Boström-Einarsson, Lisa (2016) ***Habitat degradation and competition for resources in coral reef fishes*****. PhD thesis, James Cook University.**

Habitat degradation and competition for resources in coral reef fishes

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Thesis submitted by

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in July 2016

for the degree of Doctor of Philosophy

within the College of Science and Engineering,

James Cook University

Acknowledgments

First and foremost I would like to thank my supervisors Geoff Jones, Phil Munday and Mary Bonin. Thanks to Geoff for giving me the freedom to explore many ideas throughout this dissertation, and for always providing the big-picture perspective in such an elegant and succinct way. Thanks to Phil for your relentless enthusiasm towards new results and new ideas, and for your ‘outside-of-the-box’-insights. And last but not least, thanks to Mary for being my cheerleader from day one and for dedicating so much time and energy towards every aspect of this thesis. What an amazing privilege to have this dream team on my side for the past six (!) years, throughout my Honours and PhD theses. It goes without saying that I couldn't have done this without you, and I’m forever grateful for your support and mentorship along the way.

This thesis has involved a large amount of fieldwork in Kimbe Bay, Papua New Guinea. None of the experiments would have been possible without the support of Mahonia Na Dari Conservation Centre and Walindi Plantation Resort. I had some amazing volunteers and lab mates who assisted in the field and helped maintain my sanity. Scott Hansen, Lucy Quayle, James Black, Phil Smith, Rhys Cornish and Lisa Vitale - I truly appreciate all your hard work. Jacob Eurich and Sir Chancelot Macdonald - the Jones lab would not be the same without you!

Throughout the marathon journey that is a PhD I was fortunate enough to be surrounded by a group of amazing people. In particular, April Boaden, Amelia Wenger and Ashton Gainsford - I am so grateful to have shared this journey with you.

Big thanks also to my family: Mum, Dad, Ingela, Lina, Oskar and Maya. Your enthusiasm and support can be felt across oceans and continents, and I appreciate all that you’ve done for me. *Jag saknar er ofantligt mycket varje dag, älskar er*!

Finally, thanks to Hugo for being there, literally every step of the way. The past four years would have been infinitely less fun, exciting and adventurous without you. I’m so excited to see where our post-PhD(s) adventures take us!

Statement on the contribution of others

The research presented in this thesis was funded by Australian Research Council grants to Geoff Jones and supported by the ARC Centre of Excellence for Coral Reef Studies and College of Science and Engineering at James Cook University, Townsville, Australia. An Endeavour International Postgraduate Research Scholarship awarded to Lisa Boström-Einarsson (LBE) provided additional support in the form of a stipend and tuition fees. The Graduate Research School at James Cook University provided support in the form of two grants; one supporting conference travel, and one as a write-up grant. Mahonia Na Dari Conservation Centre in Kimbe Bay, Papua New Guinea provided logistical support during field work.

This thesis was supervised by Geoff Jones, Phil Munday and Mary Bonin (MCB), who all provided guidance and editorial assistance on all chapters, and contributed to the development of ideas explored in each chapter. Chapter 2 is a review chapter, synthesising the collective knowledge of competition in reef fishes. As such, it builds on the work of a large number of authors that make up the content of the review. LBE and MCB worked together on compiling the data set that forms the basis for the review (Appendix 2), and in developing the questions and topics covered in the review. LBE produced the figures and online interactive data visualisation with input from all authors. Writing of the manuscript was truly a collaborative effort, with all authors contributing intellectual input to the drafting and revision of the manuscript. All data described in Chapters 3,4 and 5 were collected specifically for this thesis (by LBE), have not been published elsewhere and did not include externally collected data.

The work was conducted under JCU ethics permit A1899.

General Abstract

Habitat loss and degradation are among the most pressing threats to the persistence and diversity of species. They can directly lead to declining abundance through the loss of resources, or indirectly through disruption of important ecological interactions such as competition and predation. Coral reef ecosystems around the globe have experienced a decline in coral cover in the past few decades due to a suite of anthropogenic disturbances. Living corals not only provide the structural foundation in the reef ecosystem, but also critical resources such as food, shelter and suitable sites for reproduction for reef fishes. The loss of live coral often leads to a well-documented decline in reef fishes that associate with the coral reef matrix. However, our understanding of the causes of these declines is limited and the mechanisms are poorly understood. Habitat loss may directly impact on fitness parameters or population processes, or it may influence them indirectly by altering interactions such as competition for resources, successful sheltering from predators and habitat selection. *The overall objective of this thesis is to explore how habitat degradation influences competition for resources in a common, habitat associated coral reef fish.*

Competition over resources is recognised as a fundamental process in ecology, with important consequences for species coexistence, the distribution of species and the regulation of populations. The role of competition in the ecology of reef fishes has been the topic of debate over several decades. While early research in the 1980's focused on the partition of resources between species (i.e niche partitioning) or the chance colonisation of space (i.e 'lottery hypothesis'), others focused on alternate theories to explain patterns of density dependence (e.g. disturbance, predation, recruitment limitation). Since then, a large body of work has accumulated, with field experiments greatly increasing our understanding of the prevalence and importance of competition in coral reef fish communities. **Chapter 2** compiles and synthesises the results of

experimental tests of competition and shows that evidence for competition is pervasive, thus confirming its important role in structuring reef fish communities. Competition was found to be important both within and between species, with 72% of intraspecific tests and 56% of interspecific tests demonstrating a demographically significant consequence of competition. Competition within species (intraspecific competition) is likely to be particularly intense, given that individuals of the same species are likely to have a high degree of overlap in their resource requirements. A majority of studies of intraspecific competition explored numerical responses (i.e. survival or abundances) to competition. 59% found a negative effect of increasing conspecifics on their overall survival, while relatively few studies investigated sub-lethal effects of competition. Considering levels of competition depend on the availability of resources, the intensity of competition is likely to increase in response to habitat loss and degradation. However, the review emphasised the paucity of studies which have considered links between competition and resources, and the extent to which habitat loss and degradation alter the effects of competitive interactions are poorly understood.

A species' competitive response to habitat loss may affect multiple demographic parameters, and these effects may occur over different time scales. However, few studies have manipulated resource availability and documented the effects of habitat loss over time while measuring multiple demographic parameters. In **Chapter 3** I evaluate the consequences of habitat loss on the abundance, body condition and behaviour of a common coral reef fish over four months following an experimental reduction in the availability of live coral habitat. I identified natural aggregations of *Pomacentrus moluccensis* sheltering in *Acropora* coral colonies, and experimentally reduced live coral tissue by exposing 60% of the coral colony to crown-of-thorns starfish. Throughout the four month post-disturbance period, *P. moluccensis* showed a strong association with the remnant live habitat on treatment colonies, and avoided the recently dead coral habitat. Densities within this live habitat increased following the disturbance, but gradually dropped until they matched those of control colonies, indicating density dependent mortality. Surprisingly, liver samples indicated that individuals on treatment colonies with 60% loss of live coral habitat had a higher body condition than those on control colonies with no habitat loss. Video analyses revealed *P. moluccensis* on treatment colonies opportunistically feeding on the algal matrix growing on the recently dead coral branches. These results indicate that successful competitors benefit by gaining access to a novel food source along the edge of prime shelter space within live coral. This edge effect allows species with a degree of flexibility in their resource requirements to benefit from living at a habitat boundary. Chapter 3 highlights a species complex response, both positive and negative, to habitat degradation.

While Chapter 3 demonstrated the importance of live coral in promoting the survival of habitat associated fishes, it is still unclear what causes the mortality of less successful individuals. It is commonly hypothesised that fish mortality is increased as a consequence of the loss of shelter space between branches as dead corals become overgrown by algae. In **Chapter 4,** I tested this hypothesis by quantifying changes in sheltering behaviour of a common damselfish, *Pomacentrus moluccensis*, following the death of its host coral colony. Recently dead colonies of *Acropora* were allowed to accumulate algae and invertebrates over a period of five weeks. Groups of *P. moluccensis* were then placed on either live or dead coral colonies, startled using a visual stimulus, and their sheltering responses compared. *Pomacentrus moluccensis* stopped sheltering amongst the coral branches immediately following the death of the coral, despite very little change in shelter space. Instead, most individuals swam away from the dead coral into the surrounding water where they were more exposed to predators. I argue that live coral is a necessary cue that elicits the appropriate behavioural sheltering response to potential predators. Findings in Chapter 4 suggest that the disruption of this cue poses a great threat to coral-associated fishes on degrading reefs.

Partial habitat loss clearly results in temporary crowding of reef fishes which may lead to density dependent habitat selection. Individuals are faced with the decision of either joining high density populations crowded into remnant high quality habitat or opting to move to low quality habitat. **Chapter 5** investigates how habitat loss influences habitat selection, and ultimately the distribution, of *P. moluccensis*. In a survey of habitat use on 49 transects along the coral reef crest I found that *P. moluccensis* adults only chose dead coral colonies when the average density per live coral colony was higher than under natural conditions. These high densities on live coral colonies only occurred on reefs where >50% of colonies on were dead. This suggests that the loss of habitat causes crowding on remnant live coral until some fish start using less preferred dead colonies. I then conducted a choice experiment to investigate if density dependent habitat selection was the mechanism underlying this pattern. When presented with the choice of two colonies, fish were more likely to choose a near empty alternate colony when the other colony was severely crowded with conspecifics. The consequences of this behaviour are likely to be two-fold; first adult fish are forced to inhabit dead coral, and second their presence may encourage juvenile larvae to recruit to this unsuitable habitat if these recruits use conspecific presence as a cue to determine habitat quality. Chapter 5 provides the first example of how habitat loss induces density dependent habitat selection, adding to the growing body of work showing that habitat loss is impacting on critical ecological interactions on coral reefs.

