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

Thesis submitted by

Mary Catherine Bonin

(BA, GDipResMeth)

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DECLARATION OF ETHICS

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

Signature   Date

STATEMENT OF CONTRIBUTION OF OTHERS

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GENERAL ABSTRACT

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

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

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

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

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

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

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

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