblages associated with coral colonies that were in 3 distinct phases of health. We hypothesised that the nature and strength of association between individual species and live coral would determine how fish assemblages differed between live, degraded and algal-covered coral colonies.

## Materials and methods

### *Sampling*

The study was conducted in the lagoon at Lizard Island on the northern Great Barrier Reef (14° 40’ S; 145° 28’ E). Data were collected during February to March 2004. Fish assemblages associated with individual coral colonies (~11000 to 14000 $cm^3$) of *Seriatopora hystrix* and *Pocillopora damicornis* (Pocilloporidae) were surveyed at depths between 2 to 6 m on 3 large reef complexes within the lagoon (Bird Islet, Front Reef, Vicki’s Reef). Both coral species form sturdy, compact colonies and are common throughout the Indo-Pacific on upper reef slopes exposed to strong wave action. On each reef complex, colonies were classed into 3 health categories: (1) live; (2) degraded, and (3) degraded with recent algal growth. These 3 categories represent the successive stages of coral health resulting from either bleaching or predation by crown-of-thorns starfish (COTS) (Marshall and Baird 2000). Colonies were surveyed simultaneously, and no colony was surveyed more than once during the study period. A total of 1541 fish were recorded: 558 individuals from 67 *S. hystrix* colonies (n = 20 live, 31 degraded and 16 algal-covered colonies), and 983 individuals from 118 *P. damicornis* colonies (n = 37 live, 45 degraded and 36 algal-covered colonies).

Fish assemblages on each colony were initially surveyed from a distance of 3m to minimise observer disturbance, after which the interior branches of the colony were examined for cryptic fish species. All fishes seen to directly utilise the colony were counted, identified to species and assigned to 1 of 3 ontogenetic categories: (1) ‘recruit’ (<1 mo on reef), (2) ‘juvenile’ (>1 to 4 mo on reef), and (3) ‘adult’ (Randall et al. 1997, G. P. Jones unpubl. work, www.fishbase.com). Coral colony volume ($\pi \times r^2 \times h$ [cm], where $r$ = radius and $h$ = height from base of coral) and coral health category were recorded.

*Data analysis*

There was no significant correlation between the density of fishes associated with different colony sizes within each coral species (*S. hystrix*: $r^2 = 0.001$, $p = 0.7$; *P. damicornis*: $r^2 = 0.006$, $p = 0.3$); therefore, all survey data within each coral species and coral loss category were combined. Non-parametric multivariate analysis of variance (NPMANOVA, Bray-Curtis dissimilarity matrices, Anderson [2001]), were used to test whether population abundances within pooled ontogenetic categories differed among the 3 coral health categories, both within and between coral species. Significant differences in assemblage structure were analysed using similarity of percentages (SIMPER) (PRIMER version 5). Specifically, we determined the contribution of each fish species to the average similarity within and between assemblages associated with individual coral colonies, both within and between coral species.

All fish species were categorised into functional groups based on feeding, shelter and settlement-habitat requirements to test whether the association with coral health categories differed among functional groups (Randall et al. 1997, M. Srinivasan pers. comm.). We used the following 5 functional groups: (1) obligate coral use (OBLIG: associated with live coral throughout ontogeny), (2) corallivorous (CORAL: both obligate and facultative coral feeders), (3) coral-dwelling (DWELL:

use live coral as shelter throughout ontogeny), (4) coral settling (SETTL: settle to live coral, no association as adults), and (5) others (OTHER: no strong association with live coral at any stage in the lifecycle). NPMANOVA was used to examine the structure of functional groups among the 3 coral health categories, within and between coral species. Significant differences among coral colonies in the number of functional groups were analysed using SIMPER analysis (similarity percentages) to identify species that contributed most to similarities within and dissimilarities between assemblages.

Patterns in the diversity of functional groups associated with different coral health categories were compared using distribution-free randomisation tests in ECOSIM (Gotelli and Graves 1996). Diversity was calculated using rarefaction, which estimated the expected richness and associated variance of random sub samples of each functional group between coral health categories within each coral species.

We tested whether the abundance of distinct ontogenetic stages differed among the 3 coral health categories, both within and between each coral species, using NPMANOVA (using Bray-Curtis dissimilarity matrices). Significant differences were analysed using SIMPER analysis to identify species that contributed most to similarities within and dissimilarities between the fish assemblages associated with coral health categories.

## Results

### *Live colonies*

There were significant differences between the structures of fish assemblages associated with live colonies of *Seriatopora hystrix* and *Pocillopora damicornis* (Table 2.1). Total abundance on *P. damicornis* colonies was significantly lower than on *S. hystrix* colonies, but *P. damicornis* fish assemblages were more diverse (Fig. 2.1). *P. damicornis* colonies were numerically dominated by both coral-dwelling planktivorous damselfishes (Pomacentridae) and non-coral associated, benthic-feeding wrasses (Labridae) (Fig. 2.2). In comparison, obligate coral-dwelling gobies (Gobiidae) numerically dominated *S. hystrix* colonies, and coral-dwelling damselfishes (Pomacentridae) and non-coral associated wrasses (Labridae) and damselfishes (Pomacentridae) were abundant (Fig. 2.2). Corallivores (Chaetodontidae) and coral settlers (Labridae, Pomacentridae) were present in low numbers on *P. damicornis* but were absent from *S. hystrix* (Fig. 2.2).

Table 2. 1. *Seriatopora hystrix* and *Pocillopora damicornis*. Non-parametric multivariate analysis of variance (NPMANOVA) comparisons between fish assemblages associated with live coral colonies, live and degraded colonies, and degraded and algal-covered colonies of 2 coral species. Data are p-values. *p ≤ 0.05.

| **Coral health category** | ***S. hystrix* vs. *P. damicornis*** | ***S. hystrix*** | ***P. damicornis*** |
|---|---|---|---|
| Live | 0.0002* | | |
| Live vs. degraded | | 0.02* | 0.1 |
| Degraded vs. algal-covered | | 0.001* | 0.0002* |

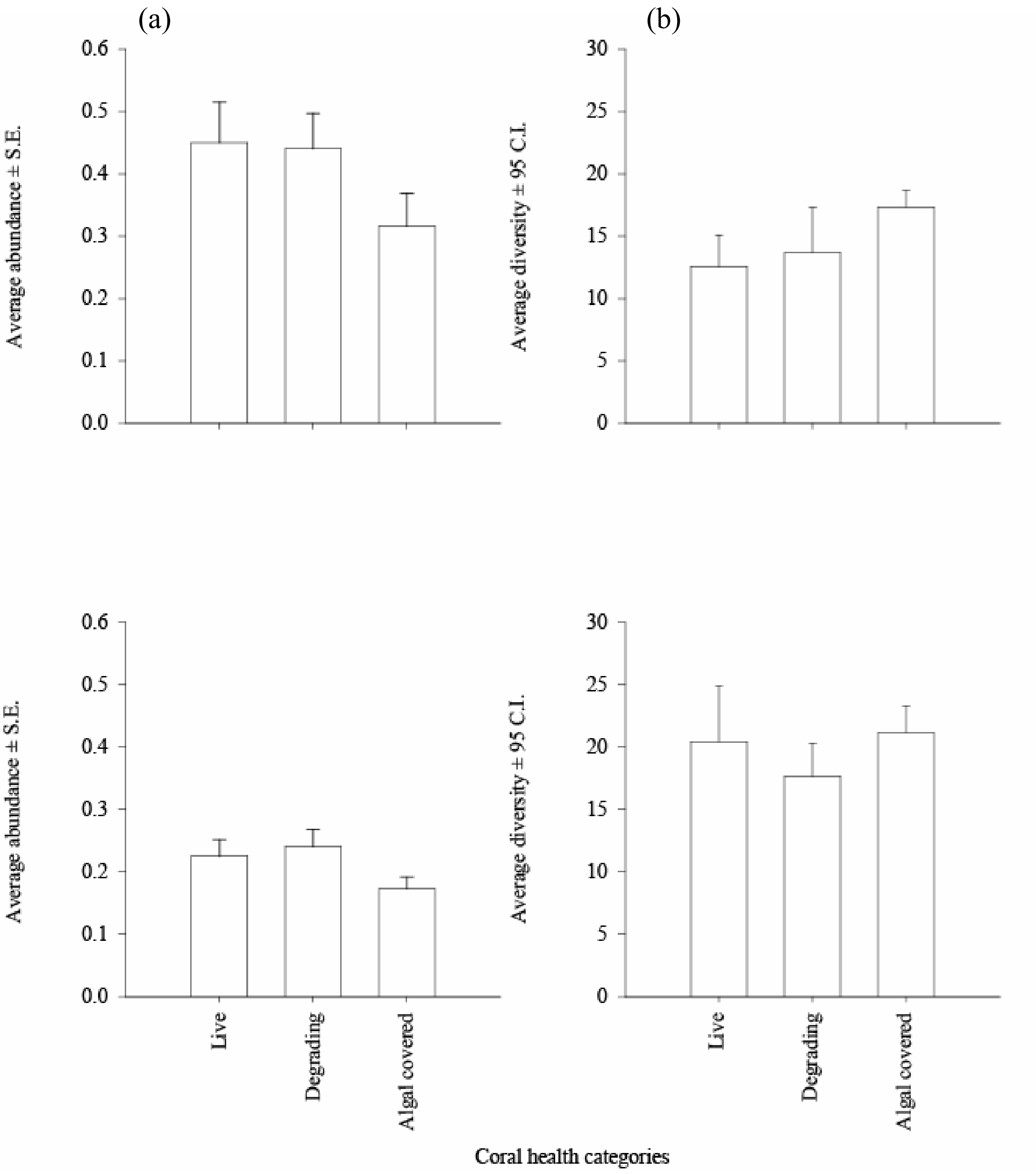

Fig. 2. 1. *Seriatopora hystrix* and *Pocillopora damicornis*. Relationship between coral health (live, degraded and algal-covered) and average species total abundance (± S.E.) and average species diversity (± 95 C.I.) of fish assemblages on colonies of 2 coral species, (a) *S. hystrix* and (b) *P. damicornis*.

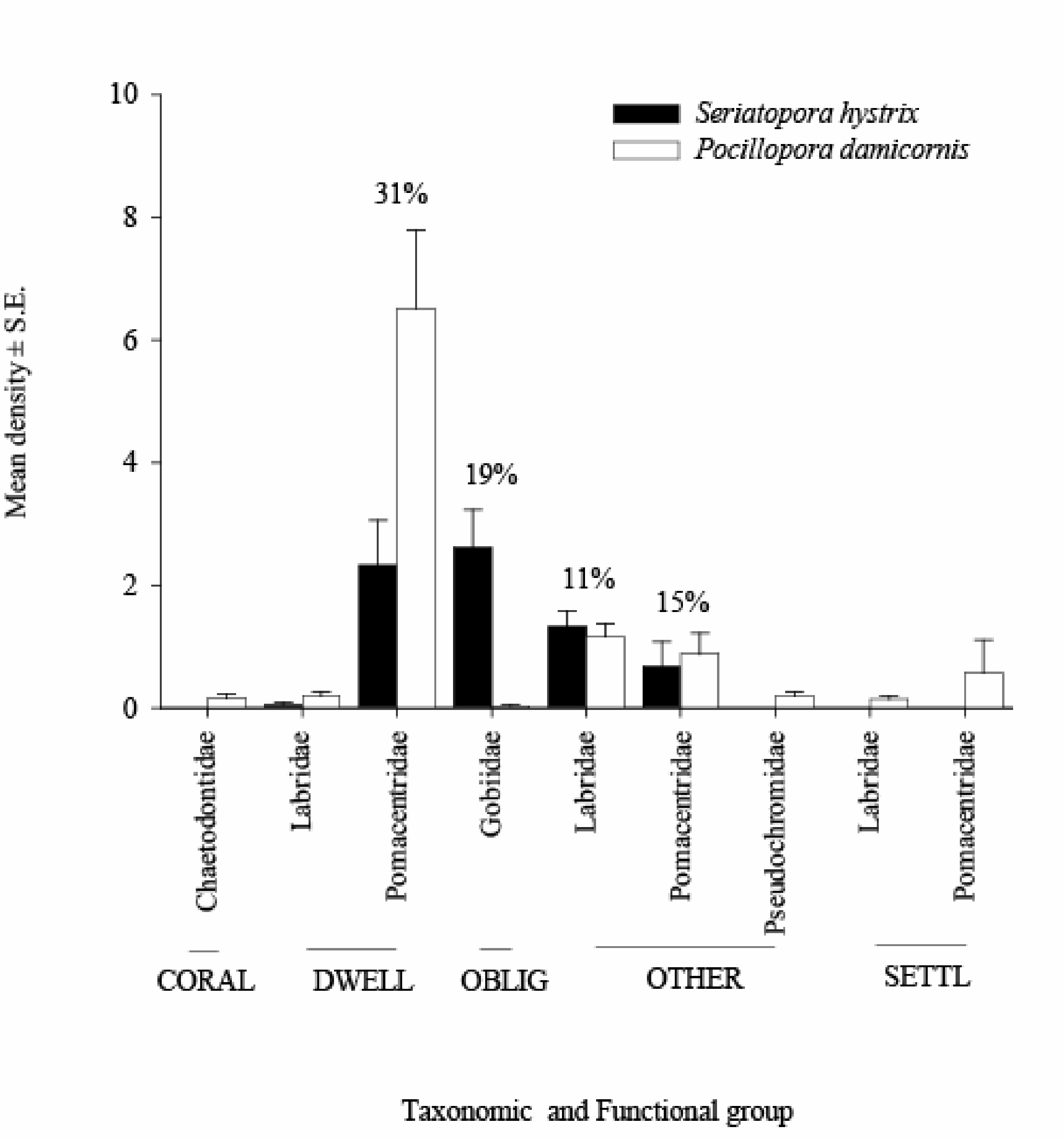

Fig. 2. 2. *Seriatopora hystrix* and *Pocillopora damicornis*. Density (mean ± S.E.) and the contribution of taxonomic and functional groups to the average dissimilarity between fish assemblages associated with live colonies of 2 coral species. Functional groups - CORAL = corallivorous species (both obligate and facultative); DWELL = species dwelling on live coral; OBLIG = species that are obligate coral users; OTHER = species with no association with live coral; SETTL = species that settle to live coral. Percentages above bars: families contributing > 10 % to dissimilarity.

*Live versus degraded colonies*

There were no significant differences in fish total abundance or diversity between live and degraded colonies within each coral species (Fig. 2.1). However, assemblage structure differed between live and degraded colonies for *S. hystrix*, but not *P. damicornis* (Table 2.1). For *S. hystrix* colonies, there was a greater abundance of coral-dwelling species (mainly planktivorous damselfish—Pomacentridae) in degraded colonies (Fig. 2.3a) and a low overall abundance of juvenile stages (Table 2.2). In contrast, for *P. damicornis* there were fewer non-coral associates (mainly benthic feeding wrasses—Labridae) and coral-associated species (coral-dwelling damselfishes and corallivores—Pomacentridae and Chaetodontidae, respectively) on degraded colonies compared to live colonies (Fig. 2.3b).

Table 2. 2. *Seriatopora hystrix* and *Pocillopora damicornis*. Non-parametric multivariate analysis of variance (NPMANOVA) of comparison of ontogenetic fish-assemblage structure associated with live, degraded and algal-covered colonies of 2 coral species. Data are p-values. *$p \leq 0.05$.

| | ***S. hystrix*** | | ***P. damicornis*** | |
|---|---|---|---|---|
| **Ontogenetic stage** | **Live vs.degraded** | **Degraded vs. algal-covered** | **Live vs. degraded** | **Degraded vs. algal** |
| Recruit | 0.2 | 0.0004* | 0.5 | 0.4 |
| Juvenile | 0.02* | 0.01* | 0.1 | 0.0002* |
| Adult | 0.9 | 0.500 | 0.1 | 0.07 |

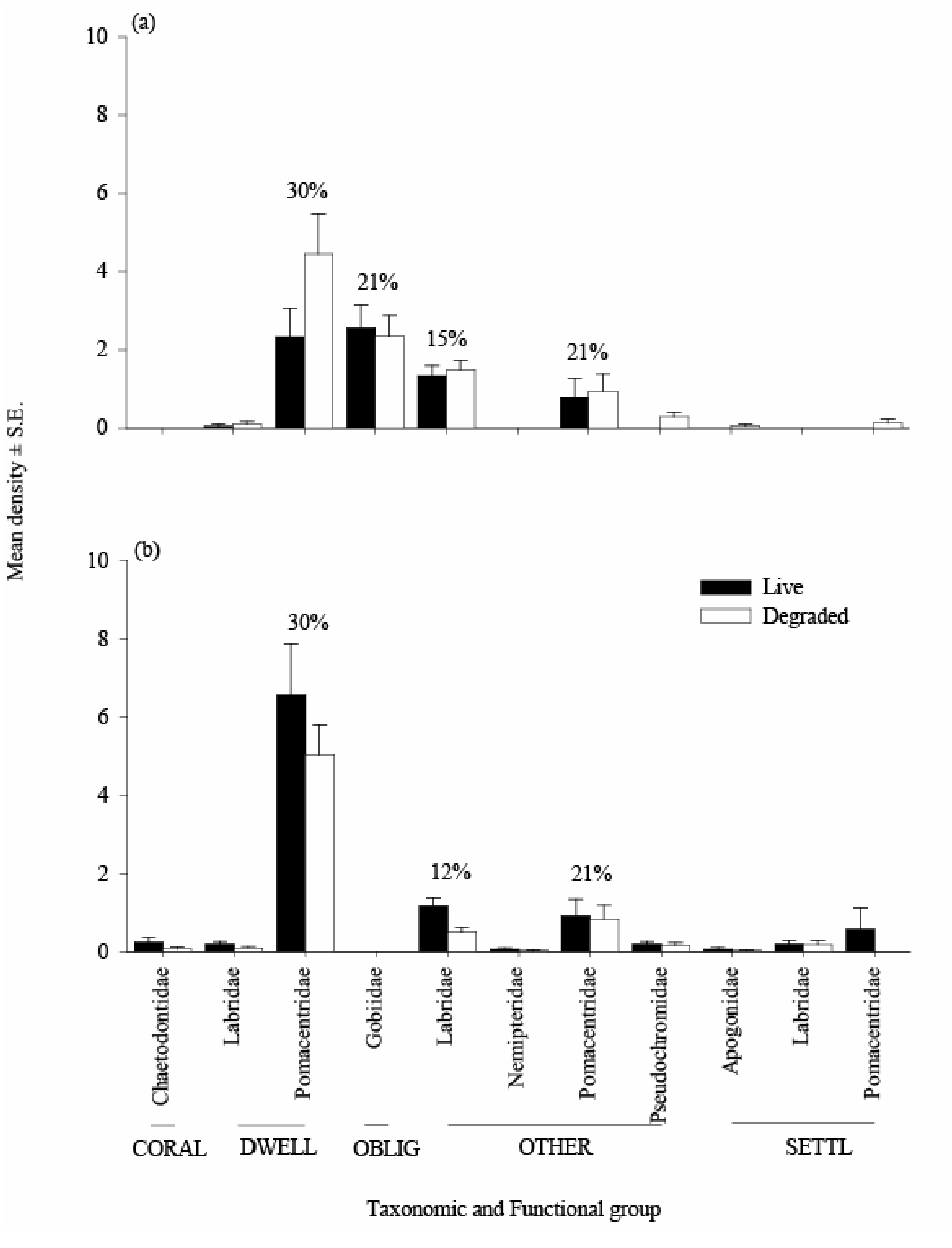

Fig. 2. 3. *Seriatopora hystrix* and *Pocillopora damicornis*. Density (mean ± S.E.) and the contribution of taxonomic and functional groups to the average dissimilarity between fish assemblages associated with live and degraded colonies of 2 coral species: (a) *S. hystrix* and (b) *P. damicornis*. Functional groups - CORAL = corallivorous species (both obligate and facultative); DWELL = species dwelling on live coral; OBLIG = species that are obligate coral users; OTHER = species with no association with live coral; SETTL = species that settle to live coral. Percentages above bars: families contributing > 10% to dissimilarity.