In summary, this thesis has investigated effects of habitat degradation on key ecological processes determining the distribution of reef fishes, competition for resources and their interaction with the coral reef habitat. It showed complex demographic responses to coral loss that include both positive and negative effects. It established that

live coral is critical, not just for the structure it provides, but also for eliciting adaptive behavioural responses to the threat of predation. Moreover, this thesis provides the first demonstration of the crowding hypothesis in the marine environment and is the first to investigate how density dependent habitat selection is affected by habitat degradation. The outcomes of this research highlight the importance of living corals in the ecology and behaviour of coral reef fishes, and their complex responses to coral reef habitat loss and degradation.

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Chapter 1

General Introduction

1.1 Resource availability and competition in dynamic ecosystems

The distribution, abundance, and quality of resources are major drivers of ecological patterns and processes in ecosystems. The term ‘resource’ refers to any substance or factor that is utilised by an organism that contributes to its survival, growth, or reproduction (Tilman 1982). Resource use is intrinsically linked to interactions between individuals because consumption of a finite resource reduces the amount available to others. Competitive interactions between individuals over limited resources can control vital demographic rates that determine population size (Hairston et al. 1960), shape spatial distributions (Fretwell and Lucas 1969) and ultimately determine the structure of communities. While resources can be derived from external sources like rainfall and sunlight, many are provided by the local habitat in which an organism lives. Given the importance of habitat in providing critical resources to organisms, habitat structure has far-reaching effects on ecological interactions such as competition and predation, the distribution and abundance of species, and the structure of ecological communities (Menge and Sutherland 1976, Tilman 1982, Morris 1988, Tilman et al. 1994).

Habitat loss and degradation has become one of the primary causes of extinction in disturbed ecosystems and a major threat to the survival of endangered species (Tilman et al. 1994, Pimm et al. 1995). Habitat loss further disrupts ecosystems by causing population declines in many species as resources become depleted (Bender et al. 1998, Gibbons et al. 2000, Stuart et al. 2004). Reductions in species richness, population declines, and extinctions fundamentally change ecosystem functioning and alter the structure of animal and plant communities (Larsen et al. 2005, Dobson et al. 2006). Although the effects of habitat loss and degradation on species abundance are relatively well-known, little is known of the underlying demographic mechanisms and how they are mediated by behavioural responses in a changing landscape.

Competition occurs where individuals exploit limited resources (Begon et al. 1986). The intensity of competition should increase in response to declining resources and/or increasing population density, leading to density-dependent changes in the demographic rates that control population size. Hence competition plays a role in regulating populations and setting a carrying capacity in population growth models (Gause 1934). While it is recognised as a key ecological process, the exact role and relative importance of competition in regulating populations and structuring communities has historically been debated. Given that individuals of the same species share similar diet and microhabitat preferences, competition within species (intraspecific competition) has long been recognised as important in regulating and shaping populations (Schoener 1973). Similarly, competition between species was found to increase with the degree of overlap in resource requirements (Schoener 1983), so that ecologically similar species are more likely to compete over shared resources. Manipulative field experiments illustrated how species distributions could be shaped by competition (Connell 1961, 1983). More recently, studies with experimental designs sufficient to distinguish and compare the strength of inter- and intraspecific competition have been undertaken (e.g. Underwood 2002, Cross and Benke 2002, Forrester et al. 2006) demonstrating that these processes should not be considered independently. However, the relative importance of inter- and intraspecific competition remains poorly understood in most ecosystems, despite the large body of research that has accumulated on competition in general.

Field ecologists measure the potential effects of competition on individuals by the controlled manipulation of either resource abundance, population density, or the presence/absence of competing species (Underwood 1986). Although a majority of studies have measured effects of competition on numerical parameters like abundance, density, or biomass (Gurevitch et al. 1992), competition may cause changes in these parameters through sub-lethal effects on individual performance (Smith and Tyler 1972). Density dependent changes to body condition (e.g. Choquenot 1991, Stewart et al. 2004), growth (e.g. Petranka and Sih 1986, Lewis et al. 2001) and reproductive outputs (Carrete et al. 2006) have been linked to competitive interactions in a wide range of organisms. Such changes in individual growth and condition due to competition may then indirectly increase mortality by making weaker competitors more vulnerability to predation (Holt 1984, Jeffreys and Lawton 1984, Hixon 1991). In addition, if species are competing for space then subordinate competitors may be excluded from refuges and therefore more vulnerable to predation (Vessey 1987, Holbrook and Schmitt 2002). Less successful competitors may be subordinate by virtue of competitive ability, or through ontogeny, given that larger individuals are often the strongest competitors (Jeffries and Lawton 1984). Hence, while predation may be the proximate cause of death, the intensity of competition may drive predation rates. Given that habitat structure can often mediate the effects of predation and competition (Jeffreys and Lawton 1984, Holt 1987, Hixon and Menge 1991), the impact of habitat change will influence not only the essential resources provided by the habitat, but also the strength of critical ecological processes that regulate populations.

1.2 Behavioural interactions in heterogeneous landscapes

Habitat quality plays a major role in determining the distribution of species in heterogeneous landscapes (e.g. Milinski 1979, Dreisig 1995, Mobæk et al. 2009, Bradbury et al. 2015) and responses to spatial changes in the availability of resources can be directly manifested through changes in densities following disturbance events (e.g. Fahrig 2003, Cushman 2006). However, changes in individual behaviour frequently represent the first response to habitat loss and degradation, and often underpin subsequent demographic impacts on populations and ecosystems (Candolin and Wong 2012, 2015). Heterogeneous landscapes are composed of habitat patches of varying quality and animals may distribute themselves to extract maximum per capita benefit from available resources, described formally in the *ideal free distribution* model (IFD, Fretwell and Lucas 1969). IFD predicts that species will be distributed within a landscape to maximise their fitness (Morris 1987). In this model, individuals select a habitat based on quality, and all else being equal, distribution patterns will reflect the quality and quantity of resources provided by habitat patches (Fretwell 1972). The value of a habitat patch will vary with the density of individuals that use its resources, such that the more individuals access a certain habitat patch, the lower the quality, or 'suitability' of that patch. While IFD describes the spatial distribution of animals in a landscape, it is driven by behaviours like habitat selection and movement at an individual level (Fretwell and Lucas 1969).

Density dependent habitat selection is expected to occur when densities in high quality habitat patches reach a certain threshold (Macarthur and Levins 1964, Milinksi 1979), at which point individuals may actually achieve a higher fitness by choosing lower quality habitat patches (Parker 1970, Bergman et al. 2007). The propensity to move may depend on both the relative densities of resource competitors in the different habitat patches and also differences in resource quality and/or quantity. Where habitat degradation is moderate, behavioural process such as density dependent habitat selection may buffer species populations from the negative effects of declining resources by providing individuals with the capacity to alter their habitat use to maximise fitness. However, where habitat degradation is extreme, density dependent habitat selection and intense competition may separate the winners and losers, with displaced individuals unlikely to survive and reproduce due to a shortage of alternative habitat patches of sufficient quality to support them. Hence, investigating behavioural responses is critical to understanding and forecasting the long-term consequences of habitat change on animal communities.

1.3 Crowding in response to habitat loss

Habitat loss has the potential to affect species distributions and resource use because it directly modifies the amount of resources available in a landscape. Species reliant on resources provided by the habitat are often displaced, provided they do not suffer direct mortality due to the disturbance itself (Debinksy and Holt 2000). If the disturbance event results in a compete loss of suitable habitat across large spatial scales, displaced individuals are likely to suffer high mortality and local extinction may occur (Tilman et al. 1994). However, many disturbances leave remnant patches of suitable habitat adjoining disturbed habitat patches (Fahrig 2003), and these provide some degree of refuge in disturbed landscapes. Aggregation of surviving individuals into remnant live patches can lead to crowding and short-term increases in density following habitat loss, especially for mobile dispersive species (Debinski and Holt 2000). However density dependent interactions are likely to gradually reduce populations back to a level that can be supported by the habitat (i.e. its carrying capacity). This process, the ‘crowding effect’, has been described in numerous ecosystems, including insects communities on grasslands (Collinge and Forman, 1998), ladybugs in Chilean alfalfa fields (Grez et al. 2004) and birds in logged Canadian forests (Schmiegelow et al. 1997). Because crowding alters the per capita resource availability, it could alter the relative value of remnant habitat patches, thus leading to density dependent habitat selection. In theory, this process occurs in two stages; 1) individuals leave dead habitat in search of remnant live habitat which then becomes crowded with both displaced individuals and prior residents and 2) crowded conditions force some individuals to choose alternate habitat. Modelling studies have suggested that the effects of habitat loss on populations will vary depending on the quality of the remnant habitat (Pulliam and Danielson 1991). In situations where the low quality habitat is disturbed, the population is reduced, but persists through time. In contrast, when the high quality habitat is disturbed, the population collapses because the lower quality habitat is unable to sustain the population (Pulliam and Danielson 1991). While density dependent habitat selection and the crowding effect have been demonstrated independently, no empirical studies to date have investigated the direct link between habitat loss and density dependent habitat selection.

1.4 Behavioural cues for habitat quality and 'ecological traps'

The ideal free distribution and density dependent habitat selection assume individuals can assess habitat quality to make informed decision about habitat use. Animals use cues (e.g. visual, auditory, olfactory, or chemical signals) to asses the quality of a habitat, the presence of competitors and predators, and to inform appropriate decisions. Under natural conditions individuals are likely to exhibit behavioural responses to such cues that elicit a habitat choice that will enhance their fitness (Gates and Gysel 1978). However in highly disturbed environments, the link between the cue and the quality of the habitat may be disrupted and a normally adaptive behaviour may become maladaptive. For example, altered or introduced environments can mimic cues emitted by natural environments, which elicits a maladaptive behavioural response ('ecological traps', Dwerrnychuk and Boag 1972, Schlaepfer et al. 2002). For example, many bird species are attracted to nest on agricultural pastures because they are structurally similar to native grasslands (Schlaepfer et al. 2002). Chicks in these nests have low survival rates compared to nests in native grasslands because mechanical harvesting of crops often occurs before the chicks have fledged (Bollinger et al. 1990). While the concept of ‘ecological traps’ relates specifically to habitat selection, other behaviours are also likely to be affected by habitat loss. The concept has therefore been expanded to include any behaviour that used to be adaptive, but is now maladaptive through human interference (‘evolutionary traps’ Schlaepfer et al. 2002). For example, beetles mistake brown beer bottles as females and attempt to mate with the bottles, reducing reproductive success (Gwynne and Rentz 1983). Moreover, habitat degradation can also potentially lead to the alteration or loss of the cue itself, without altering the quality of the resource provided by the habitat (Gilroy and Sutherland 2007). Understanding which of these alternatives applies is essential to anticipate indirect and complex animal responses to habitat loss.

1.5 Habitat loss on coral reefs

Coral reef ecosystems have been experiencing an unprecedented loss of hard corals in recent decades, with an average 20% decline in live coral cover on reefs worldwide (Gardner et al. 2003, Bruno and Selig 2007, Wilkinson 2008, De’ath et al. 2012). In particular, reefs in close proximity to urban areas have suffered a suite of anthropogenic impacts (Alongi 2002). These include increased nutrient outputs from agriculture (Fabricius and De’ath 2004), elevated levels of suspended sediment caused by deforestation (Richmond 1993), rising ocean temperatures (Hoegh-Guldberg 1999, Hughes et al. 2003) and over-harvesting of reef species (Jackson et al. 2001). More recently, outbreaks of corallivorous crown-of-thorns starfish (COTS, *Acanthaster planci,* Pratchett et al. 2014), coral disease (Harvell et al. 2002) and mass bleaching events (Hoegh-Goldberg 1999) have devastated reef ecosystems further (Pandolfi et al. 2003, Bellwood et al. 2004, Bruno and Selig 2007). Coral reefs are among the most diverse ecosystems on the planet and their global decline represents a major threat to marine biodiversity.

Live corals provide the majority of structural complexity on coral reefs, and degradation of these biogenic habitats is often followed by significant declines in the abundance of associated reef fishes (Jones and Syms 1998, Halford et al. 2004, Wilson et al. 2006). Reef fish that exhibit a high degree of specialisation to live coral habitat during both their juvenile and adult life phases are particularly vulnerable (Syms and Jones 2000, Munday 2004). In addition, while many species do not have a close association with live coral in later life stages, many reef fish rely on live coral habitat in the recruitment phase (Jones et al. 2004). Obligate coral-dwelling and corallivorous species suffer the greatest declines following coral loss and habitat degradation on coral reefs (Syms and Jones 2000). However, species that do not depend on coral throughout their life are also affected by coral loss (Jones et al. 2004), sometimes years after the degradation event (Pratchett et al. 2008). Despite well-documented declines in reef fishes following habitat loss and degradation the underlying mechanisms remain largely unknown.

1.6 Habitat degradation, resource competition, and habitat selection in reef fishes

Given the reliance on live corals in many reef fish, responses to habitat loss are likely to fall in to one of three categories following coral death; affected fish are either going to suffer direct mortality, be displaced into remnant habitat, or remain on dead coral colonies . First, individuals can suffer direct mortality immediately following the disturbance event because they have lost essential resources. In particular, corallivorous fish are likely to be rapidly affected because their primary food source has been lost (Pratchett et al. 2006, Graham et al. 2007, 2009). Second, following a disturbance that causes coral mortality, coral-associated fishes may move to remnant patches of live coral habitat. Reef fish are known to leave recently dead corals in favour of live coral nearby (Coker et al. 2012), where they are likely to encounter aggression from prior residents (Almany 2004, Geange and Stier 2009, Coker et al. 2013). However, displaced individuals naturally increase the densities of organisms in receiving aggregations (Pulliam and Danielson 1991). Coral reef fishes are often susceptible to density dependent interactions, like competition for resources (Ward et al. 2006) and aggression (Boström-Einarsson et al. 2014) leading to both lethal (Brunton and Booth 2003) and sub-lethal outcomes (Booth 1995). Density dependent interactions in crowded conditions are therefore likely to force local densities to return to a level sustainable by the environment. Third, individuals may stay on dead coral habitat if they are unable to relocate to remnant live habitat. Coral specialists are rarely found on dead coral (Bonin 2012) and often experience negative effects of living on dead coral, such as reduced growth (Feary et al. 2009) and higher mortality (e.g. Bonin et al. 2009, Lönnstedt and McCormick 2014). The mechanisms responsible for these effects remain unclear, however altered interactions between species may cause some of the effects of habitat degradation in reef fish assemblages.

Many reef fish interactions are underpinned by competition for resources. While the exact resource fish gain from their association with live coral is often unknown, it is likely that coral death reduces or alters the resources available to individuals. The degradation of coral habitats can therefore lead to increased competition over finite resources. Experimental studies investigating the link between habitat loss and competition in reef fish are rare, however evidence suggests that reductions in habitat quality are likely to alter or exacerbate effects of competition (McCormick 2012, Boström-Einarsson et al. 2014). Given that the ultimate cause of mortality in coral reef fishes is almost exclusively predation (Hixon and Carr 1997), and competition for shelter space is common in reef fishes (Schmitt and Holbrook 2002) it seems likely that sheltering behaviour and habitat use could be influenced by coral mortality. Behavioural responses to declining coral cover and increasing spatial heterogeneity of reef habitats are however poorly understood. In particular, the roles of crowding by displaced individuals in remnant live habitat, the potential for density dependent habitat selection, and the consequences of living on dead habitat have not been investigated.

1.7 Aims

The overall aim of this thesis was to investigate the effects of coral loss on the behavioural interactions among coral reef fishes as a precursor to the long-term ecological changes on coral reefs. As a model species I selected the lemon damsel, *Pomacentrus moluccensis*, an obligate coral-dwelling damselfish (Pomacentridae) often found in dense aggregations on plating *Acropora* coral colonies on shallow reefs. These fish are live coral specialists (Bonin 2012), and are known to retreat into the branches of their coral colony hosts to escape predators or other perceived threats (Beukers and Jones 1998). They are highly sedentary and site-attached with typical home ranges rarely exceeding 1m (Booth 2016). This makes them highly amenable to experimental manipulation and also reduces their ability to relocate long distance if their local habitat is disturbed. Specifically, I address the effects of coral death on the intensity of competition, foraging responses, sheltering behaviour, crowding, and density dependent habitat selection. These topics are addressed in four data chapters with the following specific objectives:

1. *Synthesise the current knowledge of competition over resources in reef fishes, discussing its relative importance in regulating reef fish communities and likely consequences of habitat loss*
2. *Examine whether partial habitat degradation leads to crowding in remnant habitat in a common reef fish species, and investigate potential effects of crowding on both aggression and foraging behaviour*

3. *Evaluate how sheltering behaviour of a common reef damselfish is affected by the death of its coral colony host*
4. *Explore the effects of habitat loss on crowding and density dependent habitat selection in a habitat associated reef fish*

Chapter 2 addresses the historical debate over the role of competition in the ecology of reef fishes and provides a synthesis of the current knowledge on the prevalence and importance of competition in reef fishes, by evaluating the outcome of 173 experimental tests from 72 publications. This comprehensive review highlights the importance of competition in structuring reef fish communities. In addition, this chapter further identifies crucial knowledge gaps in the reef fish literature regarding competition, several of which are addressed in subsequent chapters of this thesis.

Few studies have documented effects of partial habitat loss over time using multiple measures of individual performance. In **Chapter 3** I address this by evaluating consequences of habitat loss on the abundance, body condition and behaviour of a common coral-reef fish over time and following a major disturbance event. I follow natural aggregations of damselfish on experimental coral colonies which have been partially degraded *in situ*. Throughout the experiment (~4 months) I monitored densities of *P. moluccensis* within live and dead habitat portions of experimental coral colonies and compare to control (undisturbed) colonies. This allows a unique perspective of how habitat use changes over relative short time-frames following the disturbance event. I use video-recordings of aggregations to evaluate how agonistic interactions and feeding behaviour are affected by the loss of habitat. Finally, liver samples allow the assessment of body condition of surviving individuals at the conclusion of the experiment. The study provides a holistic view on how changes in habitat use and behaviour following habitat loss affect demographic variables of a common reef fish.

In **Chapter 4** I aim to quantify changes in sheltering behaviour of *P. moluccensis*, following the death of their coral colony. I allow recently dead colonies of *Acropora* to accumulate algae and invertebrates over a period of five weeks and place groups of *P. moluccensis* on either live or dead coral colonies. I then record their sheltering behaviour following a visual startle using video recordings. This study is the first to explicitly test sheltering behaviour over a gradient of habitat degradation, and provides evidence to the importance of live corals in eliciting the correct behaviour response in reef fishes. The outcomes of this study suggests that the disruption of this link poses a great threat to coral-associated fishes on degrading reefs.

Chapter 5 investigates how habitat loss influences habitat selection, and ultimately the distribution of *P. moluccensis*. I use observations of habitat use during an ongoing degradation event to investigate how the distribution of adult *P. moluccensis* is affected by the loss of live coral. I further investigate how the habitat use of adults affects habitat selection in recruiting juveniles. Finally I use a manipulative choice experiment to test whether *P. moluccensis* engages in density dependent habitat selective behaviour. This chapter gives a comprehensive view of how distribution and habitat selection is influenced by habitat loss and provides the first evidence for density dependent habitat selection in the marine environment. As such it adds to the growing body of work outlining how reef fish communities are affected by disturbances.

Chapter 2

The prevalence and importance of competition among coral reef fishes

A version of this chapter has been published as: Bonin MC, **Boström-Einarsson L**, Munday PL, Jones GP. 2015. The prevalence and importance of competition among coral Reef Fishes. Annual Reviews of Ecology, Evolution and Systematics 46:169–190.