### *Degraded versus algal-covered colonies*

Total abundance was lower on algal-covered colonies (Fig 2.4) and assemblage structure differed between degraded and algal-covered colonies of both coral species (Table 2.1). For both corals, algal-covered colonies had fewer coral-dwelling fish species (predominantly planktivorous damselfishes—Pomacentridae) and greater numbers of non-coral associated species (primarily benthic-feeding labrids—Labridae, damselfishes—Pomacentridae—and blennies—Blenniidae) (Fig. 2.4). Obligate coral dwellers (F. Gobiidae) were absent from algal-covered colonies of *S. hystrix* (Fig 2.4a), and corallivores (Chaetodontidae) were absent from algal-covered colonies of *P. damicornis* (Fig. 2.4b). There was a low abundance of coral-settling species on degraded and algal-covered colonies of both coral species (Fig. 2.4). In addition, there were significant differences in the abundance of different ontogenetic stages between degraded and algal-covered colonies of both coral species (Table 2.2): recruits were absent from, and juveniles were present in very low numbers on algal-covered colonies of *S. hystrix*, and both juvenile and adult stages were present in low numbers on algal-covered *P. damicornis* colonies.

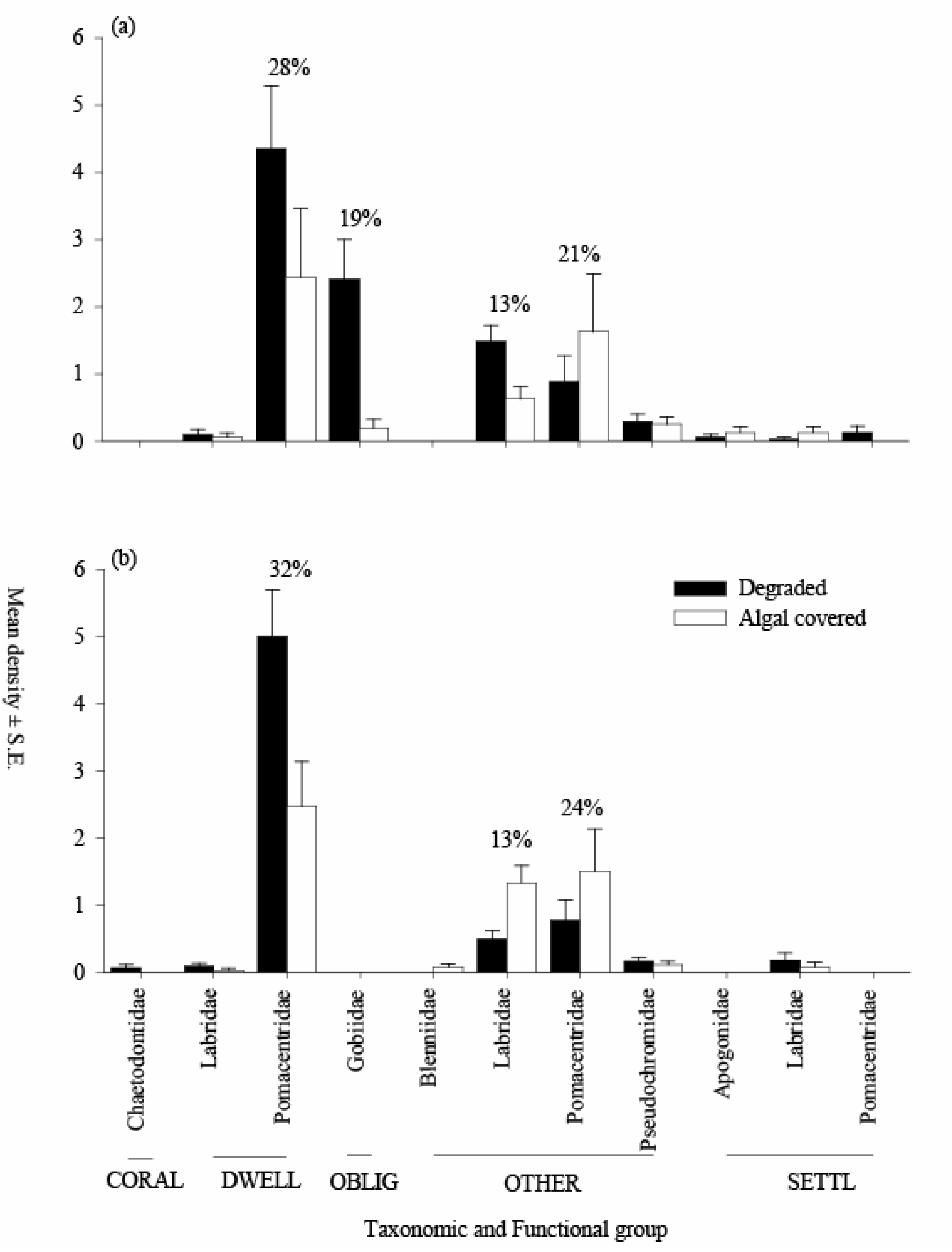

Fig. 2. 4. *Seriatopora hystrix* and *Pocillopora damicornis*. Density (mean ± S.E.) and the contribution of taxonomic and functional groups to the average dissimilarity between fish assemblages associated with degraded and algal-covered colonies of 2 coral species: (a) *S. hystrix* and (b) *P. damicornis*. Functional groups - CORAL = corallivorous species (both obligate and facultative); DWELL = species dwelling on live coral; OBLIG = species that are obligate coral users; OTHER = species with no association with live coral; SETTL = species that settle to live coral. Percentages above bars: families contributing > 10% to dissimilarity.

## Discussion

Although there is little consensus on the degree to which fish assemblages are reliant on characteristics of the underlying substratum (Jones and Syms 1998) I found that the abundance, diversity, size structure and functional groups of coral-associated fish assemblages differed among live, degraded, and algal-covered coral colonies. Degraded colonies of both coral species had lower numbers of corallivores than live colonies, whereas non coral-associated fishes numerically dominated algal-covered colonies. However, in contrast to previous studies (e.g., Hughes 1994), fish assemblages on algal-covered colonies were not more diverse than those on live or degraded coral colonies. Lower total abundance of fishes on algal-covered colonies was primarily due to the low abundance of a small subset of planktivorous damselfishes (e.g. predominantly *Pomacentrus moluccensis*) that numerically dominated assemblages associated with live colonies of both coral species, and that typically form numerically-abundant, mixed-aged groups on small coral colonies on Indo-Pacific coral reefs (Brunton and Booth 2003). In the present study, planktivorous damselfishes were abundant on both live and degraded coral colonies, but were much less abundant on algal-covered colonies. Consequently, although the proportion of benthic feeders was greater on algal-covered colonies than on live and degraded colonies, the lower abundance of planktivorous damselfishes was the key reason overall abundance was lower on algal-covered colonies.

Significant differences in the composition of fish assemblages, at both taxonomic and functional levels, were observed both between coral species and coral health categories. Numerous studies have shown that the local-scale abundance of coral-associated reef fishes is correlated with specific biological or structural characteristics of corals (Munday 2000; Holbrook et al. 2002a). Differences in the local-scale distribution of coral species may have a substantial effect on both the abundance and diversity of fish assemblages (Holbrook et al. 2000). As there are important differences in the susceptibility to degradation and ability to recover from disturbance among corals (Baird and Marshall 2002), differences in the use of species coral species may influence the extent to which fish assemblages are affected by coral degradation.

We observed low numbers of newly settled fishes and juveniles on algal-covered colonies than on live and degraded colonies. Although previous studies have suggested that the loss of live coral may have demographic consequences for coral-associated fishes (Jones and McCormick 2002), there has been little empirical evidence to support this idea (but see Booth and Beretta 2002; Jones et al. 2004). Many coral reef fishes exhibit distinct patterns of habitat use at settlement and throughout their juvenile stage (Booth and Wellington 1998). In the Indo-Pacific, as many as ~ 60% of coral reef fish species appear to associate with live coral during the early stages of their lifecycle (Jones et al. 2004). Clearly, with this level of reliance on live coral, the loss of the live coral could exert a negative influence on settlement and postsettlement movement in a range of coral reef fish species (Lewis 1998, see Chapter 3). Fluctuations in the availability of suitable habitat for a range of species may be an important process in driving local population dynamics (Jones and Syms 1998). If live coral loss results in decreased settlement and thus lower numbers of new recruits and juveniles of some species, lasting changes in the local-scale composition of fish communities may occur as a result, including changes in species composition

(Syms and Jones 2000; Jones et al. 2004), trophic structure (Lewis 1998), and size structure (Munday 2004b) (see Chapter 3).

Partial mortality of coral is a dominant feature within degraded habitat landscapes (Connell et al. 1997; Baird and Marshall 2002). In the present study, degraded coral colonies consisted of up to 30% live coral cover. Degraded colonies of *S. hystrix* supported significant numbers of obligate coral-dwelling gobies. Coral-dwelling gobies comprise a number of species that spend most of their adult life within the confines of a single live coral colony (Munday 2000; Munday et al. 2001), and depend on the colony for shelter and sites for reproduction (Munday 2002). Although the complete loss of live coral dramatically reduces the abundance of these fishes (Munday et al. 2001; Munday 2004b), this study demonstrates that partial mortality of the host colony provides enough suitable habitat for individuals to remain within the confines of the colony. The extremely limited mobility of most gobies (Nilsson et al. 2004), coupled with increased predation risk during movement (Stewart and Jones 2001) and strong interspecific competition for suitable habitat (Munday 2001; Munday 2004a) may reduce any potential benefit of emigrating to a healthier colony and may explain why these obligate coral-dwelling fishes remain in partially degraded coral colonies (see Chapter 4).

There is increasing evidence that the reductions in live coral cover associated with a variety of both anthropogenic and natural disturbances may have profound effects on the structure of coral-associated fish assemblages. In the present study I observed differences in total abundance, species diversity, the abundance of particular functional groups, and the size structure of fish assemblages among live, degraded, and algal-covered coral colonies. This study suggests that the health of corals plays an important role in structuring their associated fish assemblages, and that the specific effects of coral degradation on fish communities will depend on the coral species and the taxonomic and functional composition of its associated fish assemblage.

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# CHAPTER 3: HABITAT CHOICE, RECRUITMENT AND THE RESPONSE OF CORAL REEF FISHES TO CORAL DEGRADATION

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Feary, D.A., Almany, G.R., Jones, G.P., McCormick, M.I. (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia* 153 (3): 727-737

## Abstract

The global degradation of coral reefs is having profound effects on the structure and species richness of associated reef fish assemblages. Historically, variation in the composition of fish communities has largely been attributed to factors affecting settlement of reef fish larvae. However, the mechanisms that determine how fish settlers respond to different stages of coral stress and the extent of coral loss on fish settlement are poorly understood. Here, we examined the effects of habitat degradation on fish settlement using a two-stage experimental approach. First, we employed laboratory choice experiments to test how settlers responded to early and terminal stages of coral degradation. We then quantified the settlement response of the whole reef fish assemblage in a field perturbation experiment. The laboratory choice experiments tested how juveniles from 9 common Indo-Pacific fishes chose among live colonies, partially degraded colonies, and dead colonies with recent algal growth. Many species did not distinguish between live and partially degraded colonies, suggesting settlement patterns were resilient to the early stages of declining coral health. Several species preferred live or degraded corals, and none preferred to associate with dead, algal-covered colonies. In the field experiment, fish recruitment to coral colonies was monitored before and after the introduction of a coral predator (the crown-of-thorns starfish [COTS]) and compared with undisturbed control colonies. Starfish reduced live coral cover by 95% to 100%, causing persistent negative effects on the recruitment of coral-associated fishes. Rapid reductions in new recruit abundance, greater numbers of unoccupied colonies and a shift in the recruit community structure from one dominated by coral-associated fishes before degradation to one predominantly composed of algal-associated fish species were observed. These results suggest that while resistant to coral stress, coral death completely alters the process of replenishment of coral reef fish communities.

## Introduction

Habitat loss and degradation have been major factors responsible for declining populations (Vitousek et al. 1997), loss of biodiversity (Brooks et al. 2002) and the disruption of ecosystem services (McCarty 2001; Malcolm et al. 2006) in terrestrial environments. It has been estimated that almost one-half of the land surface has been modified by human activities (Vitousek et al. 1997) and more extinctions have been attributed to habitat loss than any other factor (Dirzo and Raven 2003). Habitat loss and degradation has been caused by a number of mechanisms, including human predation and extinction of important predators and herbivores (Lyons et al. 2004), habitat transformation for farming or development (Vitousek et al. 1997), introduction of exotic species (Seabloom et al. 2006) and most recently, climate change (Sala et al. 2000; Walther et al. 2002).

One of the central issues in conservation biology has been to identify the characteristics that render species prone to habitat change (Lampila et al. 2005; Cushman 2006). A key factor appears to be their level of specialisation, particularly a strong association with features of a habitat that are susceptible to anthropogenic disturbance (McKinney 1997; Hughes et al. 2000; Kotze and O'Hara 2003, see Chapter 4). Habitat specialists may be highly dependent on particular habitats throughout their lives or they may pass through critical stages in their life cycle that render them highly responsive to changes in the quantity or quality of their habitat (Halpern et al. 2005; Moore and Elmendorf 2006, see Chapter 4). For open populations, the decline and extirpation of suitable recruitment habitat can potentially be a major determinant of population decline and extinction.

There is increasing evidence of the widespread loss or modification of a range of habitats in shallow marine environments (e.g., Farnsworth and Ellison 1997; Alongi 2002; Duarte 2002; McClanahan 2002; Steneck et al. 2002). The risk of extinction from loss of marine habitats is increasing as the scale of habitat loss expands (Dulvy et al. 2003; Munday 2004b; Kappel 2005). Coral reefs appear to be particularly susceptible to a range of natural and anthropogenic disturbances that have reduced coral cover on a global scale (Hoegh-Guldberg 1999; McClanahan 2002; Gardner et al. 2003; Hughes et al. 2003). While clearly significant for corals, recent work also indicates that coral reef fish assemblages often exhibit dramatic changes in structure and loss of biodiversity in relation to declining coral cover (Jones and Syms 1998; Halford et al. 2004; Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006, see Chapter 2). While coral reef fish communities comprise the full spectrum of coral-dependency, from specialists in obligate association with a single coral species

(Munday et al. 1997; Munday 2004a), to those found on almost any substratum (Green 1996), the magnitude of the changes in fish communities in response to habitat change suggests a widespread reliance on the underlying coral reef habitat. However, the demographic mechanisms responsible for changes in fish community structure in response to habitat disturbance are poorly understood.

The life history transition during which larvae undergo metamorphosis into juveniles and take up residence on coral reefs is a critical period for reef fishes. At settlement juveniles can exhibit strong habitat selection for particular coral substrata (Tolimieri 1995; Öhman et al. 1998; Holbrook et al. 2002a), particular depths or reef zones (Srinivasan 2003) and can also use the presence or absence of conspecifics or other fishes as settlement cues (Jones 1987; Sweatman 1988; Booth 1992, 1995). The dynamics and distribution of adult fish populations, and how they ultimately respond to disturbance, may be strongly influenced by habitat-limited recruitment (Schmitt and Holbrook 2000; Syms and Jones 2000; Booth and Beretta 2002). Recent work suggests that a large proportion of reef fishes may preferentially recruit into live branching corals, even many of those not necessarily associated with corals as adults (Jones et al. 2004). Species-specific differences in coral preferences and levels of specialisation are likely to influence how fish assemblages respond to live coral loss (Syms and Jones 2000; Munday 2004b; Gardiner and Jones 2005, see Chapter's 2 and 4). However, our understanding of the extent of habitat selection at the time of recruitment, and the effects of coral death on fish recruitment require further investigation.

Although phase shifts in the structure of coral reef fish communities may begin with the effects of habitat change on recruitment, support for this hypothesis has been limited to a few monitoring studies (Booth and Beretta 2002; Jones et al. 2004). Further experimental studies are needed to understand the extent of the relationship between fish recruitment and coral degradation. For example, while we know that reef fishes are choosy at settlement, we do not know at what stage of declining coral health they begin discriminating among corals. That is, do they avoid settling into bleached corals (which may recover) or do they only distinguish among living and dead (algal-covered) substrata? Also, Wilson et al. (2006) showed that the nature of fish community change depends upon the type of disturbance, distinguishing among disturbances that kill corals while leaving the structure intact (e.g., bleaching, crown-of-thorns starfish [COTS]) from those that destroy the structure as well (e.g., storms, mechanical damage). While several studies have experimentally established the response of fishes to the mechanical disturbance of reefs (Lewis 1998; Syms and Jones 2000), there have been no experimental demonstrations of the effects of the loss of living coral tissue only.

The aims of this study were two-fold. Firstly, we set out to test whether the selection of benthic microhabitats by larvae of several common Indo-Pacific reef fishes was influenced by the health of coral colonies. To do this, habitat choice experiments were conducted in laboratory aquaria to examine the degree to which juveniles distinguished between live colonies, partially degraded colonies, and dead colonies with recent algal growth. We hypothesised that habitat specialists were more likely to distinguish between habitats within the aquaria than habitat generalists. We also hypothesised that the nature and strength of association between newly-settled fishes and healthy coral would determine how they responded to habitat degradation. We tested this second hypothesis in an experiment conducted in the field. Coral colonies were experimentally degraded by introducing a coral predator, the crown-of-thorns starfish, and we monitored and compared natural settlement to degraded and control colonies.

## Materials and methods

### *Laboratory preference experiment*

Settlement-stage larvae of several common Indo-Pacific damselfishes (Pomacentridae) were collected using light traps (Stobutzki and Bellwood 1998) from the lagoon at Lizard Island on the northern Great Barrier Reef, Australia (14°40'S; 145°28'E). The species collected were assigned to 3 habitat use categories based on patterns of adult habitat use (Randall et al. 1997; Allen et al. 2003): live coral-associated species (*Chromis viridis, Pomacentrus moluccensis*), degraded coral associates (*Chrysiptera flavipinnis*, *Chrysiptera rollandi*, *Pomacentrus amboinensis, Pomacentrus nagasakiensis*), and species associated with dead, algal-covered corals (*Dischistodus prosopotaenia*, *Pomacentrus chrysurus* and *Pomacentrus wardi*). Larvae were held prior to trials in featureless glass aquaria supplied with filtered seawater and aeration.