2.1 Abstract

Although competition is a recognised as a core ecological process, its prevalence and importance in coral reef fish communities has been historically debated. This review compiles and synthesises the results of 173 experimental tests of competition from 72 publications. Evidence for competition is pervasive both within and between species, with 72% of intraspecific tests and 56% of interspecific tests demonstrating a demographically significant consequence of competition (e.g. a decrease in recruitment, survival, growth or fecundity). Several factors are highlighted that can interact with the effects of competition, making it more difficult to detect in field experiments. In light of this evidence, the role of competition in shaping coral reef fish communities is discussed and emphasised as one of several processes that contributes to species coexistence. Finally, this review considers some of the complex ways that climate change may influence competition and provide suggestions for future research.

2.2 Introduction

Competition is a fundamental process in ecology and the foundation of many classic ecological theories, from formulations of population growth, to models of interacting species, to explanations of coexistence and the structure of communities. It has been invoked to explain almost every spatial and temporal pattern in ecology, from local resource subdivision to global patterns in biodiversity, from the outcome of brief encounters between individuals to long-term adaptation and coevolution. Competition can be defined as the *“interaction between individuals brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the fitness of at least one of the individuals”* (Begon et al. 1986). However straightforward this seems, the role of competition in ecology remains one of the most hotly debated topics (Simberloff 1982, Roughgarden 1983). It has divided ecologists over key issues such as the mechanisms of coexistence, the importance of competition versus other ecological processes, density-dependent versus independent processes, and contemporary versus historical factors in ecology. Our understanding of the significance of competition has been greatly advanced by field experiments, with a large body of empirical research showing that both intra- and interspecific competition commonly influence the demographic drivers of distribution, abundance and community structure (Connell 1983, Schoener 1983, Underwood 1986, Gurevitch et al. 1992). While a general rule as to when and where competition is and is not important is yet to be formulated, experiments continue to refine and expand our understanding of this ubiquitous yet elusive process.

Coral reef fish communities have been fertile ground for testing established theory and developing new ideas concerning the ecological role of competition (Sale 1980, Jones 1991, Jones and McCormick 2002, Hixon 2011, Forrester 2015). Pioneering researchers in the early 1970’s were fascinated by the high diversity of reef fish communities and mechanisms of coexistence under conditions of seemingly intense competition for living space. Not surprisingly, the established view from terrestrial systems that coexistence and stability stem from competition-induced niche partitioning (MacArthur and Levins 1967) was transposed to coral reefs (Smith and Tyler 1972, 1973). However, this theory of *"limiting similarity"* was not a comfortable fit with early observations on the ecological overlap among reef fishes and the apparent instability of communities. In the mid-70's, Peter Sale proposed his *"lottery hypothesis"* as an alternative model of competitive coexistence (Sale 1976, 1977). This novel and contentious theory argued that competing species with identical resource requirements and similar competitive abilities could coexist through chance colonisation of vacant space. The theory assumes that space is a limited resource and when an individual dies, the first-available recruit of any species recolonises the vacant space. The ensuing debate over the importance of niche partitioning versus lottery competition dominated the early growth of this field, peaking in the early 1980's (Figure 2.1). Coral reefs provided a natural laboratory for field experiments, with the first critical tests of competition for shelter sites (Robertson and Sheldon 1979) and living space (Robertson et al. 1981) published at this time.

Challenges to the assumption that reef fish communities were limited by the availability of space emerged during this period of intense debate. Talbot et al. (1978) proposed that disturbance and predation keep communities in a non-equilibrium state below carrying capacity, reducing the intensity and importance of competition. In the early 1980s, another new model of reef fish population dynamics and community structure was put forward – the *"recruitment limitation"* hypothesis (Victor 1983, Doherty 1983). As with the lottery hypothesis, this idea emphasised the importance of variable recruitment, but it also argued that larval settlement is insufficient to lead to resource limitation or density-dependent population regulation resulting from competition. It was based on empirical observations on the degree to which fluctuations in recruitment drive adult population size, as well as pioneering experiments that failed to detect evidence of interspecific competition (Doherty 1983). By the end of the 1990s, it also became widely accepted that predation is another major factor reducing populations to below carrying capacity (Hixon 1991). During the period 1985-1995, the view that competition was rare in reef fish communities was pervasive and research attention waned (Figure 2.1). However, despite a preoccupation with recruitment and predation, studies on competition never completely ceased. This period saw the first demonstrations of intraspecific competitive effects on survival (Jones 1987a,b) and the first demonstrations of the effects of interspecific competition on reef fish distributions (Robertson and Gaines 1986, Clarke 1989).

By the early 1990s, the dichotomous views of the past weakened and a pluralistic view that recruitment, predation and competition may all be interacting to influence reef fish ecology gained increasing acceptance (e.g. Jones 1991, Hixon 1991). Rather than single factor models, the next decade was dominated by discussion over the relative importance and strength of density-dependent and independent processes and their underlying causes (Jones 1990, Caley et al. 1996, Hixon and Webster 2002). While the density-dependent effects of predation dominated the literature, the study of competition regained momentum (Figure 2.1). Evidence accumulated that competition could drive patterns of abundance and distribution across coral reef habitats (Robertson 1996), influence energetic factors such as growth and reproduction (Forrester 1990, Jones and McCormick 2002) and that competition for shelter can strongly influence mortality (Hixon and Webster 2002).

Interest in competition has continued to grow and a large body of literature addressing this process has been published over the last 15 years (Figure 2.1). Increasing attention has been fuelled in part by the global degradation of coral reef habitats and the likely exacerbation of the importance of competition as a result of declining resources (e.g. Bonin et al. 2011). Forty years on, there is a clear need for a review of studies on

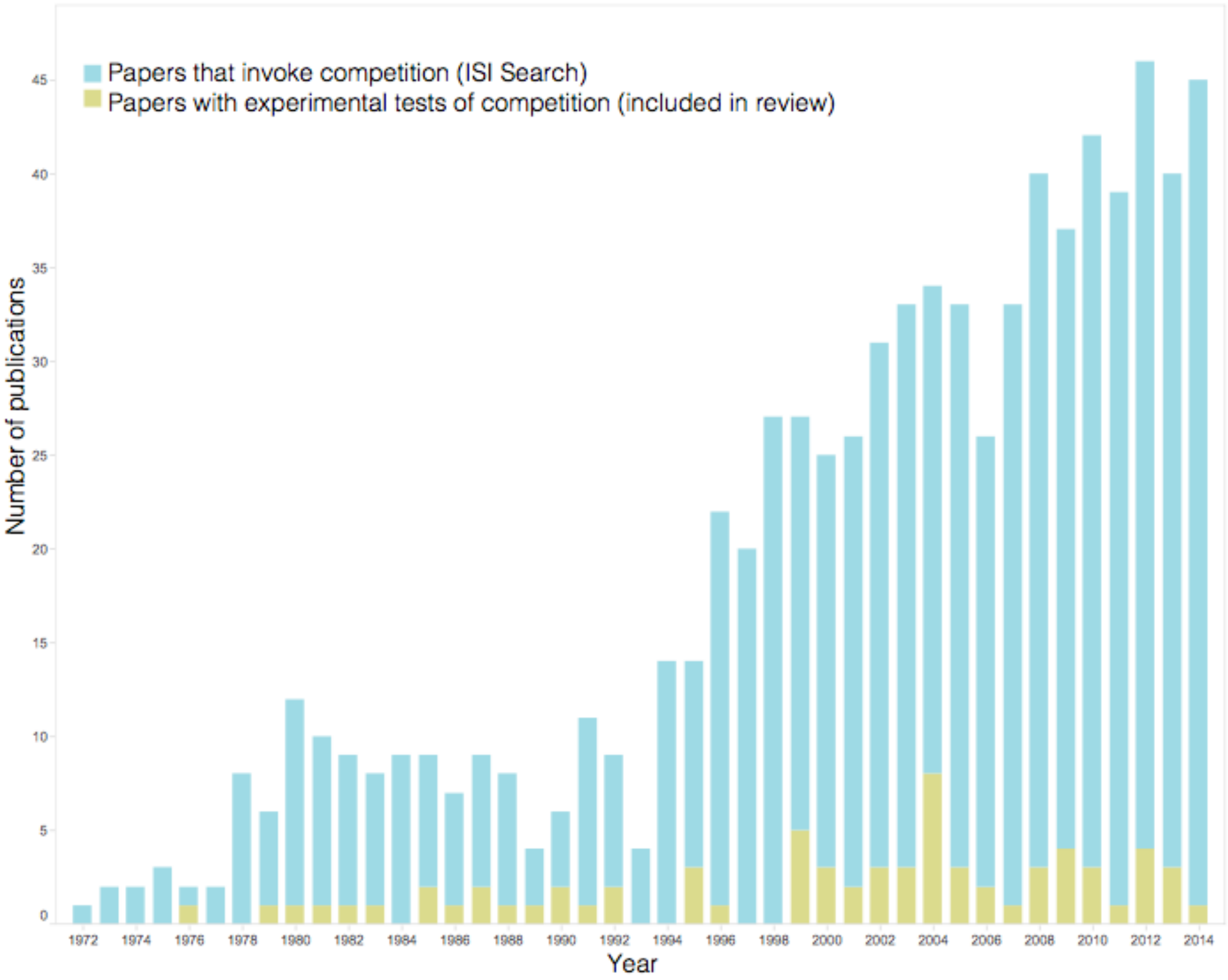

Figure 2.1. Trends over the past 42 years in the annual numbers of publications that have invoked (blue bars) or have experimentally tested (green bars) competition within or among coral reef fish species. The number of papers that have invoked competition was determined through an ISI Web of Science survey using the search term: [(competit* AND Coral* AND reef* AND fish*) OR (resource AND partitioning AND coral* AND reef* AND fish*) OR (resource AND sharing AND coral* AND reef* AND fish*) OR (stability AND coral* AND reef* AND fish*) OR TOPIC: (space AND sharing AND coral* AND reef* AND fish*) OR (resource AND limitation AND coral* AND reef* AND fish*)] for the years 1972-2014. The results of this search were then manually filtered to exclude all papers not focused on coral reef fishes, reducing the list to 707. The final tally (n=724) includes additional references cited in the two key books on coral reef fishes (Sale 1991, 2002) that were not picked up in the survey. The number of publications that provided experimental tests of competition (n=72) was determined using the criteria outlined in the review.

competition in reef fishes, which will enable us to appreciate the diverse ways in which competition affects populations and communities, and recalibrate our understanding of the significance of this process. This review provides a comprehensive synthesis of the roles of both intra- and interspecific competition in structuring coral reef fish populations and communities. Specifically, this review:

1. Evaluates the different approaches from which competition can reliably be inferred and compiles those papers that provide adequate tests.
2. Synthesises the evidence for both intra- and interspecific competition, and the strength of these effects on key demographic parameters.
3. Discusses how competition interacts with and may be confounded by other factors such as habitat quality and predation.
4. Revisits the old debates with new data, including evidence for early views such as resource partitioning and the lottery hypothesis.
5. Assesses the likely future role of competition among reef fishes in a changing world.

2.3 What constitutes good evidence for competition?

Although theoretical and observational studies are valuable for generating predictions about the role of competition in ecological communities, manipulative experiments are necessary to provide definitive evidence (Connell 1983, Underwood 1986). Ideally these experiments demonstrate an effect of competition on a vital demographic parameter (e.g. recruitment, survival, growth, fecundity). At the very least they must demonstrate that competitors produce changes in patterns of abundance, distribution, or resource use that are indicative of changes to these parameters. The different experimental approaches that can be applied fall under three general categories—competitor density manipulations, resource availability manipulations, and dominance experiments (see Sidebar).

Experimental approaches for measuring competition

Competitor density manipulations either add or remove competitors from experimental plots on natural reefs, or stock them in various densities on experimental reefs. The simplest version involves manipulating competitor presence/absence, whereas an even better approach is to establish three or more competitor density treatments, as this allows for tests of density dependence in demographic parameters. Densities chosen should reflect those that occur naturally for the study species and include treatments at the higher end of this range.

Resource availability manipulations can be useful for identifying the specific resource that is limited in a study system. A resource is either supplemented or reduced in its availability, and changes in at least one demographic response variable are measured.

Dominance experiments involve replicated trials that place a pair of competitors together and test for dominant-subordinate relationships, as indicated by a shift in resource use by the subordinate individual in the presence of the dominant. Experiments that only show evidence of aggression do not provide good evidence of competition, unless they also demonstrate a consequence in terms of resource use or a fitness parameter.

For this review, the literature was thoroughly searched and studies were included if they met the following three criteria: 1) they were field or laboratory-based experimental studies of coral reef fishes, 2) they involved a competitor density manipulation, resource manipulation, and/or dominance test, and 3) they measure a demographically significant consequence of competition (i.e. a change in abundance, distribution, resource use, recruitment, survival, growth or fecundity). Despite the fact that a total of 724 studies of reef fishes over the past four and a half decades have invoked competition, the selection criteria produced a total of 72 papers, across at least 50 species, that provide direct experimental evidence for intra- and/or interspecific competition among coral reef fishes (Figure 2.1). Most of these papers include multiple experimental tests of competition, because competitive effects are tested across several species, different life history phases, or use more than one experimental approach. For these papers each experimental test of competition on a focal species was catalogued on a per experiment basis at each life history stage tested. For example, if the reciprocal effects of two species were tested on each other in an experiment, this would be recorded as two separate tests of competition (i.e. one for each focal species). The resulting 173 experimental tests of competition form the basis for this review. A database was compiled that includes information on the original citation, the type of experiment, the species and life stages, the response variables measured, details of the outcome, and notes on the primary conclusions of the authors. This database is provided online, in both spreadsheet format (Appendix 2) and also as an interactive figure that may serve as a functional resource for further exploration of the literature and concepts reviewed here.

2.4 Evidence for intraspecific competition

A review of 75 experimental tests of intraspecific competition from 52 publications revealed that 72% of experiments provide evidence that this process influences the local distribution, resource use or demographic rates of coral reef fishes (Figure 2.2a). Most experiments have examined effects of intraspecific competition during the juvenile stage, either due to changes in the density of the juveniles themselves (30 experiments) or adult conspecifics (22 experiments). An additional 21 experiments tested for intraspecific competition among adults. Given that these experiments were conducted on 29 different focal species from 5 families (Appendix 2), it is clear that reef fishes are commonly affected by intraspecific competition.

Distribution and Resource use

Sixteen experiments have explored changes in the local distribution and resource use of reef fishes due to competitive interactions with conspecifics (Appendix 2). A majority of these demonstrate shifts in the distribution or resource use of planktivores following manipulation of dominant competitor densities (Coates 1980, Forrester 1991, Webster and Hixon 2000, Webster 2004, Whiteman and Côté 2004). In all cases dominance hierarchies were established based on body size, with larger fish excluding smaller ones from access to preferred feeding positions or larger prey items. Intraspecific competitors may also exclude subordinates from accessing high quality refuges (Bucheim and Hixon 1992, Hobbs and Munday 2004, Coker et al. 2012). For example, conspecific damselfish may compete for prime predator refuges within coral colonies (Holbrook and Schmitt 2002) and larger gobies may usurp smaller conspecifics from protective shrimp burrows (Thompson 2005).

Recruitment

There is increasing evidence that recruitment (i.e. the input of juveniles into a population) is affected by competitive interactions with conspecifics. Since Sale (1976) first investigated this issue, 14 experiments have evaluated how competitors affect the input of new recruits. Given that recruitment is inherently difficult to measure, it is perhaps not surprising that approximately half of these experiments failed to detect an effect of intraspecific competitors (Figure 2.2b). This may indicate that resident conspecifics do not influence the settlement and/or early post-settlement mortality of some coral reef fishes (Doherty 1983, Forrester 1999, Webster 2003). However, Forrester (1995) demonstrated that recruitment patterns can sometimes be strongly influenced by conspecifics, with the number of recruits of the bridled goby, *Coryphopterus glaucofraenum*, decreasing by a third across a naturally occurring range of adult densities. Although adult gobies do not appear to discourage settlement itself, they occupy a finite number of shelter holes, leaving the new settlers more vulnerable to predation (Forrester 1995, 1999). This negative influence of adults on the availability of shelter sites for settling juveniles has also been described for two damselfish, *Dascyllus flavicaudus* and *D. trimaculatus,* with the presence of resident conspecifics reducing the density of recruits by 94% and 74% respectively (Schmitt and Holbrook 2000). However in some cases the presence of conspecifics may enhance rather than reduce recruitment (Figure 2.2b). Sweatman (1985) demonstrated that the presence of conspecific adults increased the number of settlers for three damselfish species, presumably because adult presence indicated a high quality habitat.

Survival

With a total of 44 experiments, this is by far the most common response variable measured to assess the effect of intraspecific competition among coral reef fishes. Although many early studies failed to detect an effect of interspecific competitors (Robertson and Sheldon 1979, Doherty 1982 and 1983, Jones 1987a), two experiments by Jones (1987b, 1988) provided the first indication that they could induce density-dependent mortality in reef fishes. Negative effects of conspecifics on survival have subsequently been demonstrated in 59% of experiments (Figure 2.2c). The most commonly cited resource implicated in competition-induced, density-dependent survival is shelter space from predators. Such competition is especially intense among small-bodied species that are closely associated with specific shelter sites, including gobies (Forrester 1995, Forrester and Steele 2000, 2004, Wilson 2005, Samhouri et al. 2009), blennies (Buchheim and Hixon 1992), wrasses (Caselle 1999), and damselfish (Schmitt and Holbrook 1999a, Schmitt and Holbrook 2007). Death of competitors is usually attributed to predation rather than injuries sustained during interactions with competitors.

Holbrook and Schmitt (2002) provided the first conclusive evidence that competitive interactions are the underlying source of density-dependent predation mortality. Infrared underwater video revealed that subordinate damselfish competitors were displaced to high-risk peripheral areas as they jostled for shelter space at the centre of coral colonies. This intense competition led to density-dependent mortality because as the densities of conspecifics increased, a larger proportion of individuals were displaced into shelter sites with higher risk of predation. Although most experimental work to date has demonstrated negative effects of conspecifics, a small proportion (7%) has shown positive effects of conspecific density on survival (Figure 2.2c). Survivorship of juvenile damselfish *Dascyllus albisella* and *Pomacentrus amboinensis* was enhanced in larger groups (Jones 1988, Booth et al. 1995). However in both cases, increased densities of conspecifics came at the costs of reduced growth and delayed maturation, leading the authors to conclude that while group living may be beneficial, there are costs associated with intraspecific competition.

Growth and Reproduction

Of the 28 experiments that have measured intraspecific effects on growth, 64% have observed negative effects of competition (Figure 2.2e). Doherty (1982) provided the first evidence that conspecific densities could influence growth, with the average body size of the damselfish *Pomacentrus wardi* smaller in large groups compared to smaller groups. By individually tagging fish, Jones (1987a, b) later confirmed that juveniles of the congener *Pomacentrus amboinensis* not only grew less at higher densities, but that this also translated into delayed maturation. Given that conspecifics often have near complete overlap of their resource requirements, competition over food is often cited as the mechanism underlying reduced growth at increasing densities of conspecifics (Jones and McCormick 2002, Hixon and Jones 2005). Alternatively, several studies have demonstrated that crowded individuals expend more energy and have increased metabolic costs than less crowded fish. Fish at high densities engage more frequently in aggressive interactions, increase the distance covered while foraging, and increase time searching for shelter, all of which may serve to reduce growth (Booth 1995, Forrester et al. 2006, Johnson 2008, Samhouri 2009, Samhouri et al. 2009). A single study has described a facilitative effect of conspecifics on growth, where the presence of larger conspecifics enhanced growth of the damselfish *Dascyllus aruanus* (Booth 2004). However, this positive effect of conspecifics was only seen on food-supplemented reefs, suggesting that conspecifics enhanced growth only when food was abundant. The study is unique in that it highlights how the availability of resources may alter the strength of intraspecific competition in reef fishes.