In each trial, 3 coral colonies (*Acropora cerealis*), each in a different category of health, were placed in a large, circular 300 L tank filled with filtered seawater. The 3 coral colonies were randomly arranged in a triangular configuration along the sides of the tank with equal distance between colonies. The condition of the 3 colonies was as follows: live (100% live coral cover), degraded (> 75% reduction in live coral) and algal-covered (dead coral with 1 - 2 week old algal growth). All colonies were 20 - 30cm$^2$ in diameter. Three larvae of the same species were introduced into the centre of the tank between 2000 and 2100 hours and their colony choice was recorded the following morning at 0500, and subsequently every 30 min until 1300. Three larvae were used within each trial to ensure that species natural behaviour at settlement was shown. Twenty-one individuals of each species were tested over 7 trials (n = 7). Individuals < 10cm from a colony were deemed to be associated with that colony. Coral colonies were only used in a single trial and tanks were cleaned between trials.

Since individuals within each trial could not be separately identified, the average abundance of all individuals (within each fish species) associating with each of the 3 colony categories was quantified over all 7 trials. As the data did not satisfy the assumptions of normality and homogeneity of variance required by ANOVA, Kruskal-Wallis one-way analysis of variance on ranks was used to examine whether significant differences in habitat association, between the 3 health categories, were apparent within each fish species. Any significant differences found in habitat associations within species were then examined using *post hoc* Mann-Whitney *U* tests, to determine the importance of each habitat in influencing species habitat associations. The Mann-Whitney *U* test is a nonparametric alternative to the t - test for comparing differences in population means and has the advantage of not requiring normal probability distribution for the data. We identified potential metrics when these tests showed significant differences ($p \leq 0.05$).

### *Field disturbance experiment*

The field experiment was conducted in Kimbe Bay, West New Britain, Papua New Guinea (5°30'S, 150° 05'E). All invertebrate predators were removed from 10 colonies of *A. cerealis* (20 – 30 $cm^2$ diameter) on each of 3 reef complexes (A, B, C). Over a 2 to 3 month period, naturally settling fishes were collected every 3 to 4 days from each colony using hand nets and clove oil as an anaesthetic (Munday and Wilson 1997). Surveys and collections were conducted at reef C from April to June 2005 and at reefs A and B from August to September 2005. After this 2 to 3 month period, all colonies on each reef were completely caged with small wire-mesh cages. On each reef a single COTS was introduced into each of 5 randomly selected cages ('experimental'), whereas the remaining 5 colonies were left unmanipulated ('control'). Cages and COTS remained in place for 2 days and were then removed. Experimental colonies lost from 95% to 100% of live coral cover, whereas there was no reduction in live coral on control colonies. Natural settlement of fishes was then quantified every 3 to 4 days from June to November 2005 on reef C, and September to November 2005 on reefs A and B.

The average abundance and species richness of new settlers associated with replicate coral colonies (between experimental and control) was quantified within each reef, based on the entire sampling time before and then after introduction of COTS. Both the average abundance and average species richness of new settlers associated with coral colonies within each reef, over each sampling period, were then analysed using repeated measures analysis of variance (ANOVA), with the average abundance and average species richness of new settlers as dependent variables.

Factors in each repeated measures model were reefs (A, B, C), treatment (control, experimental) and colony surveys through time as the repeated measure.

## Results

### *Laboratory preference experiment*

Significant differences in habitat association were apparent within the majority of study species (Table 3.1). Mann Whitney *U* - tests showed that within the species showing significant differences in habitat association, several groups were apparent; species preferentially using the live habitat, species associating with both live and degraded habitats and species preferentially found in the degraded habitat (Table 3.2). The habitat use of *P. moluccensis* and *C. viridis* both conformed to adult categories, with both using live habitats. In comparison, both *C. flavipinnis* and *P. amboinensis* were more dependent on the live coral than adult categories would predict. Adults of both species consistently associate with degraded habitats, though within laboratory aquaria both species preferentially used either live or degraded habitats. *Pomacentrus chrysurus* were predominantly found using the live habitat, while *P. wardi* associated with the degraded habitat (Table 3.2)

Table 3. 1. Kruskal-Wallis one-way analysis examining whether significant differences in habitat association in late stage larvae of 9 pomacentrid species was apparent between live, degraded and algal-covered coral habitats within aquaria. * = $p \leq 0.001$

| Species | Chi - square | df | *p* |
|---|---|---|---|
| *Chrysiptera flavipinnis* | 25.85 | 2 | * |
| *Chrysiptera rollandi* | 1.75 | 2 | 0.41 |
| *Chromis viridis* | 80.96 | 2 | * |
| *Dischistodus prosopotaenia* | 26.51 | 2 | * |
| *Pomacentrus amboinensis* | 67.19 | 2 | * |
| *Pomacentrus chrysurus* | 34.50 | 2 | * |
| *Pomacentrus moluccensis* | 236.65 | 2 | * |
| *Pomacentrus nagasakiensis* | 5.49 | 2 | 0.06 |
| *Pomacentrus wardi* | 35.37 | 2 | * |

Table 3. 2. Mann Whitney *U* - tests examining the importance of live, degraded or algal-covered habitats in influencing the habitat associations in late stage larvae of 9 pomacentrid species within aquaria. * = $p \leq 0.01$ ** = $p \leq 0.001$

| Species | Live | Degraded | p | Live | Algal covered | p | Degraded | Algal covered | p | Preferred habitat in aquaria |
|---|---|---|---|---|---|---|---|---|---|---|
| *Chromis viridis* | 17754.50 | 10686.50 | ** | 18308.00 | 10133.00 | ** | 14823.50 | 13617.50 | 0.1 | Live |
| *Pomacentrus chrysurus* | 15882.50 | 12558.50 | ** | 16189.00 | 12252.00 | ** | 14552.50 | 13888.50 | 0.5 | Degraded |
| *Pomacentrus wardi* | 12126.50 | 16314.50 | ** | 13904.00 | 14537.00 | 0.5 | 16282.50 | 12159.00 | ** | Live/ Degraded |
| *Chrysiptera flavipinnis* | 13376.50 | 15064.50 | 0.1 | 16671.00 | 11770.00 | ** | 17101.50 | 11339.50 | ** | Live/ Degraded |
| *Pomacentrus amboinensis* | 16860.00 | 11581.00 | ** | 19403.00 | 9037.50 | ** | 17079.50 | 11361.50 | ** | Live/ Degraded |
| *Pomacentrus moluccensis* | 20516.50 | 7924.50 | ** | 20754.50 | 7686.50 | * | 15424.00 | 13017.00 | ** | Live/ Degraded |
| *Dischistodus prosopotaenia* | 13427.50 | 15013.50 | 0.1 | 13413.50 | 15027.50 | 0.1 | 14356.50 | 14084.50 | 0.8 | All habitats |

Temporal changes in habitat association between 0500 and 1300 were apparent between species during the first temporal period, with the majority of species associated with all 3 habitats in the 1st temporal period (Fig. 3.1). By the 2nd or 3rd temporal periods, however, the majority of species had associated with a particular habitat and invariably remained in that habitat for the duration of the trial. Nevertheless, differences in movement between habitats were found between the study species. Species not closely associating with the live habitat were less likely to remain in distinct habitats within the aquaria, moving more frequently throughout the habitats during trials, while those associating with the live habitat would move into this habitat in the 1st or 2nd temporal periods and remain in this habitat for the duration of the trial.

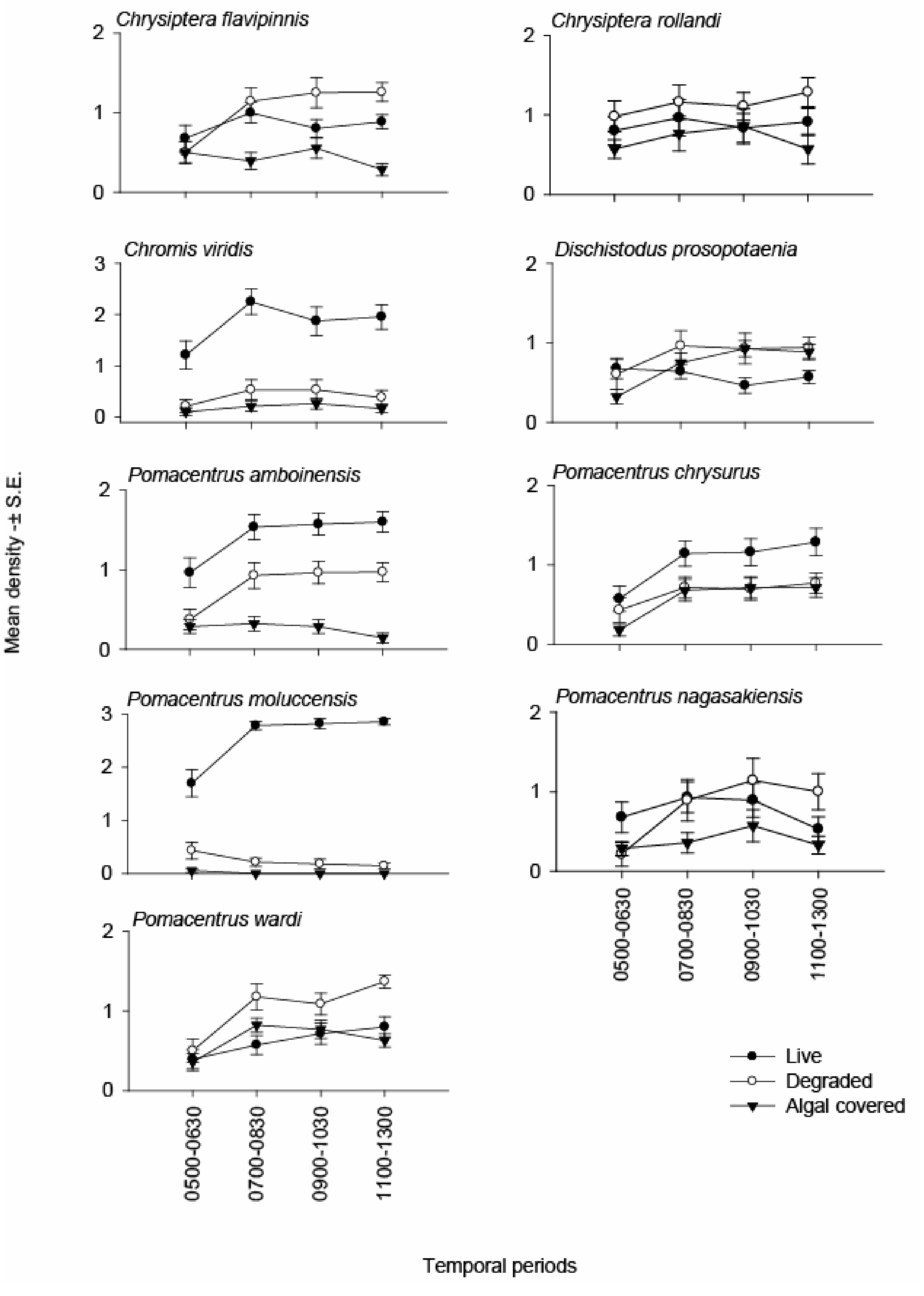

Fig. 3. 1. Mean density (± S.E.) of the late stage larvae of 9 pomacentrid species at 4 temporal periods from 0500 - 1300 in live, degraded and algal-covered habitats within laboratory aquaria. Larvae were released between 2000 and 2100 h the previous night.

*Field disturbance experiment*

Significant differences in both the abundance and species richness of new settlers associating with control and experimental treatments on all 3 reefs were apparent (Table 3.3), due to large reductions in new settlers associating with experimental colonies after live coral degradation (Fig. 3.2). Reductions in the abundance of new settlers on experimental colonies were most apparent on reefs A and B, with a 95% and 97% decrease in abundance after coral degradation, respectively, while there was a 75% decrease in new settler abundance in experimental colonies on reef C.

Table 3. 3. Repeated measures ANOVA examining whether significant differences in (a) Mean abundance and (b) Mean species richness of new settlers were apparent within each reef (Reef), between coral health treatments (Treat) over experimental trial (Time). * = $p \leq 0.01$ ** = $p \leq 0.001$

(a)

| Abundance | df | F | *p* |
|---|---|---|---|
| Reef | 2 | 3.12 | 0.06 |
| Treat | 1 | 16.94 | * |
| Reef*Treat | 2 | 9.37 | * |
| Time | 18 | 4.16 | ** |
| Time*Reef | 36 | 4.84 | ** |
| Time*Treat | 18 | 15.16 | ** |
| Time*Reef*Treat | 36 | 2.12 | ** |

(b)

| Diversity | df | F | *p* |
|---|---|---|---|
| Reef | 2 | 10.58 | ** |
| Treat | 1 | 43.29 | ** |
| Reef*Treat | 2 | 5.81 | * |
| Time | 18 | 5.65 | ** |
| Time*Reef | 36 | 2.71 | ** |
| Time*Treat | 18 | 10.34 | ** |
| Time*Reef*Treat | 36 | 1.95 | ** |

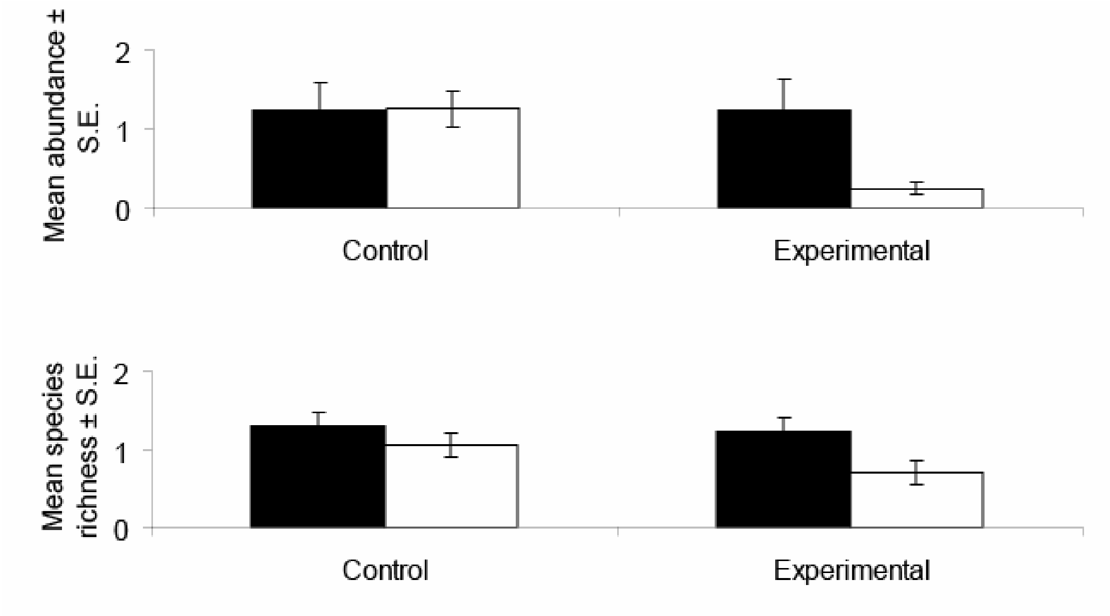

Fig. 3. 2. (a) Mean abundance (± S.E.) and (b) Mean species richness (± S.E.) of new settlers associated with control and experimental colonies between reefs, before and after caging.

Reductions in the species richness of assemblages in experimental coral colonies were also apparent throughout reefs, with at least 70% decrease in the average species richness in experimental coral colonies on all 3 reefs, after caging (Fig. 3.2). Such large reductions in the abundance and species richness of new settlers associating with experimental colonies were largely due to reductions in the settlement of 2 species strongly associated with live coral, the coral goby *Gobiodon quinquestrigatus* (Gobiidae), which reduced in proportional abundance by 12% after coral loss and the damselfish, *P. moluccensis*, which decreased in proportion by 100% on degraded colonies (Fig. 3.3). In comparison, although fluctuations in both the abundance and species richness of newly settled fishes were observed on control colonies, the magnitude of these changes was significantly less than that observed on experimental reefs (Fig. 3.2).

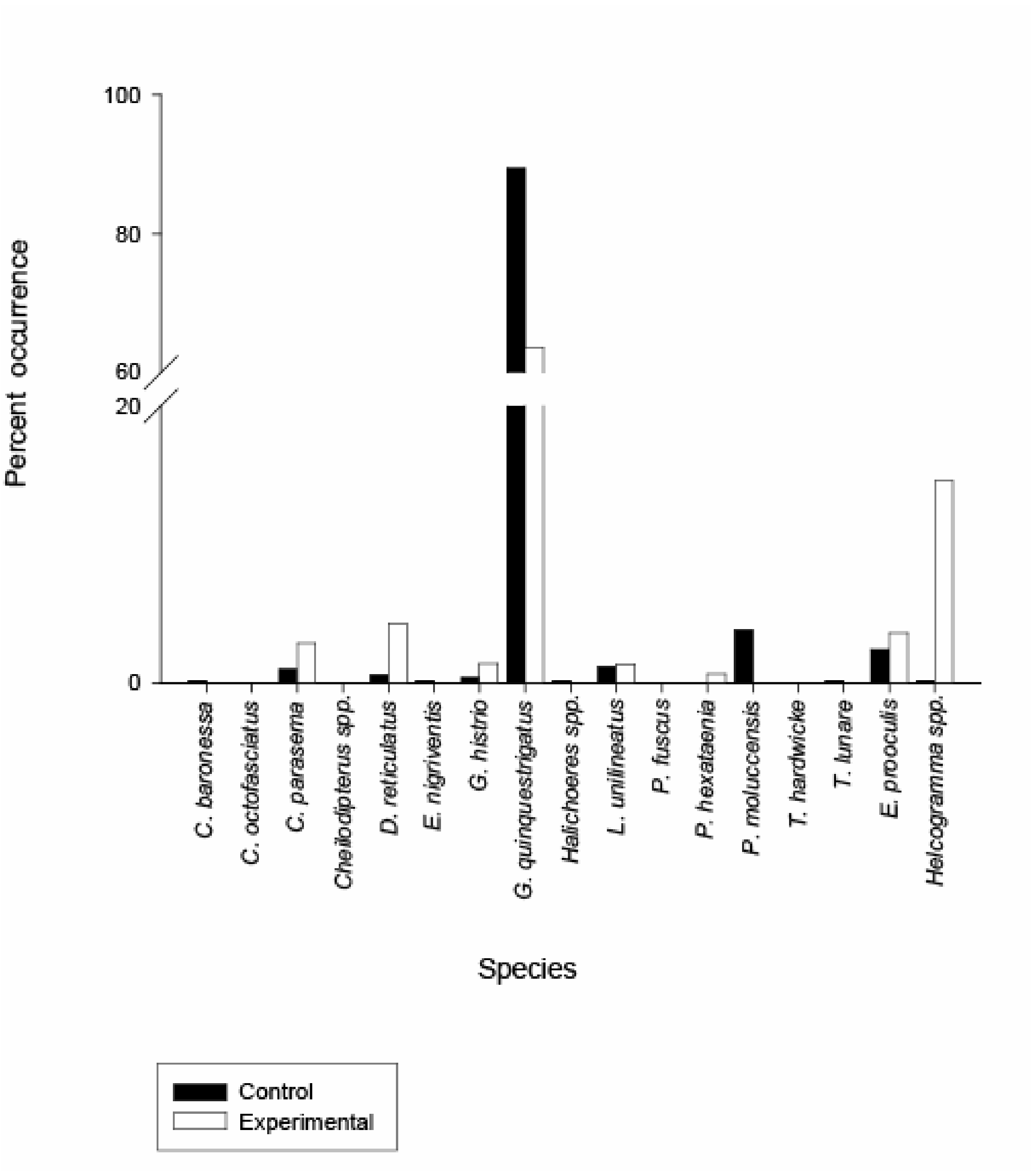

Fig. 3. 3. Percent occurrence of all fish species associated with *in situ* control and experimental colonies after caging.