There is also strong evidence that intraspecific competition can influence reproduction in coral reef fishes, with 71% of the 14 experiments observing reduced reproductive fitness due to competitors (Figure 2.2e). Early studies demonstrated a delay in age of maturation due to reduced growth (Jones 1987a, Forrester 1990, Booth 1995), whereas more recent experimental work has shown decreased rates of egg clutch production (Samhouri 2009, Forrester et al. 2011), clutch size (Wong et al. 2008), and larval size (McCormick 2006) when fish breed among higher densities of conspecifics. In an unprecedented eight-year study covering multiple generations of the bicolor damselfish *Stegastes partitus*, Hixon et al. (2012) demonstrated that fecundity decreases with increasing conspecific density but this competitive effect was mediated by habitat structural complexity. Adult damselfish living on reefs with high habitat complexity and ample refuge space from predators displayed density dependent egg production per nest whereas damselfish on reefs with low habitat complexity displayed density-independent egg production.

2.5 Evidence for interspecific competition

Because early studies failed to detect interspecific competition, the initial perception was that competition among coral reef fishes occurred primarily within species rather than between them (Jones 1991). However our knowledge on interspecific competition among reef fishes has grown considerably and now includes 98 experimental tests from 34 publications (Appendix 2). These experiments have been conducted on 39 focal species from 5 families and 50 examine interspecific competition among adults (Appendix 2). The remaining 48 test the effect of interspecific competition during the juvenile stage, whether in the presence of heterospecific juveniles (29 experiments) or adults (19 experiments). Over half (56%) of these studies detected an effect of interspecific competitors on at least one demographic response variable (Figure 2.2f), indicating that interspecific competition among reef fishes is much more prevalent than once thought.

Distribution, Abundance, and Resource use

With 58% of 43 experiments demonstrating effects of interspecific competitors (Appendix 2), there is ample evidence that they can influence the spatial distribution of coral reef fishes, both across reef zones (Robertson and Gaines 1986, Robertson 1995) and among microhabitats (Ebersole 1985, Clarke 1989, Srinivasan et al. 1999, Munday et al. 2001, McCormick and Weaver 2012). However these interactions are usually highly asymmetric, with the distribution of one species in the pair strongly affected by the presence of the other but not vice versa. The removal experiment by Robertson and Gaines (1986) is a prime example. They tested competitive relationships among five species of surgeonfish that exhibit high dietary overlap and defend feeding territories along the reef slope. Of the 27 interacting species pairs, only 3 had competitive relationships that were not strongly asymmetric. In the vast majority of pairings, one species was consistently more

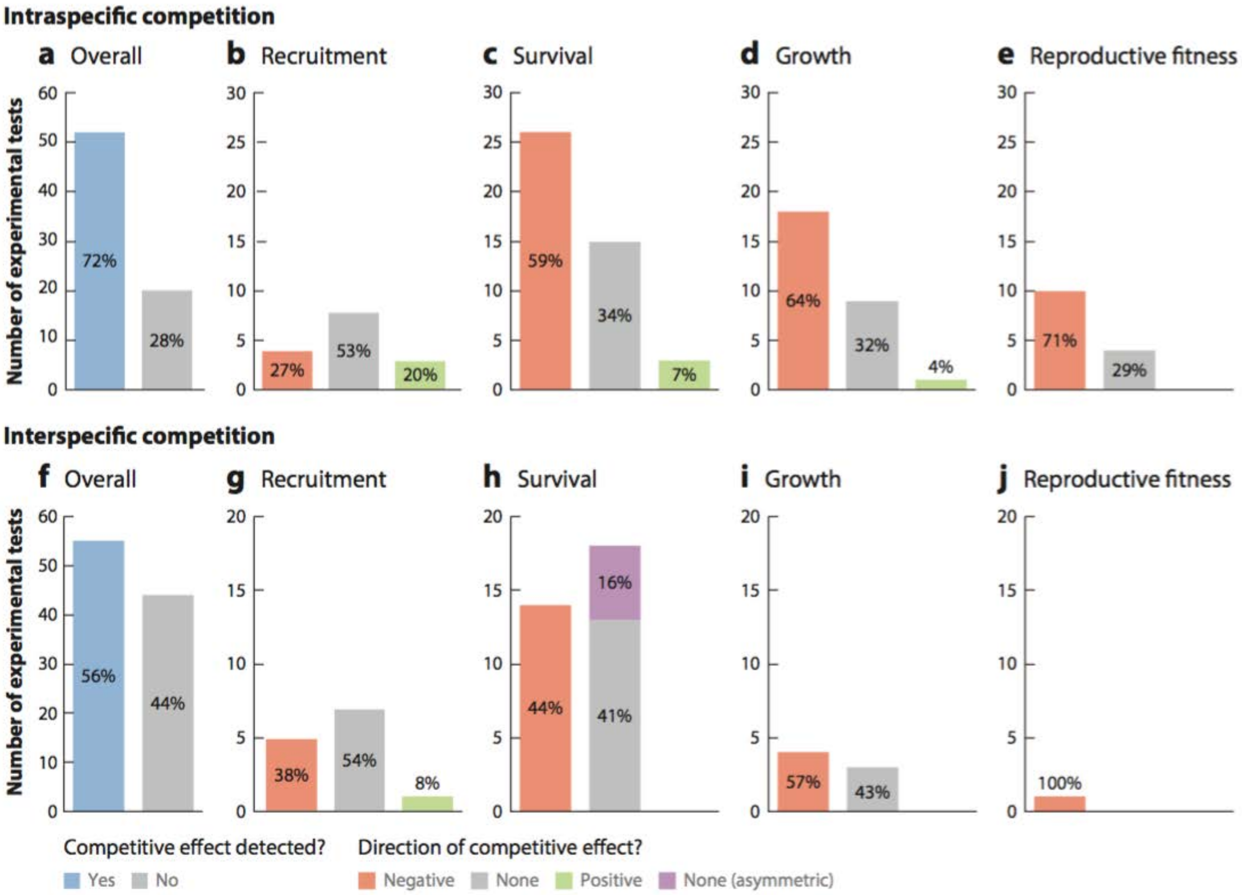

Figure 2.2. Summary of the evidence for intra- and interspecific competition among coral reef fishes from the 173 experimental tests included in this review. Overall counts (intraspecific: panel a, interspecific: panel f) indicate the number of experimental tests that found evidence of competition across all response variables (i.e. a change in abundance, distribution, resource use, recruitment, survival, growth or fecundity). Panel b-e (intraspecific) and g-h (interspecific) provide details on the outcome of competition on the four key demographic parameters. A negative effect (red bars) indicates a decline in that response variable due to competition and a positive effect (green bars) indicates an increase in that response variable with increased density of competitors. In the case of interspecific competitive effects on survival (panel h), tests on a focal species that found no evidence of competition (grey bars) are distinguished from those in which the species has been shown to be dominant in an asymmetric competitive pairing (purple bar).

aggressive and defended territories that would otherwise be used by the subordinate species. Likewise, strong competitive asymmetries are also evident in experiments that have demonstrated effects of interspecific competitors on coral reef fish abundance (Robertson 1996, Schmitt and Holbrook 1999b, Munday et al. 2001, Schmitt and Holbrook 2003, Holbrook and Schmitt 2004). In the first study to demonstrate interspecific competition among juvenile coral reef fishes, Schmitt and Holbrook (1999a) manipulated the presence of two coral-associated damselfishes, *Dascyllus flavicaudus* and *D. aruanus*, on experimental patch reefs and compared population growth rates after three months. The population of *D. aruanus* declined by ~55% in the presence of *D. flavicaudus*, a striking result when compared to the 50% population growth observed in the absence of this competitor. In contrast, the presence of *D. aruanus* had a negligible influence on the population growth of *D. flavicaudus* highlighting the asymmetry in this competitive pairing.

Recruitment

Since Doherty's (1983) pioneering removal experiment, which found no effect of the removal of the territorial damselfish *Pomacentrus wardi* on the recruitment of a congener, only a handful of other studies have examined the potential for interspecific competitors to influence the recruitment of coral reef fishes. Sweatman (1985) was the first to present experimental evidence that their presence influenced recruitment patterns, with the richness and abundance of recruits tending to be higher on artificial reefs without resident damselfish *Dascyllus aruanus* and *D. reticulatus*. Similarly, studies by Almany (2003, 2004) have shown that the prior residence by adult damselfishes can influence the recruitment of other species. Negative effects of these prior residents on recruitment were apparent mainly for other damselfish species, whereas their effect was neutral or positive for wrasse, butterflyfish, and surgeonfish (Figure 2.2g).

Survival

As with intraspecific competition, survival is the most common demographic response variable measured to assess interspecific competition among reef fishes. Although a number of early studies (Doherty 1982, 1983, Jones 1987b, 1988, Munday 2001) found no evidence of its effect, 44% of the 32 experimental tests to date have detected a significant negative effect of interspecific competition on the mortality of a focal species (Figure 2.2h). Of the 18 experiments that did not find evidence of interspecific competition, 15% involved dominant asymmetric competitors that were shown to have strong effects on another species, but a reciprocal test showed that the subordinate did not affect their survival (Figure 2.2h). Carr et al. (2002) found that survival of juvenile bicolor damselfish, *Stegastes partitus*, was density-dependent only in the combined presence of congener *S. leucostictus,* adult conspecifics, and predators, suggesting interspecific competitors are important in population regulation. Density-dependent mortality was induced by interference competition for shelter space with the highly aggressive beaugregory damselfish, *S. leucostictus*. Bonin et al. (2009b) conclusively demonstrated an effect of an interspecific competitor on the survival of a coral reef fish. They manipulated the densities of two damselfishes with similar microhabitat preferences and found that survival of juveniles of the damselfish *Chrysiptera parasema* (recently revised as *Chrysiptera arnazae,* Allen et al. 2010) was substantially reduced on reefs where they shared the microhabitat with the more dominant damselfish, *Dascyllus melanurus.* In a subsequent study with these two species, Boström-Einarsson et al. (2014) showed that per capita survival of *C. parasema* decreased with increasing density of *D. melanurus* (i.e. was density-dependent) and that this effect of interspecific competition was stronger than that of intraspecific competition. Likewise, a series of studies have shown that the presence of interspecific competitors can reduce the survival of juvenile wrasses (Geange and Stier 2009, Geange 2010, Geange et al. 2013). Notably, the outcome of competition between two wrasses depends on their sequence of arrival onto the reef. When juveniles arrive simultaneously, *Thalassoma quinquevittatum* is the dominant competitor and the likelihood of mortality of *T. hardwicke* increased by 196% in its presence. However, if *T. hardwicke* has only 5 days prior residence it becomes the dominant species in the pairing and increased the probability of mortality by 93% *T. quinquevittatum* (Geange and Stier 2009). Hence, the outcome and strength of competition between species may vary depending on the particular conditions under which competition is occurring.

Growth and Reproduction

Compared to the burgeoning literature on survival, only 8 experiments have measured sub-lethal effects of interspecific competition among reef fishes (Figure 2.2i-j). The first experimental tests failed to find any evidence of interspecific competitive effects on growth (Jones 1987b, 1988). However, Clarke (1992) demonstrated that competition between the spinyhead blenny, *Acanthemblemaria spinosa*, and the roughhead blenny, *Acanthemblemaria aspera*, influenced both growth and fecundity. Where these two species co-occur, competitively dominant spinyheads exclude roughheads from occupying shelter holes positioned higher above the substratum (Clarke 1989). These higher positions are preferred by both species because they have greater availability of planktonic food. Clarke's (1992) resource manipulation experiment showed that the consequences of occupying shelter holes closer to the substratum were a reduction in feeding rate, spawning frequency, and clutch size for both species. A subsequent aquarium experiment suggested that the lower metabolic demands of the subordinate competitor allowed it to persist in the lower quality microhabitat despite the costs of competition. This remains the only study to illustrate an effect of interspecific competition on reproductive fitness (Figure 2.2j), though since that time two other studies have demonstrated interspecific effects on growth. Munday (2001) found that a tradeoff in competitive ability and the magnitude of fitness consequences allowed a coral-dwelling goby that was an inferior competitor to persist in a lower quality microhabitat, while Forrester et al. (2006) manipulated the densities of two gobies and found that the growth of both species declined with increasing densities of the other. Despite the lack of attention, interspecific competitors clearly have the potential to influence growth and reproduction in coral reef fishes through competition for food.

2.6 The relative strength of intra- and interspecific competition

From this review of the literature it is clear that both intra- and interspecific competition can have a significant influence on coral reef fish distribution, abundance, and demographic rates. But is one of these processes more important than the other? Comparing the strength of intra- and interspecific competition (Gurevich et al. 1992) can provide insight on the relative importance of these processes in structuring reef fish communities. Intraspecific competition might be expected to be more intense than interspecific competition because conspecifics exhibit greater overlap in resource use. However when there are strong competitive asymmetries, dominant species may have greater effects on subordinate species than intraspecific competition in subordinate species. Although it has long been recognised that intra- and interspecific competition should be measured simultaneously to judge their relative importance (Underwood 1986), experiments that do so are still incredibly rare in the coral reef fish literature (but see Forrester et al. 2006, Boström-Einarsson et al. 2014). To address this knowledge gap, standardised effect sizes (Cohen’s d) were calculated with 95% confidence intervals (Nakagawa and Cuthill 2007) across studies that measured competitive effects on the survival of a focal species at a particular density level, in both the presence and absence of interspecific competitors. In each calculation, the estimate of survival with only conspecifics present was considered as the "control" and the survival estimate with interspecific competitors present was designated as the "treatment". Positive values of d indicate instances where intraspecific competition was stronger than interspecific competition (i.e. survival was lower in the presence of conspecifics compared to heterospecifics at that density level), and negative values of d indicate instances where interspecific competition was stronger than intraspecific competition (i.e. survival was lower in the presence of heterospecifics compared to conspecifics). Five studies had experimental designs that permitted this comparison and reported the necessary statistics for effect size calculation. Four of these papers measured the effects of competition across several pairs of competing species or in several habitat types, yielding a total of 15 effect size values for comparison (Figure 2.3). For several species pairings (e.g. the wrasses *Thalassoma hardwicke* versus *T. quinquevittatum, Gomphosus varius* versus *T. quinquevittatum*) strong competitive asymmetries led to significantly stronger intra- or interspecific effects on survival, depending on the focal species considered. However in the majority of these interactions (9 out of 15) the 95% confidence intervals around the effect sizes spanned zero, indicating that the strength of intraspecific and interspecific effects on survival were not different in magnitude (Figure 2.3). This outcome is similar to that of Gurevich et al. (1992), who reported no difference in the strength of intra- and interspecific effect sizes in their meta-analysis of competition experiments on primary producers and carnivores. Admittedly, this is a small sample size from which to draw conclusions and the lack of experiments that have manipulated both intra- and interspecific competitors across multiple densities means this remains a critical gap in our knowledge.

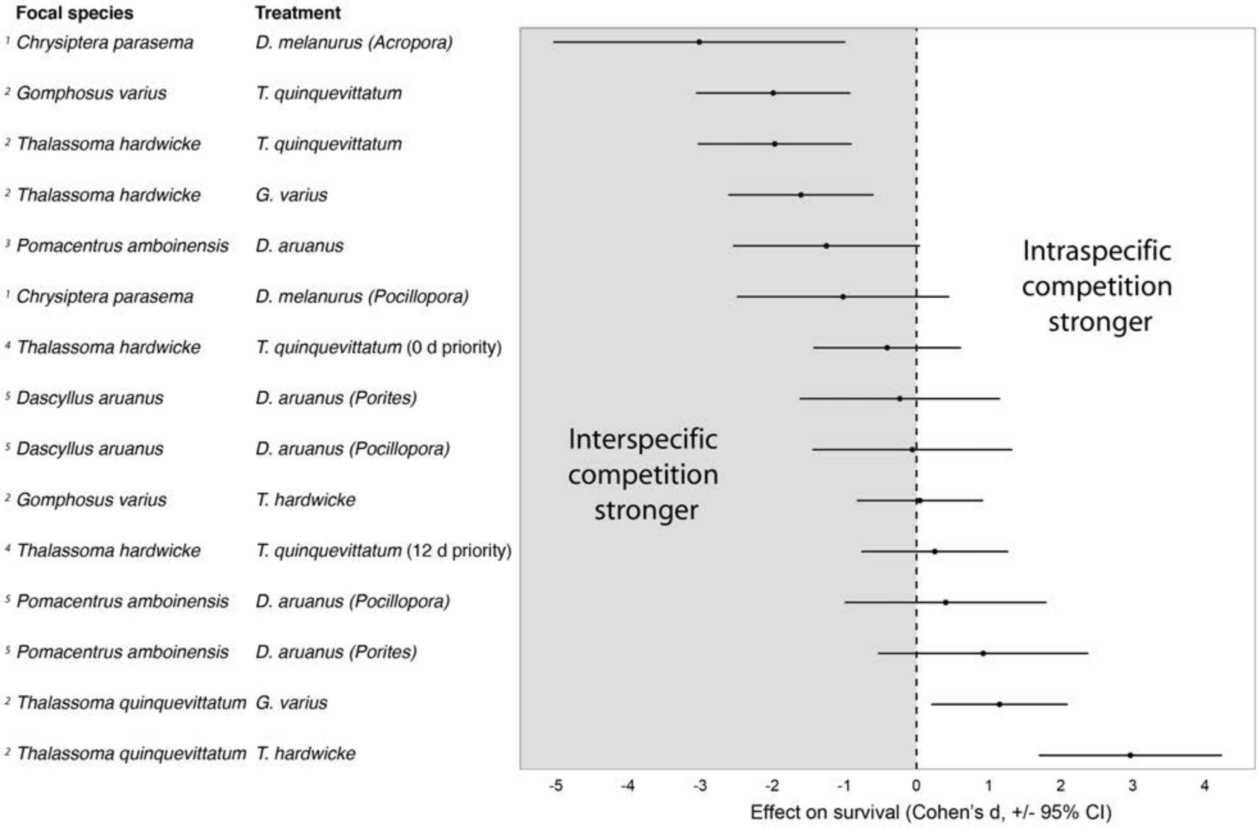

Figure 2.3. Standardized effect sizes (Cohen's d, ± 95% Confidence Intervals) of competition on the survival of a focal coral reef fish species. Each effect size estimate provides an indication of the relative strength of intra- and interspecific competition for the focal species. Negative d-values (shaded area) indicate that the effect of interspecific competition was stronger than intraspecific competition for that focal species. Positive d-values indicate that the effect of intraspecific competitors was stronger than interspecific competitors at a given density level. Effect sizes were calculated from mean and variance statistics as reported in the following references: Bonin et al. 2009b[1], Geange et al. 2013[2], Jones 1987b[3], Geange and Stier 2009[4], Jones 1988[5].