Changes in the composition of communities associating with experimental, opposed to control colonies, were apparent after caging (Fig. 3.3). Within experimental colonies, increased abundances of combtooth blennies (Blenniidae) and triplefins (Tripterygiidae) (e.g., *Ecsenius prooculis*, *Helcogramma* spp.) were observed settling into the habitats, while decreased abundances of species more closely associated with live coral were found within the habitats (Fig. 3.3). On experimental colonies fishes closely associated with algal resources (e.g., blennies and triplefins) comprised only 1.8% of the assemblage 2 weeks before live caging, which increased to 18% 2 weeks after cages were taken off and over 90% after 8 weeks. In comparison, little change in the composition of new settling species associating with control colonies was apparent before and after caging (Fig. 3.3).

Significant temporal changes in both the abundance and species richness of new settlers were apparent between treatments (Table 3.3). Degradation of experimental colonies led to temporal reductions in both the abundance and species richness of new settlers associating with experimental colonies 2 weeks after coral loss (Fig. 3.4). In comparison, little change or an increase in the abundance and species richness of new settlers were apparent in control colonies over the same time period (Fig. 3.4).

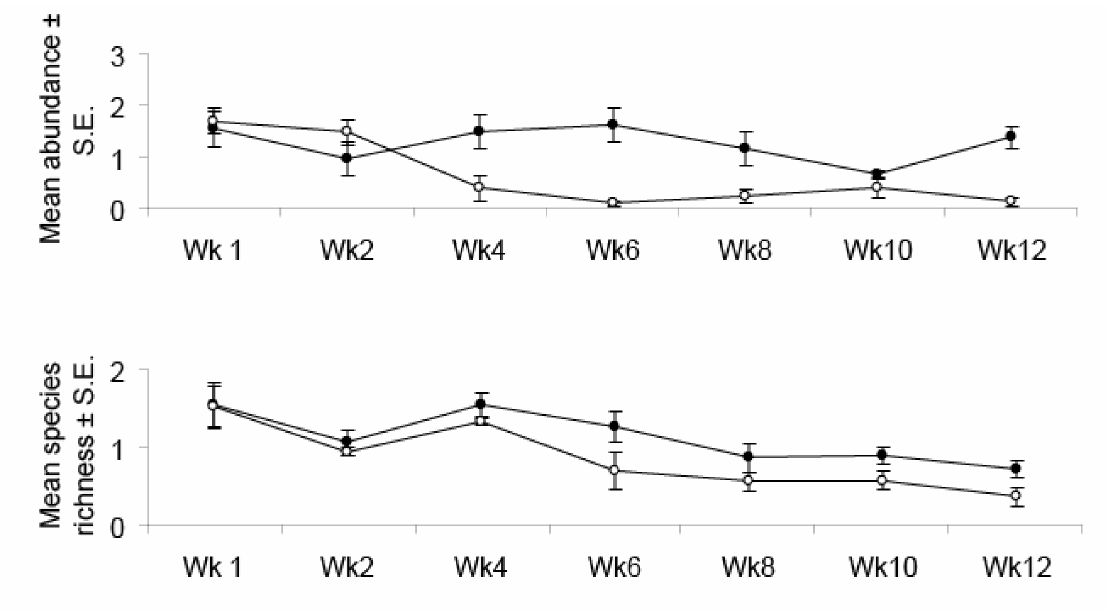

Fig. 3. 4. (a) Mean abundance (± S.E.) and (b) Mean species richness (± S.E.) of new settlers associated with control and experimental colonies between reefs every 2 weeks (T) after experimental coral degradation.

Although no significant difference in % occupancy was apparent between control and experimental colonies before caging (ANOVA, F = 0.344, df = 1, p = 0.565), reductions of live coral cover (following caging) on experimental colonies resulted in a significantly higher frequency of empty colonies during subsequent sampling periods than control colonies (ANOVA, F = 60.54, df = 1, p < 0.001). Across all 3 reef complexes, 4 weeks before live coral loss an average of 52% (± 7.4 S.E.) of experimental colonies contained at least one individual, whereas 4 weeks after caging and live coral degradation only 9% (± 4.2 S.E.) of experimental colonies were occupied. In contrast, the percent occupancy on control reefs increased during the experiment: 4 weeks before caging an average of 45% (± 10 S.E.) of control colonies were occupied by at least 1 individual, whereas 4 weeks after manipulation an average of 74% (± 6.4 S.E.) of control colonies were occupied.

## Discussion

Our results support an emerging view that settlement is likely to be a crucial bottleneck that determines the impact of coral degradation on reef fish biodiversity and community structure (Booth and Wellington 1998; Jones et al. 2004). A high level of habitat selection at settlement, combined with a high community-wide reliance of juveniles on live branching corals, will cause a major shift in recruitment regimes following severe disturbance to coral reef habitat. This mechanism could account for the dramatic changes to reef fish communities in response to declining live coral cover (see also Halford et al. 2004; Jones et al. 2004; Garpe et al. 2006; Graham et al. 2006; Wilson et al. 2006, see Chapter 2)

The majority of study species preferentially associated with either live or partially degraded coral colonies within laboratory aquaria, and none of the species examined preferentially associated with dead, algal-covered colonies. This suggests that many species will be resilient to the early stages of degradation, but not once coral death and algal overgrowth have occurred. Preferences for live and degraded habitats at settlement were apparent in fishes that both associate with live coral throughout their lives (e.g., *P. moluccensis*) (Booth 2002; Booth and Beretta 2002) and for many with little to no use of live coral colonies throughout the juvenile or adult stage (e.g., *P. chrysurus*) (Allen et al. 2003). Hence, adult responses to declining coral cover may be more a result of settlement preferences than adult habitat requirements (Jones et al. 2004).

Variations in the availability of appropriate settlement habitat may influence settlement patterns in a variety of reef associated fishes (Holbrook et al. 2000), and can affect both local species richness and population abundance (Schmitt and Holbrook 2000). However, few studies have experimentally examined the role of habitat alteration in structuring reef fish settlement patterns, with most studies strictly observational, and therefore unable to distinguish habitat changes from other potential causative factors (Booth and Beretta 2002). In this study, reductions in live coral on experimentally degraded *in situ* colonies led to reductions in both the abundance and species richness of newly settling fishes, a pattern observed in other studies (Booth and Beretta 2002). Although reductions in the settlement of a range of fish species were apparent on experimentally degraded colonies, such community decline was primarily due to reduced settlement of the coral-associated goby, *G. quinquestrigatus* and the coral-associated damselfish, *P. moluccensis*. Both fishes dominated live coral colonies, settling in large numbers in this habitat. Degradation of colonies by COTS predation and subsequent growth of algae reduced the number of new settlers of both fishes, with virtually no individuals of either species found on degraded colonies.

A physical reduction in available shelter occurs when degraded coral colonies are colonised by algae (i.e. algae reduces the amount of available space between coral branches) (Munday 2001) and this may decrease the suitability of colonies for new settlers, independent of live coral loss (Öhman et al. 1998). However, relatively immediate reductions in the abundance and species richness of new settlers on dead *in situ* colonies that had accumulated only light algal growth (2 weeks) were apparent in this study. This observation suggests that the loss of live coral itself was responsible for decreased settlement (Garpe et al. 2006). An increasing array of work is now showing that a variety of cues (i.e. chemical, auditory and visual) can form vital indicators for reef naïve fish larvae to initiate benthic settlement behaviour (Lecchini et al. 2005a; Lecchini et al. 2005b). In the present study, degradation of experimental coral colonies may have reduced or even negated such settlement cues, resulting in significant declines in new settlers associating with the degraded habitat.

A range of factors may have increased the loss of new settlers on algal-covered corals between surveys (every 3 - 4 days), such as predation or interspecific competition for resources (Steele and Forrester 2002; Webster 2002). However, post settlement exploration and movement of new settlers into preferred habitats may have occurred, independent of ontogenetic changes in habitat use (Webster and Hixon 2000; Munday 2001). Exploration of habitats at settlement is a well known behaviour in both terrestrial and aquatic animals (Stamps and Krishnan 1995; Leis and Carson-Ewart 2002; Hawkins et al. 2003). Habitat exploration is thought to allow animals to examine potential habitats (Leis and Carson-Ewart 2002), targeting habitats where reproduction and survival (i.e. fitness) will be highest (Haughland and Larsen 2004). Within the present study, exploration of aquaria habitats at dawn was found, with species moving between habitats before associating with a preferred habitat. As individuals utilising preferred habitats can show increased juvenile growth (Jones 1997; Munday 2001) or survival (Wellington 1992; Munday 2001), post-settlement movement into preferred habitats may have positive effects on the demographic structure of reef fish populations (Munday 2004a). It is possible that *in situ* settlement occurs in two phases, beginning with a coarse-scale selection of appropriate habitat, followed by early post-settlement movement into preferred substrata (sensu Finn and Kingsford 1996; McCormick and Makey 1997) and may be an important behavioural choice for successful settlement and recruitment in a range of reef associated fishes in degraded habitats.

Associations with algal biomass at settlement have been shown in a small number of taxonomic groups (e.g., Green 1998; Shima 2001), however few studies have examined the response of reef fish settlement to increased algal resources following coral degradation. The majority of work has focused on the role of algal resources in structuring the abundance and species richness of adults within degraded coral reef habitats (McClanahan et al. 1999; McClanahan et al. 2001). Such work has shown that the algal biomass can provide a considerable array of resources for a range of coral reef fishes, including sites for foraging (Ceccarelli et al. 2001; Townsend and Tibbetts 2004), shelter (Wilson 2001; Clarke and Tyler 2003) and reproduction (Neat 2001). However, this study provides some of the first evidence that shifts in reef fish community structure from the numerical dominance of live coral associates to one where algal associates numerically dominate can occur through changes in fish settlement with coral degradation and algal biomass increase (but see Booth and Beretta 2002). Such alterations in reef fish settlement patterns following reef degradation may then have strong and persistent influences on both the species richness and abundance of coral-associated reef fish communities (Schmitt and Holbrook 2000).

This work has fundamental implications in understanding the response of coral reef fish communities to increasing levels of live coral degradation. As the availability of suitable live coral settlement habitat decline on degraded reefs, the abundance of many coral-associated fish species will rapidly decline and will be replaced by species that preferentially associate with degraded, algal-dominated habitats (Jones et al. 2004). We can predict that such changes in recruitment may then interact with species longevity to determine the time scale of effects of live coral loss on reef fish community structure. Within fishes with short life spans and high population turnover rates, substantial reductions in new settler abundance and richness with live coral loss may have relatively immediate, negative effects on community replenishment (Munday and Jones 1998; Booth and Beretta 2002). In comparison, for longer lived species, we can predict that reductions in recruit abundance with live coral loss may have little effect on their population abundance in the short-term, with significant effects on the community apparent at much longer time scales (Pratchett et al. 2006b). Recent research has argued that phase delays in the response of the associated reef fish community to coral loss may be due to a coupling of the adult fish with the coral reefs physical complexity (Graham et al. 2006). Broad reductions in the structure of reef fish communities may then be linked to the breakdown of the coral reefs physical complexity (Lewis 1998; Syms and Jones 2000; Graham et al. 2006). Although the loss of the underlying coral reef structure will have detrimental effects on the community abundance of a range of reef associated fishes (Sano et al. 1984; Gratwicke and Speight 2005; Wilson et al. 2006), we predict that reductions in new settler abundance and richness with loss of the living coral tissue only will play a substantial role in altering the replenishment and ultimately the structure of the reef associated fish community within degraded reef systems.

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# CHAPTER 4: THE INFLUENCE OF RESOURCE SPECIALISATION ON CORAL REEF FISHES RESISTANCE TO CORAL DISTURBANCE

Feary, D.A. (2007) The influence of resource specialisation on coral reef fishes resistance to coral disturbance. *Marine Biology* 153: 153-161

## Abstract

Ecological theory predicts that habitat generalists are less prone to decline or extinction in response to habitat disturbance than habitat specialists. One mechanism that may afford habitat generalists greater resistance is their ability to successfully emigrate from degrading environments. This study compared the resistance of coral specialist and generalist reef fish species to live coral disturbance. In replicate coral colonies, live coral was experimentally degraded (low, medium and high coral loss). Species resistance within the colonies was then surveyed over time. In addition, the ability of coral generalist and specialist species to migrate between degraded (100% loss) and live coral colonies was compared. Coral specialists exhibited a higher propensity to remain in colonies with low levels of coral loss. However, there was no significant difference between specialist and generalist species in resistance to either medium or high levels of coral loss; both functional groups showed low levels of resistance. In terms of migration ability, generalists migrated further than specialists and showed higher levels of successful migration over the majority of distances examined. The influence of coral specialisation on the behavioural response to coral loss may be a useful predictor of changes to coral reef fish communities in response to coral disturbance.

## Introduction

Both natural and anthropogenic disturbances are contributing to increased rates of change in natural systems worldwide (Myers et al. 2000; Fahrig 2001; Hughes et al. 2003), with corresponding declines in biodiversity (Myers et al. 2000; Bellwood et al. 2004). One of the central issues highlighted by these changes has been to identify the ecological characteristics that render species prone to decline (Foufopoulos and Ives 1999). A range of factors including ecological specialisation (Hughes et al. 2000; Harcourt et al. 2002), trophic level (Harcourt et al. 2002) and body size (Owens and Bennett 2000; Kotze and O'Hara 2003) may affect species response to disturbance, whether it be a change in abundance or extinction (Fahrig 2001, 2002).

A range of empirical studies have examined the role of habitat specialisation in determining species response to habitat loss, though these focus almost entirely on terrestrial systems (Fahrig 2001; Kotze and O'Hara 2003; Swihart et al. 2003). Such work has shown that species response to habitat loss may depend on habitat dependency (McKinney 1997; Hughes et al. 2000; Kotze and O'Hara 2003). Generalists will use an array of different habitats throughout the landscape, whereas specialists, in similar landscapes, will be restricted to a small number of preferred habitats, due to their inability to emigrate successfully between habitats (Mabry and Barrett 2002). With increased habitat disturbance, generalists may move more freely within the landscape than specialists, using unfamiliar environments to reach preferred habitats (McKinney 1997; Mabry and Barrett 2002). Specialists may ultimately be less able to cope with complete loss of preferred habitats, increasing their susceptibility to population loss and extinction (Kotze and O'Hara 2003; Fitzgerald et al. 2004).

There is increasing evidence of widespread global alteration and loss of shallow marine habitats (Watling and Norse 1998; Frouin 2000; Kennish 2002; Thompson et al. 2002) and their associated biodiversity (Roberts et al. 2002; Dulvy et al. 2003; Worm et al. 2006). The risk of extinction from loss of marine habitats is increasing as the scale of habitat loss expands (Dulvy et al. 2003; Munday 2004b; Kappel 2005). Within the marine environment, coral reef habitats appear to be particularly susceptible to a range of both natural (e.g., crown-of-thorns starfish predation episodes, coral disease and coral bleaching) and anthropogenic (e.g., over fishing, sedimentation, pollution) disturbances that have reduced coral cover on a global scale (Hoegh-Guldberg 1999; McClanahan 2002; Gardner et al. 2003; Hughes et al. 2003). While clearly significant for corals, such coral loss may have substantial effects on the associated fish communities (Jones and McCormick 2002), with recent work showing dramatic changes in coral reef fish communities with live coral loss (Halford et al. 2004; Jones et al. 2004; Samways 2005; Graham et al. 2006; Pratchett et al. 2006b, see Chapter 2). Unfortunately, our knowledge of the degree of susceptibility for the vast majority of coral reef fish species is far from complete (Jones and Syms 1998; Wilson et al. 2006). As tropical fish communities comprise species encompassing a spectrum of coral specialisations, differing levels of response to coral loss are expected to occur between species (Jones and McCormick 2002; Wilson et al. 2006, see Chapters 2 and 3).

The obligate coral-dwelling gobies (Gobiidae) are extremely good candidates with which to examine the influence of habitat dependency on species' responses to habitat loss. Several species within this family are obligately associated with corymbose and digitate corals from the families Acroporidae and Pocilloporidae, which they depend on for food, shelter, sites for reproduction and recruitment (Kuwamura et al. 1994; Munday et al. 2001; Munday 2002, see Chapter 3). Within this group of fishes, however, differing levels of habitat specificity are apparent (Munday et al. 1997; Munday 2004a), from sole use of a single coral species (Munday et al. 1999) to the broad use of a range of coral species (Munday et al. 1997; Thompson et al. 2007). Suitable coral colonies are often in limited supply and coral-associated Gobiidae will rarely leave host corals, remaining within the same colony for most of their adult life (Kuwamura et al. 1994). Although reductions in the cover of live coral are expected to have a deleterious effect on gobiid abundances, recent work has shown that they will remain in corals that have shown partial mortality (see Chapter 2), although the total loss of live coral can result in large population reductions (Munday et al. 1997; Munday 2004b, see Chapter 2).

In this study, an experiment was established to investigate differences in the ability of specialist and generalist species to successfully emigrate in response to coral disturbance. On the basis of terrestrial studies (McKinney 1997; Mabry and Barrett 2002), it was predicted that species response to disturbance would be influenced by their resource specialisation, with a reduced ability to emigrate corresponding with the degree of coral specialisation. The present study simulated a coral disturbance event by degrading live coral on replicate coral colonies. Resistance in degraded coral colonies was quantified for both coral generalist and specialist reef fish species over a

5-month period. In addition, this study compared the ability of coral generalist and specialist reef fish species to successfully migrate between degraded to remnant coral colonies over varying distances.

## Materials and methods

### *Study species*

In Kimbe Bay, West New Britain, Papua New Guinea (5°30’S, 150° 05’E) continued residence in response to *in situ* coral loss and migration ability were examined in 3 species of obligate coral-dwelling goby: *Gobiodon histrio*, *Gobiodon quinquestrigatus* and *Paragobiodon xanthosomus*. Both *P. xanthosomus* and *G. histrio* are coral specialists; *P. xanthosomus* lives in obligate association with 1 coral species, *Seriatopora hystrix*; while *G. histrio* is predominantly found in *Acropora nasuta*. *Gobiodon quinquestrigatus* is a coral generalist and utilises a large number of acroporidae species (Munday et al. 1997; Thompson et al. 2007), though within this study were only used in *Acropora cerealis* colonies.

### *Resistance*

On 3 inshore reefs (Bobs Knob, Lady Jens and Blazius) randomly selected live colonies of 3 coral species (*A. cerealis*, *A. nasuta*, *S. hystrix*), holding a single pair of 1 study species (all other resident fishes and invertebrates were cleared), had their live coral cover reduced using crown of thorns starfish (COTS). All colonies were *a priori* grouped into 3 experimental coral loss treatments: low: 20 – 30%, medium: 50 - 60%

and high: 80 – 90% coral loss. There were no significant differences in colony size within and between each coral species (ANOVA $p > 0.05$; *A. cerealis* 586.2 ± 44.0 $cm^3$, mean ± SE; *A. nasuta* 543.7 ± 36.4 $cm^3$, *S. hystrix* 518.7 ± 51.5 $cm^3$). All study species were captured using hand nets and clove oil (Munday and Wilson 1997), measured (mm Standard Length [SL]), individually tagged using subcutaneous injections of coloured elastomer *in situ* and replaced. Individuals were similar in size within species (*G. histrio* 25.0 ± 0.3 mm SL, mean ± SE; *G. quinquestrigatus* 21.6 ± 0.3 mm SL; *P. xanthosomus* 17.9 ± 0.3 mm SL), though there were significant differences in average size between species (ANOVA, $F = 122.0$, $df = 2$, $p < 0.001$).

All colonies were completely caged with wire-mesh cages and single COTS introduced into each experimental cage. In addition, colonies of each coral species holding a single pair of 1 study species were caged and left unmanipulated ('control'). COTS were constrained to feed on selected parts of experimental colonies by attaching rubble to the coral head, limiting the area of coral for the COTS to feed on. All coral loss occurred over 2 - 4 days, after which all cages (both experimental and control) and COTS were removed. Total live coral volume (before COTS disturbance) ($1/3 \times \pi \times r^2 \times h$ (cm), where r = radius and h = height from base of coral) and total degraded coral volume (after COTS disturbance) ($1/3 \times \pi \times dr^2 \times dh$ (cm), where dr = degraded radius, dh = degraded height from base of coral) were measured. Coral loss was then quantified by using the formula: total live coral volume/ total degraded coral volume * 100. There was no reduction in live coral on control colonies and no change in study species abundance over the 2 – 4 days.

All colonies were censused for individually tagged gobies every 4 - 5 days for up to 140 days (5 months; June – October 2005). Where marked fish were not located in colonies all coral colonies in the vicinity were searched. The study species are all highly sedentary, showing infrequent natural movement, limited to closely spaced live colonies (separated by up to 1m [P. Munday and M. Wong, personal communication]). As experimental coral colonies were separated from neighboring corals by sandy substratum of at least 5 – 10m, any individual not located within neighbouring colonies was deemed lost. Over the course of the experiment, 384 individuals were tagged and censused: 90 individuals in control colonies (30 individuals each of *G. histrio*; *G. quinquestrigatus* and *P. xanthosomus*), 186 individuals in colonies with low coral loss (62 individuals each of *G. histrio*; *G. quinquestrigatus* and *P. xanthosomus*), 66 individuals in colonies with medium coral loss (22 individuals each of *G. histrio*; *G. quinquestrigatus* and *P. xanthosomus*) and 42 individuals in colonies with high coral loss (14 individuals each of *G. histrio*; *G. quinquestrigatus* and *P. xanthosomus*). In control colonies the majority of study species persisted for the entire trial. In contrast, no study species in experimental colonies persisted for the entire trial. Thus, colonies where either 1 or both tagged gobies were not found were replaced with new colonies that were then experimentally degraded (as above) and their pair of resident gobiid individuals tagged and censused every 4 – 5 days (as above).

### *Migration*

To examine the ability of study species to migrate from degraded to live corals, single individuals of the 3 goby species (*G. histrio*, *G. quinquestrigatus* and *P. xanthosomus*) were individually placed in a full degraded coral (100% live coral loss), surrounded by 4 live corals (all colonies were cleared of resident fishes and invertebrates before use). Successful movement of individuals into the live coral was then quantified. All goby individuals were tagged (as above) and their SL (mm) measured before release. Live corals were positioned in a square formation around the degraded central coral and at successive trials placed at different distances away from the central coral: 0, 50, 100, 150, 200, 250 and 300 (cm). All individuals within each species were of similar size (*G. histrio* 24.8 ± 0.3 mm SL, mean ± SE; *G. quinquestrigatus* 21.7 ± 0.3 mm SL; *P. xanthosomus* 17.8 ± 0.4 mm SL), though there were differences between the average sizes of species (ANOVA $F = 115.1$, $df = 2$, $p < 0.001$). Coral colony volume ($1/3 \times \pi \times r^2 \times h$ (cm), where $r$ = radius and $h$ = height from base of coral) was recorded. There was no significant difference in colony size within and between coral species (ANOVA $p > 0.05$; *A. cerealis* 516.9 ± 39.1 $cm^3$, mean ± SE; *A. nasuta* 579.1 ± 33.9 $cm^3$, *S. hystrix* 570.3 ± 48.2 $cm^3$).

Individuals were placed within the degraded coral at 0700 – 0800 hrs, and monitored for successful movement into the live corals 24 hours later. A pilot experiment had shown that transplanted fishes moved from unfavourable habitats (i.e., degraded coral colonies) into preferred habitats (i.e., live coral colonies) within hours, with no further movement after 12 – 24 hours. Therefore, the time interval between transplantation and monitoring was deemed sufficient to encompass study species natural migration behaviour. Twenty trials at each distance were completed for each goby species; individuals were only used in 1 trial. To distinguish movement from loss of individuals, where tagged individuals were not located in live colonies after 24 hours, all coral colonies in the vicinity were searched (as above). As experimental coral colonies were separated from neighbouring corals by a sandy substratum of at least 10m, movement beyond neighbouring colonies was assumed to be negligible.

### *Analyses*

#### *Resistance*

Goby species resistance to coral loss treatments (time in coral per day after disturbance) was analysed using a two-way ANOVA. All data was 4th root transformed to meet assumptions of normality and homoscedascity. As there were significant differences in resistance between species and coral loss treatments, the nature of this difference was examined using separate one-way ANOVAs. Newman-Keuls (NK) multiple comparison tests were employed for *a-posteriori* comparison tests of the means. To protect against inflated Type I error in the multiple univariate approach, an overall alpha of 0.01 was used.

#### *Migration*

As the data did not satisfy the assumptions of normality and homogeneity of variance required by ANOVA, Kruskal-Wallis one-way analysis of variance on ranks was used to examine whether there were significant differences in successful migration between distance treatments within each goby species. Any significant difference in migration was then examined using post hoc Mann-Whitney *U* tests between species, with an alpha of 0.05.

## Results

### *Resistance*

ANOVA showed that there were significant differences in resistance both among species (ANOVA, F = 6.36, df = 2, $p < 0.01$) and coral loss treatments (ANOVA, F = 92.67, df = 3, $p < 0.001$).

No significant difference in resistance within control colonies were found among all 3 species (Table 4.1), with a high level of resistance found in all 3 species (Fig. 4.1). Less than 1% of individuals, in each study species, were lost from control colonies, with the majority of individuals remaining in colonies for the entire trial (Fig. 4.1). However, there were significant differences in resistance between coral loss treatments among species (Table 4.1). There was a significantly lower resistance to low levels of coral loss in *G. quinquestrigatus*, when comparing with either *G. histrio* or *P. xanthosomus* (NK $p \leq 0.001$) (Fig. 4.1). *Gobiodon quinquestrigatus* showed an average resistance of 41 ± 5 days (± SE), while both *G. histrio* and *P. xanthosomus* showed an average of 61 ± 6 and 61 ± 4 days, respectively (Fig. 4.1). Such significant differences in resistance among species were not found with medium and high levels of coral loss (Table 4.1). Although *G. quinquestrigatus* showed the lowest rates of resistance to both medium and high levels of coral loss among species (Fig. 4.1), there were no significant differences among coral loss treatments.

Table 4. 1. Comparisons among 3 obligate coral-dwelling gobies in their resistance to coral loss treatments: Control, Low, Medium and High coral loss.

| Habitat loss treatments | df | MS | F | p |
|---|---|---|---|---|
| Control | 2 | 0.046 | 2.116 | 0.13 |
| Low | 2 | 1.136 | 8.245 | 0.001 |
| Medium | 2 | 0.218 | 2.754 | 0.08 |
| High | 2 | 0.087 | 0.663 | 0.53 |

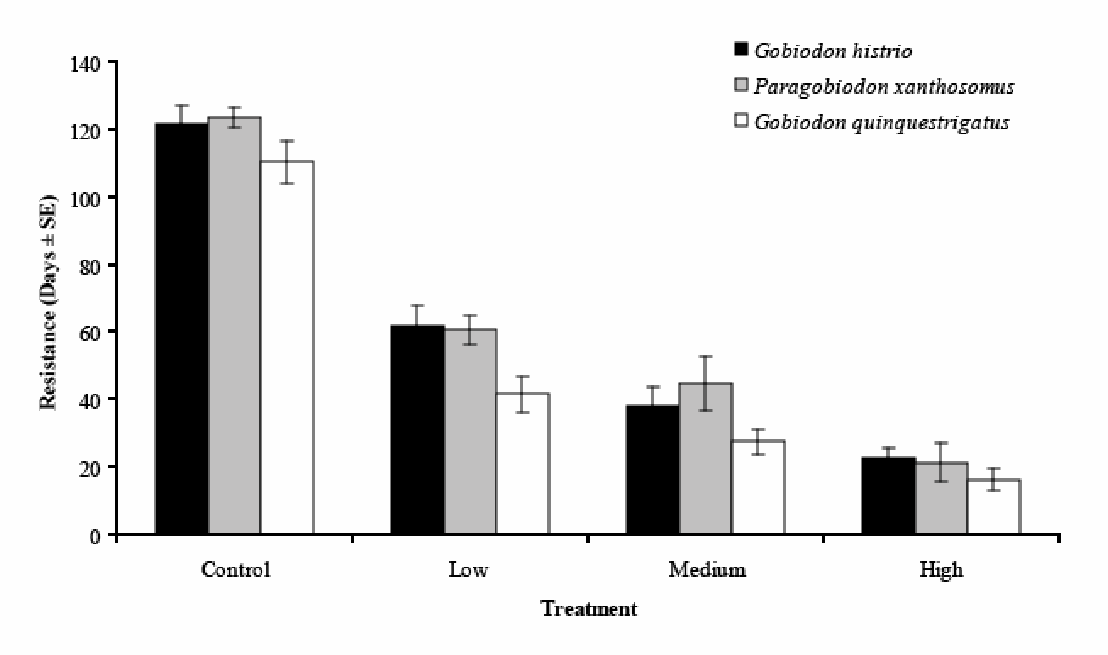

Fig. 4. 1. Resistance (time in coral per day ± S.E.) to 4 coral loss treatments (control, low, medium and high coral loss) within 3 obligate coral-dwelling gobies from habitat specialist to generalist: *Gobiodon histrio*, *Paragobiodon xanthosomus* and *Gobiodon quinquestrigatus*.

*Migration*

Although all transplanted individuals moved out of the degraded central colony within the 24 hour period, there were significant differences in successful migration to live colonies among species (Kruskal-Wallis: Chi-Square = 12.82021, df = 2, p = 0.001). Mann Whitney *U* tests showed that the coral specialists, *G. histrio* and *P. xanthosomus*, had significantly lower migration success than the coral generalist, *G. quinquestrigatus* (Table 4.2). Both *G. histrio* and *P. xanthosomus* were successful in moving between corals separated by ≤ 100 cm (75 – 80%) (Fig. 4.2). However, this successful movement decreased considerably when corals were further than 100 cm apart (10 - 25%), and no individuals of either species successfully moved between corals ≥ 250 cm apart (Fig. 4.2). In comparison, *G. quinquestrigatus* were able to successfully move between degraded and live corals up to 250 cm apart (Fig. 4.2).

Table 4. 2. Comparison of the differences in average migration between 3 obligate coral-dwelling gobies: *Gobiodon histrio*, *Gobiodon quinquestrigatus* and *Paragobiodon xanthosomus*. Tests are Mann Whitney *U*.

| Species | Rank sum | p |
|---|---|---|
| *Gobiodon histrio*<br>*Gobiodon quinquestrigatus* | 17640.00<br>21700.00 | 0.005 |
| *Gobiodon histrio*<br>*Paragobiodon xanthosomus* | 19110.00<br>20230.00 | 0.03 |
| *Gobiodon quinquestrigatus*<br>*Paragobiodon xanthosomus* | 21140.00<br>18200.00 | 0.01 |

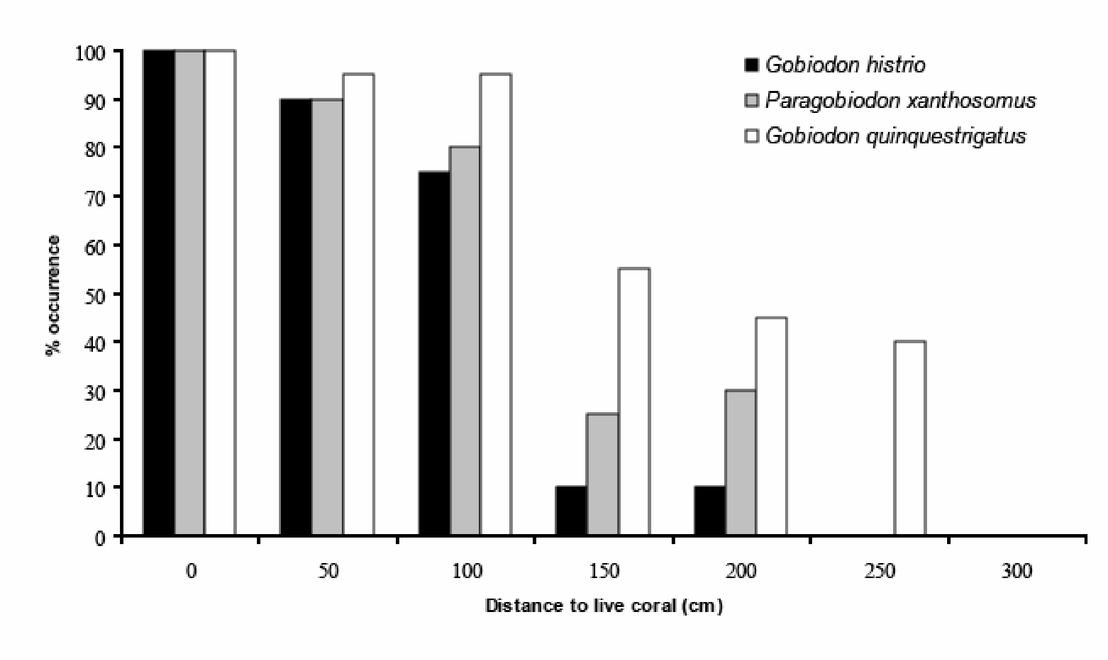

Fig. 4. 2. Relationship between successful migration from degraded to live corals and distance between corals for 3 obligate coral-dwelling gobies from habitat specialist to generalist: *Gobiodon histrio*, *Paragobiodon xanthosomus* and *Gobiodon quinquestrigatus*.

## Discussion

With the increasing disturbance to natural habitats worldwide (Myers et al. 2000; Fahrig 2001; Hughes et al. 2003), identifying the response of species to habitat loss is a central issue in conservation biology (Foufopoulos and Ives 1999; Fahrig 2001). Differential responses of species to habitat loss are well documented and a range of intrinsic factors may be important in determining this response (Hughes et al. 2000; Owens and Bennett 2000; Harcourt et al. 2002; Kotze and O'Hara 2003). This study found that differing responses to coral loss were influenced by species resource requirements. The coral specialists, *G. histrio* and *P. xanthosomus*, showed a higher level of resistance to partial coral disturbance than the coral generalist, *G. quinquestrigatus*. However, there was no significant difference in species resistance to medium or high levels of coral loss. In terms of migration ability, the coral specialists showed a significantly lower propensity to migrate from degraded into live coral colonies, with the coral generalist moving further and showing higher levels of successful migration.

Although the loss of habitat is usually closely followed by species emigration (Fahrig 2002), for species specialising on particular resources, resistance to partial habitat loss may dramatically increase an individual's ability to survive disturbance events. The Gobiidae show extremely strong interspecific competition for suitable colonies that often are in limited supply (Munday 2001; Munday 2004a) and individuals may retain single coral colonies for most of their adult life (Munday 2002). As predation risk will drastically increase with movement between corals (Stewart and Jones 2001) and the probability of finding suitable free corals will significantly decrease with increasing coral specialisation (Munday 2004a), the ability of specialists to remain within partially degraded colonies may far outweigh any benefit of immigrating to a healthier colony. In comparison, generalists are expected to use a much more broad array of habitats within the landscape (Sarre et al. 1995; McKinney 1997) and are more likely to find suitable colonies within a degraded coral landscape than specialists, increasing the probability of individuals successfully emigrating (Sarre et al. 1995; McKinney 1997). For habitat generalists the risks of movement between coral colonies may then be outweighed by the potential benefits of successfully emigrating from degraded to remnant coral colonies.

Although susceptibility to live coral loss is expected to differ between tropical reef fish species (Jones and Syms 1998), this work has shown that all 3 obligate coral-dwelling gobies show little ability to remain in corals with medium to high levels of coral loss. Each species are obligately associated with live coral colonies, depending on the colony for suitable shelter and sites for reproduction throughout their adult life (Munday et al. 1997, 2001). With the reduction of over half the coral the availability of such resources may decrease to such a level that all 3 species cannot survive within the colony (Munday et al. 1997). This result corresponds with recent work showing reductions in reef fish community abundance and diversity with declining live coral habitat (Halford et al. 2004; Jones et al. 2004; Graham et al. 2006, see Chapter 2). Although such reductions in reef fish structure will encompass species with obligate associations with live coral (Kokita and Nakazono 2001), a lower abundance and diversity of fishes with little association to the live coral cover (i.e., planktivores) can also occur with medium to high levels of live coral loss (see Chapter 2). As such levels of live coral loss are occurring more frequently within disturbance events (McClanahan 2004; Sheppard and Obura 2005), and such extreme coral disturbance events are predicted to occur on a more regular temporal scale (Hoegh-Guldberg 1999; Gardner et al. 2003; Hughes et al. 2003), relatively large, negative changes in the population structure of coral-associated reef fish communities may occur with coral disturbance (Graham et al. 2006).

Although the ability to successfully migrate between habitats may be influenced by a number of intrinsic factors (Chapman 2000), different levels of habitat specialisation may have a major influence (McKinney 1997; Mabry and Barrett 2002; McCauley 2007). In the present study the 2 coral specialists showed lower levels of successful migration between degraded and live corals than the habitat generalist. Such differences in migration success may be affected by a number of ecological factors associated with resource specialisation (Chapman 2000). However, in many empirical studies the structure of the surrounding matrix and the discrepancy in species ability to utilise different habitats within the matrix form an important determinant in migration success (Saunders et al. 1991; Ewers and Didham 2006). For generalists, the ability to move throughout marginal into preferred habitats, using marginal habitats as ecological "stepping stones" allow species to successfully disperse through the matrix and locate preferred habitats (Sarre et al. 1995; Ronce and Kirkpatrick 2001; Mabry and Barrett 2002). An unwillingness or inability to utilise marginal habitats (such as shown by many habitat specialists) may lead to species less able to exploit new habitats or disperse through the modified landscape (Ewers and Didham 2006). In this study, the coral generalist, *G. quinquestrigatus*, may have been able to use a much broader array of marginal shelter sites between degraded and live corals than the specialists, *P. xanthosomus* or *G. histrio* (i.e., small depressions in the sand and fragments of coral rubble). However, there was little behavioural difference in the response of study species when placed outside of their coral colony coral, with all 3 species rapidly moving into any close shelter (personal observation). Further work must now examine whether behavioral differences in movement influences migration ability between coral specialists and generalists.

Although resistance to coral loss may have positive effects on individual survival, remaining in degraded corals may eventually have negative effects on species persistence. If disturbances to coral reef communities are temporally short, degraded corals may regain their live coral cover (Connell et al. 1997; McClanahan 2000). Within this context, the ability of fishes to remain within the corals may result in little change to population structure (Pratchett et al. 2004). However, the possibility that disturbed coral colonies do not recover or show increased levels of disturbance within or after a disturbance event is extremely high (McClanahan 2002; Pandolfi et al. 2005). An inability or unwillingness to move between habitats may then have negative lag effects on the physiological condition and subsequent population structure of fishes associated with the degraded habitat (Booth 1995; Pratchett et al. 2004). For example, for live coral specialists that remain in degraded coral habitats, higher socially-mediated stress, due to increased coral loss and isolation, may affect species physiology (Adams 1990), leading to reduced levels of body condition and subsequent growth rate (Booth 1995; Pratchett et al. 2004, see Chapter 5). Such reductions in condition with habitat loss may then have negative long-term effects on the persistence of populations associated with the degraded habitat (Jones and McCormick 2002) due to reductions in species age of maturity and lifetime fecundity (Sogard 1994; Jones and McCormick 2002) and increased time periods in predator-vulnerable size classes (Forrester 1995; Booth and Hixon 1999) As populations of coral specialists are expected to persist in degraded landscapes, we can expect that reductions in the physiological condition of species will occur, and may be a major determinant in their population decline and extinction (Pratchett et al. 2004).

The persistence of habitat specialists and habitat generalists differed by days to weeks, while the distance successfully migrated differed by 1 - 2m. While these are seemingly minor differences, they are likely to have important demographic consequences due to the restricted spatial scales over which these species live (Munday 2004b). In a healthy coral landscape, the movement of obligate coral-associated gobies is infrequent and typically limited to movement between closely-spaced (≤ 1m) coral colonies (P. Munday and M. Wong, personal communication).

Coral disturbance events (e.g., COTS outbreaks, bleaching, etc.) often create large areas of dead coral (relative to relevant goby spatial scales) (Connell et al. 1997; Marshall and Baird 2000), thereby increasing the distance between coral colonies suitable for goby occupation (Connell et al. 1997). This can increase the risk of isolation within habitat fragments (Ault and Johnson 1998; Overholtzer-McLeod 2004). As fragmentation of coral habitats often increases with time after a disturbance event (Bunkley-Williams et al. 1997; Marshall and Baird 2000), the successful emigration of individuals will depend on both species-specific resistance (tendency to remain in a degraded colony) and migration ability (distance capable of moving). Species with high resistance and low migration ability (i.e., habitat specialists) are at greater risk of isolation because by the time the habitat degrades to below their resistance threshold, there is likely to be less suitable live coral nearby (Munday 2004b). In contrast, species with low resistance and high migration ability (i.e., habitat generalists) are more likely to move out of disturbed coral colonies early during the disturbance event when there are more suitable live coral colonies nearby, which is likely to result in greater successful migration and lower mortality of generalists within the degraded landscape (Munday 2004b).

Determining the intrinsic characteristics that influence reef fish species response to disturbance is becoming more essential with increased disturbance of coral reefs. Although several characteristics may affect reef fishes response to disturbance, for the obligate coral-dwelling gobies, different species level of coral specialisation may be important. In this group of fishes, coral specialists will resist moving from corals with low levels of coral loss for longer periods than generalists. However, medium or high levels of coral loss will result in reduced species abundance, independent of coral specialisation. Specialists will also show lower levels of successful migration from degrading to surviving corals. Such disparity in response to live coral disturbance between coral specialists and generalists may lead to a disproportionate reduction in the abundance of coral specialist gobiid species with live coral disturbance (Munday 2004b). If this pattern holds true for the array of coral-associated reef fish species, increased reductions in a range of coral specialised reef fish species may occur in disturbed coral systems (Jones et al. 2004).

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# CHAPTER 5: SUBLETHAL RESPONSE OF REEF FISHES TO LOW CORAL COVER

Feary, D.A., McCormick, M.I., Jones, G.P. (In Review) Sublethal response of reef fishes to low coral cover. *Coral Reefs*

## Abstract

Although the global decline in coral reef health is likely to have profound effects on reef associated fishes, these effects are poorly understood. While declining coral cover can reduce the abundance of reef fishes through direct effects on recruitment and/or mortality, recent evidence suggests that individuals may survive in disturbed habitats, but may experience sublethal reductions in their condition. To test this, I examined the response of 2 coral-associated damselfishes (Pomacentridae), *Chrysiptera parasema* and *Dascyllus melanurus*, to varying levels of live coral cover. Growth, persistence and the condition of individuals were quantified on replicate coral colonies in 3 coral treatments: 100% live coral (control), 50% live coral (partial) and 0% live coral (dead). The growth rates of both species were directly related to the percentage live coral cover, with individuals associated with dead corals exhibiting the slowest growth, and highest growth on control corals. Differences in the growth of individuals between treatments occurred after 29 days. There was no significant difference in the numbers of fishes persisting or the condition of individuals between different treatments on this time-scale. I argue that slower growth in disturbed habitats will delay the onset of maturity, reduce lifetime fecundity and increase vulnerability to gape-limited predation. Hence, immediate effects on recruitment and survival may

underestimate the longer-term impacts of declining coral on the structure and diversity of the coral-associated reef fish communities.

## Introduction

The destruction and degradation of shallow marine habitats is increasing at an unprecedented rate (Alongi 2002; Duarte 2002; Lotze et al. 2006). Coral reef ecosystems appear to be particularly vulnerable to a range of disturbances that are combining to threaten coral throughout tropical regions (Gardner et al. 2003; Hughes et al. 2003; Pandolfi et al. 2003; Pandolfi et al. 2005; Aronson and Precht 2006). While human impacts on coral reefs have direct and immediate consequences for coral biodiversity (Hoegh-Guldberg 1999; Knowlton 2001; Pandolfi and Jackson 2006), recent work has shown that the associated reef fish fauna will often exhibit dramatic changes in structure in relation to declining coral cover (Jones and Syms 1998; Halford et al. 2004; Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006, see Chapter's 2 and 3). Some effects occur immediately in response to the loss of living coral tissues, particularly for species that specialise on corals as a food source or shelter sites (Syms and Jones 2000; Halford et al. 2004; Jones et al. 2004, see Chapter 4). Other effects do not become apparent for several years, perhaps in response to the collapse of the 3-dimensional physical structure on dead reefs (Graham et al. 2006; Wilson et al. 2006). However, our understanding of the demographic mechanisms by which declining cover impacts on fish communities over different time scales remains limited.

Longer-term effects of declining coral cover on fish communities may arise though mechanisms that have no immediate effects on demographic rates, such as recruitment or mortality (see Chapter 3). Sublethal effects in response to a loss of resources, such as reductions in reef fish growth, physiological condition or reproductive success may not be detected for months or years after disturbance. For example, Pratchett et al. (2004) found little change in the population abundance of a small obligate corallivore (*Chaetodon lunulatus*), associated with degraded reefs, 2 years after reductions in live coral cover. However, there were significant declines in the condition of populations within the habitat, likely to have resulted from declines in the quantity and quality of available coral prey (Pratchett et al. 2004). Increasing competition for limited resources in disturbed coral habitats may gradually reduce the condition of surviving reef fishes (Booth 1995), while increased socially-mediated stress through competition may incur physiological costs (Adams 1990) that reduce both body condition and fitness (Booth 1995).

Previous work investigating the sublethal response of fishes to coral disturbance have focused entirely on obligate corallivores (e.g., Pratchett et al. 2004). While the effects can be substantial, coral-feeders represent a small proportion of coral reef fish communities (Hixon 2003). Small, coral-associated planktivores, many of which are damselfishes (Pomacentridae) often make up a larger proportion of reef fish assemblages (Sale 1991a). These fishes typically associate with live coral colonies, presumably using them primarily as shelter sites (Holbrook et al. 2000; Holbrook et al. 2002b). Significant declines in the abundance of planktivorous damselfish populations have been observed where disturbance has caused extensive coral mortality (Booth and Beretta 2002, see Chapter 2). However, even for species that exhibit no immediate change in abundance, reductions in the availability of live coral for species that use the habitat primarily for shelter, may have negative effects on their growth, physiological condition or reproductive success (Jones 1988; Jones and McCormick 2002).

As reductions in the growth, condition and fitness of species that use the habitat primarily for shelter cannot be explained by reductions in food availability, the effects of habitat loss may then be related to variations in the risk of predation on disparate habitats (Jones 1988). For example, Munday (2001) has shown that coral obligate gobies (Gobiodon) show lower growth rates in less preferred corals, dependent on the coral's interbranch space. Smaller interbranch spacing in less preferred corals may have increased the time gobies spent on predator avoidance, reducing foraging efficiency and negatively affecting growth (Munday 2001). Such correlations between habitat structure and growth rate show that reductions in preferred habitat space may have long term consequences for habitat associated reef fish populations (Booth 1995).

This study examined the response of 2 species of coral-associated, planktivorous damselfish to different levels of live coral. Under experimental conditions, I tested the effects of coral cover on short-term patterns of abundance, growth and condition on individual fish in both species. I predicted that the short-term response would be reductions in growth and/or condition rather than abundance, and that lower live coral cover would lead to lower fish growth and/or condition. In addition, I predicted that individual body size would influence short-term persistence, growth and/or condition with live coral loss, with lower persistence and lower growth and/or condition with low live coral in smaller sized individuals.

## Materials and Methods

This study was conducted at Kimbe Bay, West New Britain, Papua New Guinea (5°30'S, 150° 05'E), and examined the effects of low live coral on the persistence, growth and condition of 2 coral-associated planktivorous damselfishes, *Chrysiptera parasema* and *Dascyllus melanurus* (Pomacentridae). These 2 species are commonly associated with branching corals on isolated patch reefs in back-reef habitats in this region (Srinivasan 2003). Srinivasan (2003) showed that both species can be successfully translocated to patch reefs established for experimental manipulations.

To establish experimental reefs, 36 live colonies of *Acropora millepora*, (200 x 300 mm), were translocated to an expanse of sand 5 - 6.5 m in depth. All colonies were separated by 20m. Eight individuals of *C. parasema* were stocked on each of 18 randomly selected colonies, while *D. melanurus* individuals were stocked on the remaining 18 colonies. Subsequent immigrants were replaced until the population on each colony stabilised at 5 - 6 *C. parasema* and 6 - 7 *D. melanurus*. All individuals were then tagged for individual recognition, using subcutaneous injections of coloured elastomer *in situ*, and measured to the nearest mm (SL and TL) (reference for marking). Transplanted fish were categorised into two different size classes: juveniles and sub adults (*C. parasema*: juveniles ≤ 21mm TL, sub adults > 21mm TL; *D. melanurus*: juveniles ≤ 19mm TL, sub adults > 19mm TL) (Cole 2002; Asoh 2003; Srinivasan and Jones 2006).

Coral colonies were randomly assigned to 1 of 3 treatments: 100% live coral cover ($n$ = 12); 50% live coral cover ($n$ = 12), and 0% live coral cover ($n$ = 12). All colonies were caged with wire-mesh cages and a single crown-of-thorns starfish (COTS) was introduced into each of the coral-reduced treatment colonies. COTS were constrained to feed on selected parts of experimental colonies by attaching rubble to the coral head, limiting the area of coral for the COTS to feed on. Coral loss occurred over 2 - 4 days; all cages and COTS were then removed.

After 29 days all study species were collected, euthanised with an overdose of clove oil, and their total length (mm SL and TL) measured. Sagittal otoliths were extracted from each individual and a transverse section through the nucleus was taken (Wilson and McCormick 1999).

*Persistence*

To examine whether, within each species, there were differences in the abundance of individuals on treatments, the abundance of transplanted individuals at the start of the trial ($T_{start}$) were compared with their abundance after 29 days ($T_{end}$). Repeated measures ANOVA was used to examine whether there were significant differences in the persistence of individuals between $T_{start}$ and $T_{end}$, within each species, between size class and coral treatment. Size class (juvenile, sub adult), coral treatment (100%, 50%, 0% live coral) and time ($T_{start,}$ $T_{end}$) were factors, with number of transplanted fish on each colony as the dependent variable. Any significant difference in persistence within and between factors was examined using Tukey HSD tests.

### *Growth*

To investigate whether there were differences in growth of study species over the 29 day trial, between size class and coral treatment, 2 measures of growth were analysed: (1) change in total length (change TL) and (2) change in daily increment width, across the 29 day trial. Change in the total length of individuals within each species and size class (change TL = total length at trial end – total length at trial start) was averaged across treatments. To examine whether there were significant differences in change TL between size class (juvenile, sub adult) and treatment (100%, 50%, 0% live coral), two-way ANOVA using 4th root transformed data was used. Any significant difference in change TL within or between factors was examined further using Tukey HSD tests.

To examine the temporal change in growth rate within species, recent otolith growth was determined by measuring the size of each daily increment from the otolith margin to the 29th ring (Suthers 1998). To reduce the influence of body size on recent otolith growth within species, sagittae from individuals in similar size classes at the start of the trial were compared. Thirty individuals in each size class were analysed (10 individuals from each coral treatment) within each study species. Each measurement was repeated 3 times by a single observer without reference to the fish's identity (i.e. blind), and the mean value taken. Measurements deviating by < 10% of the mean were accepted (only 5% of measurements were excluded). Increment measurements were obtained using the image analysis package Sigma Scan™. To examine whether there were differences in daily increment width over the course of the experiment, mean increment width was analysed using repeated measures ANOVA on 4th root transformed data. Factors in the model were size class (juvenile, sub adult) and coral treatment (100%, 50%, 0% live coral), with otolith increments (29 daily increments) as the repeated measure and mean increment width as the dependent variable (Chambers and Miller 1994). Any significant difference in increment width, within and between factors, was examined using Tukey HSD tests.

*Condition*

To determine the influence of coral treatment on the body condition of both study species, between size classes, the Fulton's condition factor was calculated. Fulton's condition factor (K) was defined as:

$K = WB * 100/L^3$

where WB is gutted body weight (g) and L is standard length (mm).

To quantify the physiological condition of study species, hepatocyte vacuolation was measured (i.e., the proportion of liver tissues occupied by intracellular vacuoles). After fixing, hepatic tissues were dehydrated in a graded ethanol series and embedded in paraffin wax. Tissues were sectioned at 5 $\mu$m and sections were stained using Mayer's hematoxylin and eosin. The proportion of vacuoles in hepatic tissues was then quantified using a Weibel eyepiece, recording the proportion of points (out of 42) that intersected hepatocyte vacuoles viewed at 400 magnification. Hepatocyte vacuolation counts were repeated 3 times by a single observer without reference to the fish's identity (i.e. blind).

For each condition index, 30 individuals in each size class were examined (10 individuals from each coral treatment) within each study species. The mean value of each condition index, within species, between size class and coral treatment was taken and analysed using two-way ANOVA on 4th root transformed data.

## Results

### *Persistence*

There was no significant difference in the persistence of populations of either *C. parasema* or *D. melanurus* between size classes or coral treatments (ANOVA, $p > 0.05$), with both study species showing high levels of persistence throughout the trial period. For *C. parasema*, over 70% of transplanted individuals survived throughout the 29 day trial period, whilst 80% of transplanted individuals persisted for *D. melanurus*.

### *Growth*

There were significant differences in somatic growth of *Chrysiptera parasema* individuals among coral treatments (Table 5.1). There was significantly higher growth on the colonies with 100 and 50% coral treatments than those with no coral, with fishes on 0% coral treatments showing only ½ the growth of those on 100 and 50% coral treatments (Tukey HSD, $p < 0.01$) (Fig. 5.1). Growth on the 100 and 50% coral treatments did not differ from one another. Notably, both size classes were equally affected by coral loss (Table 5.1).

Table 5. 1. Factorial ANOVA comparing the average somatic growth of *Chrysiptera parasema* individuals over a 29 day experiment, between size classes (juvenile, sub adult) and coral treatments (100%, 50%, 0% live coral).

| Source of variation | df | MS | F | p |
|---|---|---|---|---|
| Size class | 1 | 0.005 | 0.346 | 0.558 |
| Coral treatment | 2 | 0.114 | 7.989 | 0.001 |
| Coral treatment * Size class | 2 | 0.008 | 0.560 | 0.573 |
| Error | 73 | 0.014 | | |

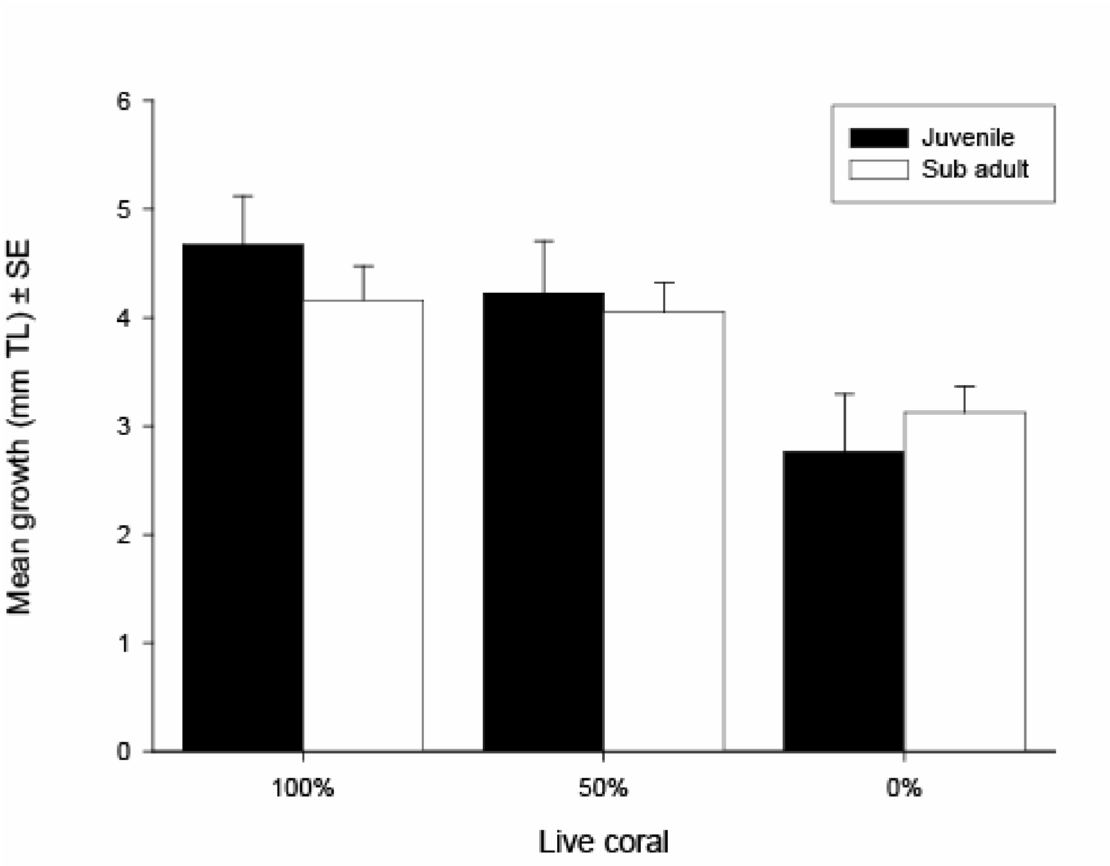

Fig. 5. 1. Mean somatic growth (mm TL) of *Chrysiptera parasema* individuals over a 29 day experiment between size classes (juvenile, sub adult) and coral treatments (100%, 50%, 0% live coral).

Moderately high variability precluded significant trends in the somatic growth of *Dascyllus melanurus* among coral treatments (Table 5.2). However, a similar trend in growth to *C. parasema* was found among treatments, though there was significantly higher growth for juveniles than sub adults for all coral treatments (Tukey HSD, $p < 0.01$). Juveniles on 100% coral treatments had an average growth of 7.16 ± 0.66 (mean ± SE, mm TL) over 29 days, while those on 50% and 0% coral treatments grew on average 6.55 ± 0.59 and 6.34 ± 0.38 mm TL, respectively (Fig. 5.2). In comparison, sub adults on 100 % coral treatments grew 5.78 ± 0.36 (mean ± SE, mm

TL) over the course of the experiment, while those on 50% coral treatments grew 5.53 ± 0.38 mm TL and those on 0% coral treatments grew 5.10 ± 0.58 mm TL (Fig. 5.2).

Table 5. 2. Factorial ANOVA comparing the average somatic growth of *Dascyllus melanurus* individuals over a 29 day experiment, between size classes (juvenile, sub adult) and coral treatments (100%, 50%, 0% live coral).

| Source of variation | df | MS | F | p |
|---|---|---|---|---|
| Size class | 1 | 0.114 | 5.125 | 0.026 |
| Coral treatment | 2 | 0.026 | 1.175 | 0.313 |
| Coral treatment * Size class | 2 | 0.005 | 0.228 | 0.797 |
| Error | 102 | 0.022 | | |

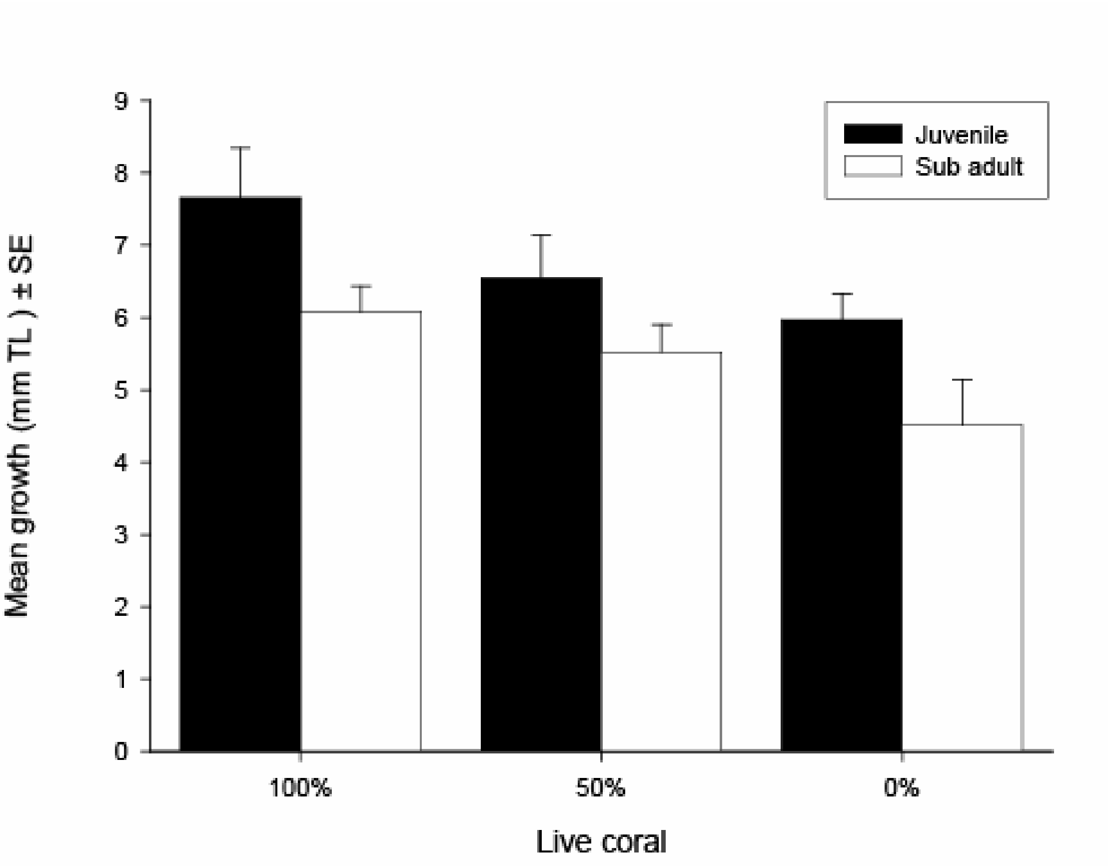

Fig. 5. 2. Mean somatic growth (mm TL) of *Dascyllus melanurus* individuals over a 29 day experiment between size classes (juvenile, sub adult) and coral treatments (100%, 50%, 0% live coral).

Data from otolith increment widths supported overall growth trends among coral treatments. There were significant differences in the mean width of daily increments in *C. parasema* between coral treatments over the trial period, but no difference between size classes (Table 5.3). Differences in mean increment width between coral treatments were due to significantly wider increments for individuals on 100 and 50% coral treatments compared to those associated with no live coral (Tukey HSD, $p < 0.01$) (Fig. 5.3). Although increment widths fluctuated in magnitude for fish from the 3 treatments over the 29 day period (as indicated by a significant Time x Coral treatment term, Table 5.3), increment widths showed a relatively consistent ranking among treatments through time. Individuals associated with 100 and 50% coral treatments had generally wider daily increments than fish on coral treatments with no live coral (Fig. 5.4). The apparent differences in otolith increment width between treatments in the 29 day period suggest that coral cover has a rapid influence on the growth profiles of these coral-associated fish (Fig. 5.4).

Table 5. 3. Repeated measures ANOVA comparing average otolith increment width of *Chrysiptera parasema* individuals over a 29 day experiment, between size classes (juvenile, sub adult), coral treatments (100%, 50%, 0% live coral) and times ($T_{start}$, $T_{end}$).

| Source of variation | df | MS | F | p |
|---|---|---|---|---|
| Size class | 1 | 1.026 | 0.010 | 0.922 |
| Coral treatment | 2 | 884.604 | 8.295 | 0.001 |
| Coral treatment * Size class | 2 | 140.211 | 1.315 | 0.278 |
| Error | 49 | 106.646 | | |
| Time | 28 | 203.067 | 15.083 | 0.000 |
| Time * Size class | 28 | 13.480 | 1.001 | 0.464 |
| Time * Coral treatment | 56 | 18.311 | 1.360 | 0.042 |
| Time * Size class * Coral treatment | 56 | 20.763 | 1.542 | 0.007 |
| Error | 1372 | 13.464 | | |

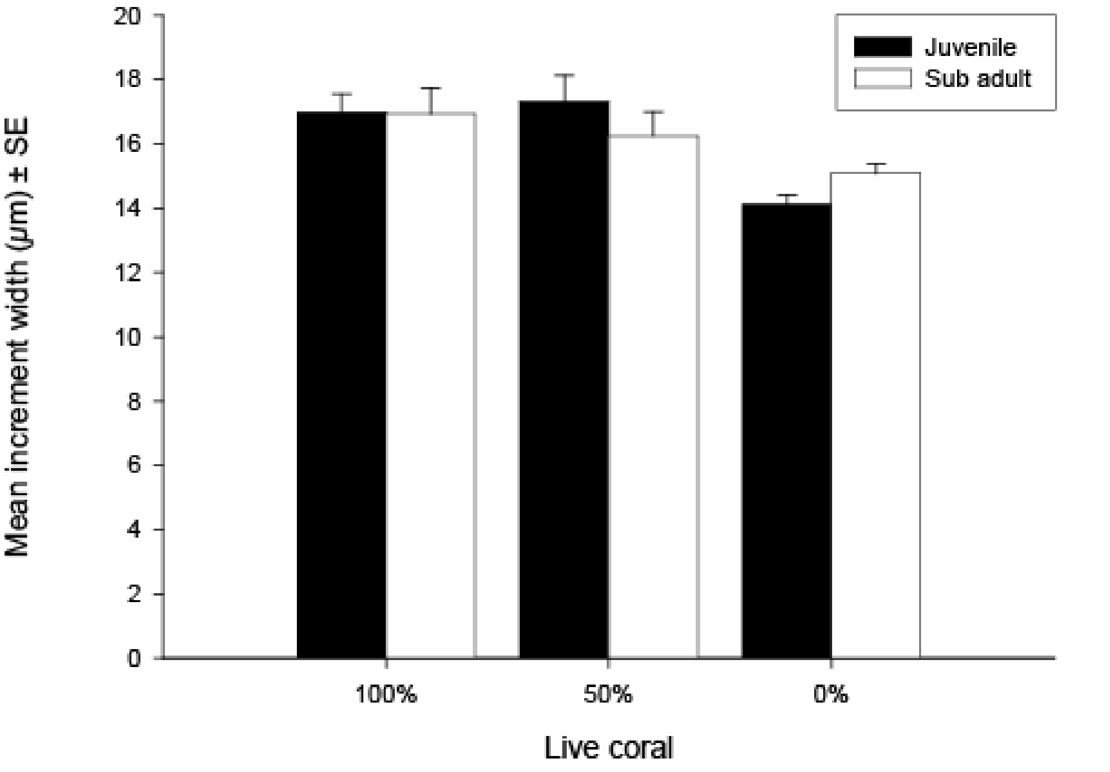

Fig. 5. 3. Mean otolith increment width ($\mu$m) of *Chrysiptera parasema* individuals over a 29 day experiment between size classes (juvenile, sub adult) and coral treatments (100%, 50%, 0% live coral).

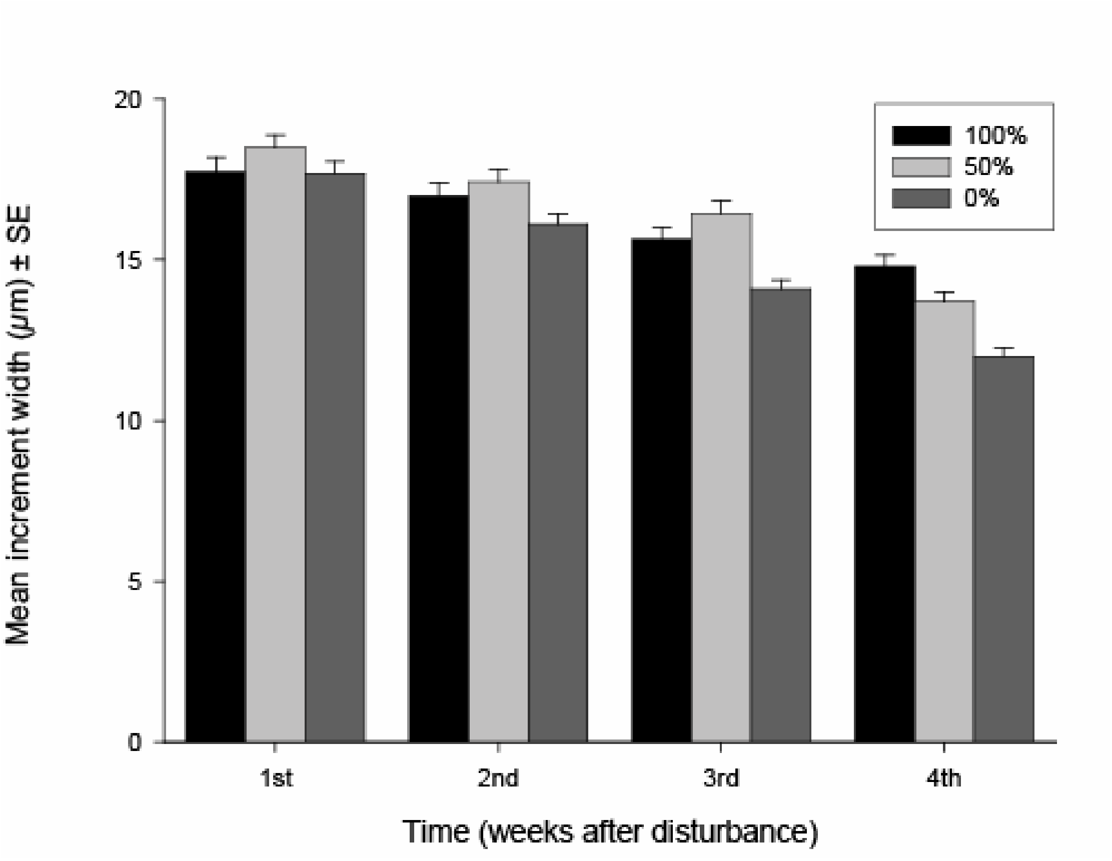

Fig. 5. 4. Mean otolith increment width ($\mu$m) of *Chrysiptera parasema* individuals over four time periods ($1^{st}$, $2^{nd}$, $3^{rd}$ and $4^{th}$ week of trial) and coral treatments (100%, 50%, 0% live coral).

There were significant differences in mean increment width between size classes and coral treatments within *D. melanurus* (Table. 5.4) with juveniles having substantially wider increments than sub adults (Tukey HSD, $p < 0.01$). Within both size classes, however, there were significantly wider increments in individuals associated with 100 than 50% coral treatments and 100 than 0% coral treatments (Fig 5.5). Juveniles associated with 100% coral treatments had a mean increment width of 19.00 ± 0.33 (mean ± SE, $\mu$m), while those associated with 50% and 0% coral treatments had mean increment widths of 16.04 ± 0.23 and 15.73 ± 0.28 $\mu$m, respectively (Fig. 5.5). In comparison, sub adults associated with 100% coral treatments had a mean increment width of 16.49 ± 0.22 (mean ± SE, $\mu$m), while those associated with 50% and 0% coral treatments had a mean increment width of 14.61 ± 0.19 and 14.92 ± 0.20 $\mu$m, respectively (Fig. 5.5).

Table 5. 4. Repeated measures ANOVA comparing average otolith increment width of *Dascyllus melanurus* individuals over a 29 day experiment, between size classes (juvenile, sub adult), coral treatments (100%, 50%, 0% live coral) and times ($T_{start}$, $T_{end}$).

| Source of variation | df | MS | F | p |
|---|---|---|---|---|
| Size class | 1 | 14.271 | 8.176 | 0.006 |
| Coral treatment | 2 | 16.267 | 9.320 | 0.000 |
| Coral treatment * Size class | 2 | 1.360 | 0.779 | 0.464 |
| Error | 54 | 1.745 | | |
| Time | 28 | 2.179 | 12.926 | 0.000 |
| Time * Size class | 28 | 0.170 | 1.005 | 0.457 |
| Time * Coral treatment | 56 | 0.199 | 1.178 | 0.176 |
| Time * Size class * Coral treatment | 56 | 0.316 | 1.877 | 0.000 |
| Error | 1512 | 0.169 | | |

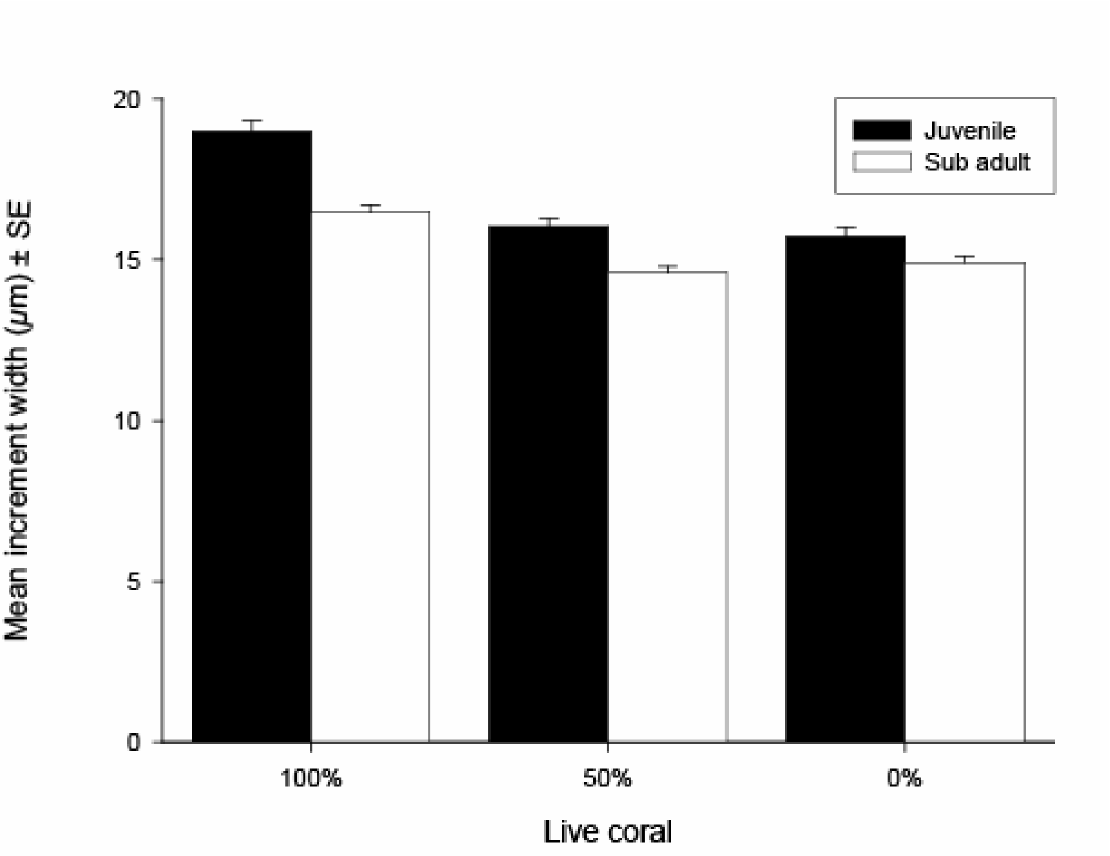

Fig. 5. 5. Mean otolith increment width ($\mu$m) of *Dascyllus melanurus* individuals over a 29 day experiment between size classes (juvenile, sub adult) and coral treatments (100%, 50%, 0% live coral).

*Condition*

A comparison of the condition of both study species suggested that there was little change in individual condition between treatments or size class over the trial period (Fig. 6). Within both species there was no significant difference in Fulton's K value (ANOVA interaction,: *C. parasema*, F = 0.94, df = 2, p < 0.001; *D. melanurus*, F = 1.48, df = 2, p < 0.001) or hepatocyte vacuolation value (ANOVA interaction: *C. parasema*:, F = 0.94, df = 2, p < 0.001; *D. melanurus*: ANOVA interaction, F = 1.48, df = 2, p < 0.001) (Fig. 6).

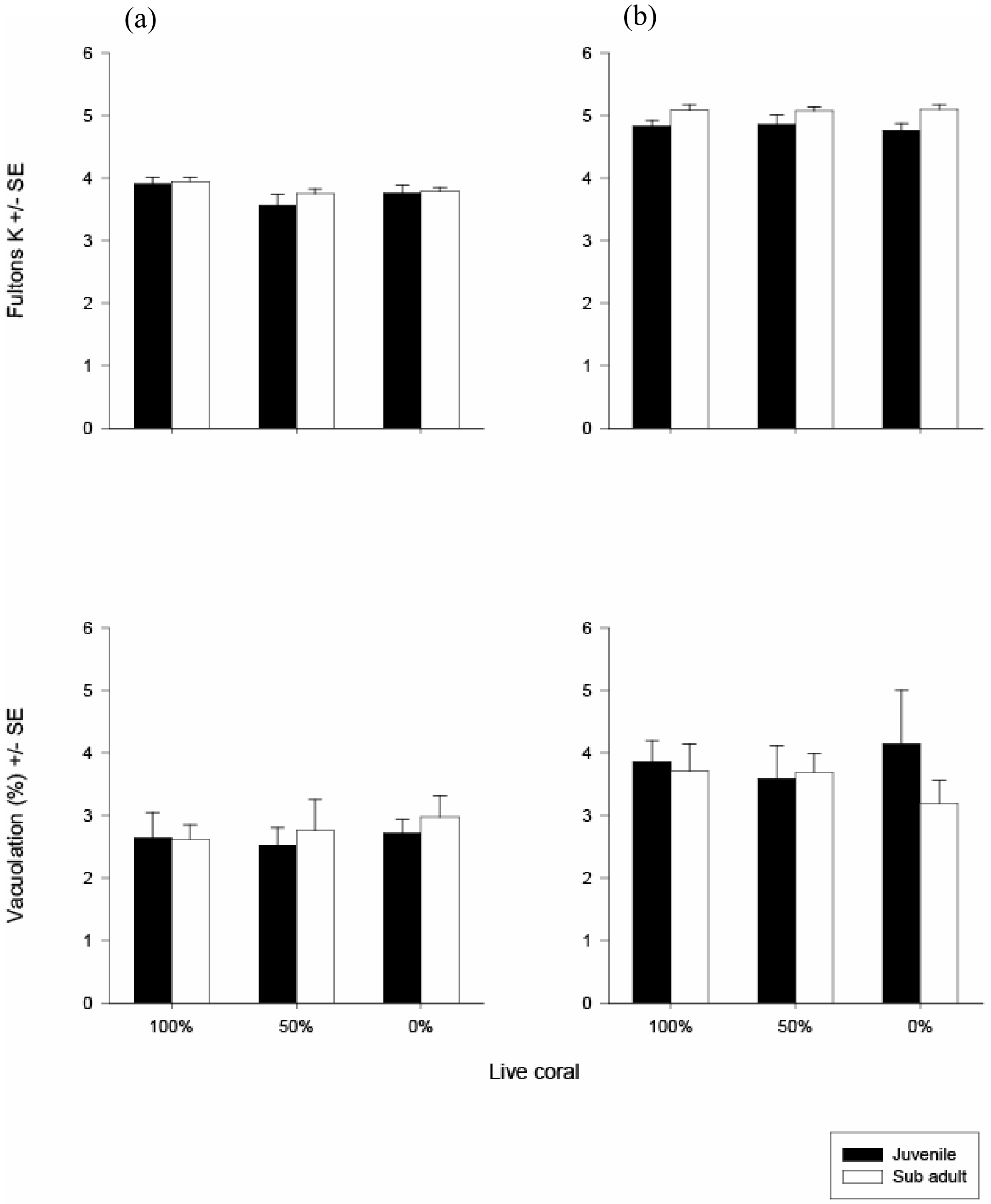

Fig. 5. 6. Comparison of condition measures: Fulton's K (K x $10^3$) and proportional occurrence of hepatocyte vacuoles between individuals of (a) *Chrysiptera parasema* and (b) *Dascyllus melanurus* between size classes (juvenile, sub adult) and coral treatments (100%, 50%, 0% live coral). Means with standard error are displayed.

## Discussion

This study supports recent work showing that coral loss can have sublethal effects on growth in coral reef fishes (Booth 1995; Pratchett et al. 2004). The present work also shows that this conclusion extends to fishes that do not rely on coral as a food source. Low levels of live coral reduced the growth of 2 planktivorous reef fishes by up to 50% of those living on undisturbed corals, without having any short-term effects on abundance or condition. Although loss or alteration of habitat can directly affect the growth of fishes, reductions in growth usually correspond with declining quality and/ or quantity of feeding resources within the habitat (Sogard 1992; Gilliers et al. 2006). However, both study species are planktivores, and thus it can be predicted that low coral cover should have had no effect on their food resources.

Both study species utilise live coral colonies for shelter (Srinivasan 2003), using the colony structure as refuge from predation (Holbrook and Schmitt 2002). Reductions in live coral and increased levels of algal overgrowth within experimental treatments will have reduced the availability of shelter space between residents (Munday 2001), increasing the potential for predation on individuals (Holbrook and Schmitt 2002). Within this study, on dead and partially degraded colonies, algal biomass rapidly filled the interstitial spaces between coral branches over the 29 days, substantially reducing possible shelter space for residents (Munday 2001). Such a loss of suitable shelter may have led to an intensification of competition between residents for suitable refugia, increasing resident's physiological stress (McCormick 2006; Trenzado et al. 2006), leading to reductions in their growth rate (Forrester 1991; Booth 1995; Munday 2001). In this study, within experimentally disturbed corals, as the quality and availability of suitable shelter space diminished for residents, increased intraspecific interactions may have affected group member's physiological stress, resulting in declines in growth rate (Trenzado et al. 2006).

Within group-forming coral-associated fishes, differences in body size between residents may create the potential for highly asymmetrical intraspecific competition for shared resources (Webster and Hixon 2000; Webster 2004). Theoretically, such asymmetry in competition can lead to some form of demographic density dependence within the group (Hixon and Jones 2005). The most common consequence of competitive interactions between residents is lower growth and survival of smaller sized residents (reviewed in Jones 1991). However, within the present study there was no significant difference in persistence of size classes between coral treatments, within each species, and no difference (i.e., *C. parasema*) or relatively higher levels of growth (i.e., *D. melanurus*) in juvenile than sub adult individuals between coral loss treatments. Although group size for both species was within the boundaries of natural *in situ* abundance (Srinivasan 2003), both species can form groups holding 2 - 3 times more individuals than utilised in the present study. Therefore, within the present research, despite the loss of habitat availability with live coral disturbance, for both species sufficient habitat was available to minimise lethal intraspecific competition for resources between residents. Therefore, I argue that the short-term response of coral-associated reef fish to changing live coral cover will be relatively similar across size classes, with high levels of persistence within disturbed habitats despite reductions in growth. However, for both study species, lethal interactions between small and large bodied residents may become density dependent on a longer temporal scale (Holbrook and Schmitt 2002; Webster 2004). Increased growth of algal biomass throughout the coral structure, coupled with the growth of resident individuals, may result in increased levels of antagonistic interactions between residents. Such increased interactions between residents may then lead to higher levels of density-dependent juvenile mortality within the population (e.g., Holbrook and Schmitt 2002).

Despite the negative effects on growth rate of remaining within disturbed colonies, there was no substantial movement of individuals away from coral-loss treatments. The majority of small-bodied coral-associated fishes show extremely low migration ability, predominantly remaining within the shelter of their host coral colony throughout their lifecycle (Forrester 1991; Munday and Jones 1998). For these species, a high level of competition for a limited supply of suitable habitats (Shulman 1985; Bay et al. 2001) may preclude successful movement of individuals between habitats throughout the reef. In addition, we can expect that mortality risk may substantially increase with emigration, due to the increased risk of predation when outside of suitable shelter (Stewart and Jones 2001; Holbrook and Schmitt 2002). Therefore, although reductions in live coral cover may reduce preferred space within colonies for resident fishes, their individual survival, to some extent, may be dependent on their ability to remain in the shelter of a coral colony (Shulman 1985; Holbrook and Schmitt 2002). We can predict that a trade-off may exist in which the potential benefits of moving to another coral colony are outweighed by the increased risk of mortality outside of the coral's shelter. An increasing number of studies are finding relatively high levels of resistance to coral decline within coral reef fish assemblages (Pratchett et al. 2004, see Chapter 2), with recent work showing persistence of obligate coral-dwelling fishes in partially degraded colonies weeks to months after coral loss (see Chapter 4). Although coral degradation is usually followed by species emigration or loss (Pratchett et al. 2006b), for fishes closely associated with the coral habitats, persistence in disturbed habitats may dramatically increase their ability to survive disturbance events (see Chapter 4).

In size structured fish populations, attainment of sexual maturity is often size based, and thus time-to-maturity is dependent on growth rate (Kirkpatrick 1984). Factors that cause fluctuations in growth rate, both social and environmental, may then have substantial effects on lifetime fecundity (Jones and McCormick 2002). The present study has shown that low live coral may lead to reduced growth in resident reef fishes. Such reductions in growth rate with low live coral may then increase individuals time to maturity and may have significant effects on the number of clutches produced throughout their lifetime (Sogard 1994; Booth 1995). We can expect that in populations associated with disturbed habitats, larval production may be poorer than from populations associated with healthy reefs (Jones and McCormick 2002). The long-term effects of such declines in larval quantity may substantially influence the replenishment of coral reef fish populations both at the local and regional scales (Jones et al. 1999; Jones et al. 2004).

Variation in growth rate may indirectly affect mortality and population size in the longer-term, through individuals remaining for long periods in small, predator vulnerable sizes (Forrester 1995; Booth and Hixon 1999). Piscivores are usually gape-limited, thus within size-structured fish populations predation rates can be affected by prey size, with higher levels of predation on smaller sized prey (St John 1999; Scharf et al. 2000). Such size dependent mortality may form an essential demographic mechanism regulating fish populations (Webster 2004; Hixon and Jones 2005).

However, reductions in the growth rate of fishes associated with disturbed habitats may increase the time period over which individuals are exposed to predation (Luczkovich et al. 1995; Persson et al. 1996). A bottleneck in the growth of individuals within the degraded habitat may then have long-term detrimental effects on the abundance and diversity of the associated fish community (Wilson et al. 2006). As habitat disturbance increases, growth rates of species associated with the habitat may decline, leading to substantially higher abundances of individuals in predator-vulnerable size classes (Forrester 1995; Booth and Hixon 1999). As predator abundance will track prey availability (Stewart and Jones 2001), we can expect that predator density may increase around disturbed habitats, enhancing predation risk for the associated community. The long-term effects of such increased predation risk may include substantial changes in the abundance, diversity and/ or size structure of the resident community (reviewed in Hixon 1991).

Phase delays in the response of the coral-associated reef fish community to coral loss may be due to a coupling of adult fishes with the coral reef's physical complexity (Graham et al. 2006). Broad reductions in the structure of reef fish communities may then be linked to the long term physical breakdown of the reef (Lewis 1998; Syms and Jones 2000; Graham et al. 2006). However, the present work has shown that reductions in the growth rate of small sized individuals (i.e., juveniles and sub adults) may also explain a phase delay in the response of reef fish communities to live coral loss. We can expect that within populations associated with degraded habitats, the loss of live coral will manifest as short-term reductions in individual growth rate, mediating any significant numerical response within the population (Jones and McCormick 2002; Pratchett et al. 2004). Such reductions in individual growth rate, however, may have negative long-term effects on the population's demographic structure within the habitat, reducing individual age to maturity, lifetime fecundity and increasing susceptibility to predation. Overall, although a variety of mechanisms may explain both the short and long-term numerical responses of reef fish communities to the alteration and loss of live coral cover, the present study suggests that a sublethal physiological response to live coral loss may play a substantial role in altering the structure of the reef associated fish community within degraded reef systems.

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# CHAPTER 6: GENERAL DISCUSSION

This thesis makes a significant contribution to our understanding of the patterns and processes important in the structure and dynamics of reef fish communities in response to coral disturbance. The patterns observed confirm recent work showing coral reef fish assemblages exhibit dramatic changes in their structure and biodiversity in relation to declining live coral (Jones and Syms 1998; Halford et al. 2004; Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006). The observational and experimental studies within this thesis, however, show that changes in reef fish community structure with coral disturbance will occur at varying temporal scales. In the short term, species-specific reductions in population abundance and diversity may be manifest through increased mortality within degraded habitats or movement of individuals between degraded and live coral habitats (Chapter 4). However, reductions in species diversity, the abundance of particular functional groups, and the size structure of coral-associated fish assemblages in response to declining coral cover may all manifest at much longer temporal scales, through reductions in resident individual's growth rate (Chapter 5) and fluctuations in the replenishment of coral-associated species within degraded habitats (Chapter 3).

Distinct changes in the structure of reef fish communities were apparent when comparing assemblages associated with colonies in sequential stages of coral degradation (i.e., from live and degraded to dead coral colonies) (Chapter 2). Within live coral colonies high abundances of coral obligates were apparent. The abundance of this functional group was lower in degraded colonies, while dead, algal-covered colonies held virtually no coral obligates (Chapter 2). Evidence in Chapter 4 suggested that changes in the abundance and diversity of coral obligates between live and degraded corals was dependent on species-specific differences in habitat dependency. Habitat generalists were less likely to persist within degraded habitats than specialists, due to their higher migration ability and lower level of resistance to coral loss (Chapter 4). I argued that if this pattern held true for the array of coral-associated reef fish species, increased reductions in a range of coral-specialised reef fish species would occur in disturbed coral systems (Jones et al. 2004). Following coral death and algal biomass increase, however, there were substantial reductions in coral obligate abundance, independent of species habitat dependency, within the disturbed habitats (Chapter 4). As increasing levels of global disturbance are accelerating the widespread degradation and death of tropical reefs, high levels of reef fish assemblage loss, substantially more than previously observed, will occur in tropical communities (Wilson et al. 2006).

I predicted that an inability or unwillingness to move away from degraded habitats may have substantial negative effects on the growth of fishes associated with the habitat (Chapter 4). Reduction in species growth rate with live coral loss was predicted to mediate any significant short-term numerical response within the population to the decline in live coral (Chapter 5). The results of this thesis conformed to this prediction and showed that low live coral can have significant effects on the growth of coral-associated fishes, without leading to substantial reductions in their population abundance (Chapter 5). Growth rates of study species were directly related to percentage live coral cover, with the lowest growth rates in individuals associated with dead colonies (0% live coral) and the highest in those within control colonies (100% live coral). I argued that such reductions in individual growth rate with live coral loss would lead to reductions in individual's maturity and lifetime fecundity within the habitat. These results show that a phase delay in the numerical response of reef associated fish communities to live coral loss may occur, mediated by a sublethal change in the physiological condition of species associated with the habitat.

Phase delays in the response of coral reef fish communities to live coral loss may also be manifest by changes in the abundance and diversity of new recruits utilising the degraded habitats (Chapter 3). Within Chapter 2 I showed that the total abundance of species was lowest in algal-covered colonies of both coral species, largely due to the low number of new recruits and juveniles associated with the habitat. A comparison of settlement preferences between common Indo Pacific reef fishes showed that both coral and non-coral associated damselfishes (Pomacentridae) avoided dead, algal-covered colonies at settlement, preferentially settling into either live or degraded colonies in the aquaria (Chapter 3). I then showed that experimental reductions in live coral cover resulted in rapid (2 - 4 weeks) and significant reductions in the abundance of coral-associated reef fish larvae settling into the habitats (Chapter 3). Such reductions in new settler abundance with live coral loss showed that the availability of suitable live coral was a significant factor in the successful settlement for a range of coral-associated reef fishes. I predicted that habitat-limited recruitment would become an important process by which changes in the composition of the coral-associated reef fish community manifest in degraded habitats (Schmitt and Holbrook 2000; Syms and Jones 2000; Booth and Beretta 2002). I argued that reductions in new settler abundance and richness, with loss of the living coral tissue, would then play a substantial role in altering the long term replenishment and ultimately the structure of the reef associated fish community within degraded reef systems (Chapter 3).

## Future directions

The patterns and processes described in this thesis suggest a number of hypotheses worthy of future investigation. The results of Chapter 3 suggest that reef fish settlement within degraded coral habitats may occur in 2 phases, with individuals using a coarse-scale selection of coral habitats (including degraded and algal-covered habitats), followed by post-settlement movement into preferred substrata. This behaviour may be important for the successful settlement and recruitment of a range of reef associated fishes in degraded habitats (sensu Finn and Kingsford 1996; McCormick and Makey 1997). However, little is known of *in situ* settlement behaviour in a range of tropical reef fish species (Leis and Carson-Ewart 2002). Recent studies have shown that a variety of cues (i.e. chemical, auditory and visual) may act to initiate benthic settlement behaviour in reef-naïve fish larvae (Lecchini et al. 2005a; Lecchini et al. 2005b). How such cues are affected by live coral loss and increased algal biomass are unknown (Chapter 3). Further insights into the importance of species specific behaviour at settlement and the possible role of benthic cues in mediating choice of substrata at settlement are needed. Understanding the role that benthic cues have on reef fish settlement patterns will be essential in understanding the response of reef associated fish communities to live coral loss.

The present research demonstrated that degradation of live coral can have a negative impact on the growth of resident fish, even when those fish do not appear to directly depend on coral for food resources (Chapter 5). I argued that within communities associating with degraded coral colonies, social mediated stress through habitat loss and increased crowding of residents may enhance an individual's physiological stress, leading to reductions in growth (Booth 1995) (Chapter 5). However, little work has examined the role of social-mediated interactions (e.g., through reduced shelter availability) in influencing the growth of coral-associated reef fish populations (Jones and McCormick 2002). Even when there is no observable change in population abundance with coral degradation, the reduced availability of suitable resources for a range of reef associated fishes and the increased interactions between individuals within degraded habitats may increase resident species levels of stress, leading to substantial changes in their growth. Further insights into the role of social-mediated interactions in influencing the growth of fishes associated with degraded coral habitats are needed.

Lastly, this work has highlighted the importance of coral death and increasing algal biomass in structuring diverse coral associated reef fish communities (Chapter 2, 3, 4 and 5). Coral death and increased algal biomass can have substantial effects on a range of tropical reef fish species with differing associations with live coral. Changes in species ecology (e.g., reduced population abundance [Chapter 2]), behaviour within habitats (e.g., reduced settlement [Chapter 3], increased emigration [Chapter 4]) and physiological condition (e.g., reduced growth [Chapter 5]) can all occur with coral death. Although changes in the population and community structure of obligate coral users (i.e. corallivores) have been shown with coral death, the majority of study species in this thesis have been fishes that do not directly depend on coral for feeding resources (e.g., planktivorous damselfishes) (Chapter's 2, 3 and 5). Why then does coral death have such an effect on these fishes? Although the availability of suitable shelter sites for these fishes may reduce with an increase in algal biomass (Munday 2001), ecological, behavioural and physiological changes in coral-associated reef fishes were found on colonies that had accumulated only light algal growth (1 - 2 weeks after coral loss). As reef fish use a variety of cues (including chemical) to recognise suitable coral reef habitats, we can predict that coral death may reduce or even negate such cues, leading to reductions in species abundance within the habitat. However, for populations associated with degraded habitats, is there an aspect of the increasingly algal biomass (i.e., physical or chemical) that fishes have an aversion to (e.g., Engstrom-Ost and Isaksson 2006)? For example, although algae utilise secondary metabolites as a chemical defence against herbivory (Paul et al. 2006), do they also exude chemicals that physically deter fishes? Further insight into the response of reef fishes to increasing algal overgrowth may lead to testable hypotheses on the role of algal biomass in structuring coral reef fish assemblages within degraded reef habitats.

This study has substantially contributed to our understanding of the future of tropical reef fish communities within an environment of increased coral disturbance. Fish communities utilising degraded coral habitats will hold higher abundances of habitat specialists than generalists, though broad reductions in community abundance will occur with coral death and algal biomass overgrowth. Disturbance and loss of live coral cover will lead to reductions in the abundance and diversity of new settlers who prefer to settle, and live in association with, live coral. In contrast, species that utilise non-coral habitats will increase in abundance in disturbed habitats. Lastly, for coral-associated fishes, fluctuations in individual growth rate will occur with live coral loss, with lower growth rates corresponding with higher levels of coral loss.

Such changes in species growth within habitats will have significant effects on individual maturity, fitness and the long term viability of populations within the habitat.

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