2.7 Factors that complicate the detection of competition

Resource identification and limitation

Identifying the specific resources that individuals compete for can be challenging, and perhaps because of this few of the studies reviewed attempted to do so. Although it is possible to demonstrate that competition is occurring without identifying the underlying resource involved, a problem can arise when interpreting the results of experiments. A number of studies have argued that resource limitation is not driving competition even though they observe strong effects of competitors (e.g. Forrester et al. 2006, Geange and Stier 2009, Samhouri 2009). The hypothesis is that behavioural interactions due to crowding, rather than a lack of resources, are the underlying cause of reduced growth or survival. This interpretation is sometimes supported by resource manipulation experiments that fail to show effects of altered resource availability. Although it seems clear that crowding incurs energetic costs and can increase the risk of mortality, authors should be cautious about interpretations that disregard resource limitation as the underlying cause of competition. The very behaviours that result in the observed costs of competition (e.g. increased aggression or moving farther from shelter) are motivated by the search, acquisition and defence of resources. Lack of an effect in resource manipulation experiments may simply indicate that the researcher was not able to identify and manipulate the specific resource that induced competition in their system. Furthermore, resource shortage is often related to its *quality* rather than its absolute quantity. As individuals become crowded, the highest quality parts of the resource will become limited well before the resource is completely exploited. Strong competition can therefore occur well below the perceived carrying capacity of the habitat because individuals may aggregate in areas of high resource quality (Clarke 1989, 1992). Although this makes it more difficult to manipulate resources and detect their degree of limitation in natural systems, resource limitation is, by its very definition, a critical component of competition.

Variation in habitat quality

Habitat variability is a good example of how variation in resource quality may obscure the effects of competition (e.g. Wilson and Osenberg 2002, Adam 2011). Wilson and Osenberg (2002) observed highly clumped distributions of *Gobiosoma* cleaning gobies, creating the impression that increased densities of conspecifics might be beneficial to survival. However, subsequent experiments revealed that competition among the gobies did have strong negative effects on settlement and survival once variation in habitat quality was accounted for. Consistently higher settlement of gobies to high quality habitat masked the negative effect of competitors. This inspired Shima and Osenberg (2003) to coin the term "cryptic density-dependence", a concept that highlights how other processes that operate in conjunction with competition may sometimes conceal its effects. Experiments that have manipulated both habitat quality and competitor density provide further evidence that habitat can have a strong influence on the detection and strength of competition (Jones 1988, Bonin et al. 2009b, Geange 2010, Geange and Stier 2010, Boström-Einarsson et al. 2014). In each of these studies, the separate and interacting effects of habitat and competitor density were isolated, and in each case the effect of altered habitat quality on reef fishes was stronger than the effect of changing competitor density. These stronger effects of habitat resulted from a range of different manipulations of its quality—from subtle changes such as switching to a less-preferred species of branching coral (Jones 1988, Bonin et al. 2009b), to reducing microhabitat complexity (Geange 2010, Geange and Stier 2010), or decreasing the percentage of live coral available (Boström-Einarsson et al. 2014). The only instance in which the effect of competition was stronger than the effect of altered habitat quality was when the competitor was given a 5-day prior residency advantage (i.e. Geange and Stier 2010). In fact, the effect of reduced habitat quality can sometimes become so strong that the effects of competition become experimentally undetectable (Boström-Einarsson et al. 2014), creating another form of cryptic density-dependence. In this instance, the process that obscures competition may be the stronger influence of predation in low quality habitat, rather than increased juvenile settlement as seen in high quality habitat. These studies collectively suggest that the habitat in which competitors interact is an important factor to consider when measuring competition among reef fishes and manipulating it can help to resolve what resources are limiting.

Predation

Predation is another factor that can muddy the water when measuring competition, especially when it comes to effects on survival. Although several previous papers have addressed the interaction between competition and predation (e.g. Gurevich et al. 2000, Hixon and Jones 2005, White et al. 2010), it is important to raise here because competition for refuge space from predators is among the most highly studied types of competition in the reef fish literature. In some of these experiments it is clear that competition is the ultimate process, with predators serving as the proximate agents of mortality (e.g. Carr et al. 2002, Holbrook et al. 2002). However, when predators are not manipulated or monitored as part of the experiment, it can be difficult to say with certainty whether it is competition, predation or some combination of these processes that underlies density-dependent mortality. Predators can potentially induce density dependence through an aggregative functional response, yet little is known about how prey densities influence the foraging behaviour of coral reef piscivores (but see Stier and White 2013). Another possibility is that the effects of predation may overshadow the effects of competition (Gurevitch et al. 2000), making it difficult to detect competition in short-term experiments, even when it is occurring (Hixon and Jones 2005). To date there is only one long-term experiment that demonstrates competitive effects on survival actually occur in the absence of predators. Hixon and Jones (2005) manipulated densities of the damselfish *Pomacentrus amboinensis* in the presence and absence of predators, and found that mortality of this damselfish became density-dependent after 10 months. This effect of density occurred even where predators were excluded, confirming that competitors can directly influence coral reef fish survival in the long-term. If predator manipulation is not logistically possible in competition experiments, data on aggression and refuge use among competitors, combined with monitoring of predator distribution and abundance across density treatments, can help test a particular hypothesis about the underlying processes driving experimental results. Clearly a deeper understanding of the interaction between competition and predation is required, and the manipulation or monitoring of predators is a necessary component of future experiments that set out to measure the effects of competition on reef fish survival.

2.8 Competition and coexistence in reef fish communities

A number of mechanisms may enable species to coexist in diverse communities when they are all competing for similar resources. Niche-based models of competition propose that competing species coexist through resource partitioning (Colwell and Fuentes 1975, Diamond 1978). In the presence of interspecific competitors, individuals use a different and/or narrower range of resources than they would if competing species were absent. As a result, niche overlap is reduced and a diverse community can coexist by each species specialising on a different portion of the available resources. Commonly, species also differ in their competitive abilities, with superior competitors gaining disproportionate access to the highest quality resources, and inferior competitors forced to use less favourable resources. The lottery hypothesis (sensu Sale 1977) is an alternative explanation for competitive coexistence. This hypothesis argues that competing species with identical resource requirements can coexist through chance colonisation of vacant space. Coexistence does not come about from resource partitioning, but instead is due to the stochastic availability of vacant space in comparison to the pool of individuals of different species that could occupy that space. However, a lottery for space is potentially ineffective at producing long-term coexistence between species without additional stabilising mechanisms, such as environmental variation that alternatively favours recruits of the different species (Chesson and Warner 1981). In long-lived species, favourable recruitment events can be stored in the population age structure and thus prevent any one species gaining a numerical advantage that would otherwise lead to competitive exclusion of other species through time (the storage effect: Warner and Chesson 1985). Ironically, the addition of environmentally dependent recruitment fluctuations changes the stochastic lottery hypothesis into the *lottery model*, where coexistence is dependent on some form of niche partitioning that influences the production of recruits of the different species that are available to settle into vacant space.

Although the lottery hypothesis was first developed for coral reef fishes, there is limited evidence for this mechanism of competitive coexistence among reef fishes (Robertson 1995). Just two studies to date (Munday 2004a, Pereira et al. 2015) have provided experimental evidence consistent with a competitive lottery in a reef fish assemblage. Munday (2004a) showed that two species of coral-dwelling gobies (*Gobiodon histrio* and *G. erythrospilus*) compete for access to vacant habitat space and have similar habitat preferences and competitive abilities at settlement. In contrast, most other coral reef fishes that are competing for limited resources appear to coexist through some form of resource partitioning (e.g. Clarke 1992), including other coral-dwelling gobies (Munday et al. 2001).

Theory and experimental tests of competition have often assumed that only one mechanism is responsible for the coexistence of competing species (Amarasekare 2003). Nowhere is this more evident than in reef fish ecology, where niche-based and lottery models have often been viewed as distinct alternatives (Robertson 1995, Munday 2004a). However, niche and lottery mechanisms are not mutually exclusive, and both could influence the coexistence of competing species (Chesson 2000, Gravel et al. 2006, Adler et al. 2007). In a new study on the two goby species mentioned above, Pereira et al. (2015) found that the mechanism of coexistence switches from a lottery at settlement to a competitive hierarchy and niche partitioning in adults. Juveniles of the two species have similar competitive ability, similar patterns of habitat use and similar relative abundance, consistent with a lottery at settlement; however, *G. histrio* becomes a superior competitor in larger size-classes. As a result *G. erythrospilus* is forced to use a greater proportion of less preferred habitat. The fitness loss for *G. erythrospilus* inhabiting alternative habitat is less than of *G. histrio,* which could explain how it can persist despite the competitive advantage of *G. histrio* in the adult stage. Indeed, this review of the literature has revealed that the strength of competition can vary through time and space, creating windows of opportunity for competing species to stake a claim on their share of available resources through a variety of different mechanisms. Modern competition theory recognises that both stochastic and stabilising factors, interacting with other processes such as predation and variation in habitat quality, are likely involved in the coexistence of fishes in diverse coral reef communities.

2.9 Competition in a changing world

Climate change and ocean acidification are dramatically changing marine environments and affecting the ecological processes that structure populations and communities of marine species (Harley et al. 2006). The ecological effects of these stressors may be especially severe on coral reefs due to the sensitivity of reef organisms to high temperatures and low seawater pH (Hoegh-Guldberg and Bruno 2010, Rummer et al. 2014). Climate change and ocean acidification could affect competition in coral reef fishes indirectly, through changes in the availability of habitat or other resources, or more directly by altering the competitive ability of individuals.

Coral reefs are being degraded due to the combined effects of climate change, severe storms, outbreaks of crown-of-thorns starfish, and poor water quality (Gardner et al. 2003, De'ath et al. 2012). Live coral cover is declining and reef habitat is becoming less structurally complex due to an increased frequency of these disturbances. Loss of coral cover and habitat structural complexity can directly affect reef fish diversity and abundance (Jones et al. 2004, Graham et al. 2006, Pratchett et al. 2008), but how these changes affect competitive interactions within and among species is less certain. Reduced availability of resources, such as preferred habitat, might be expected to intensify the effects of intra- and interspecific competition. This could exacerbate competitive hierarchies, causing dominant competitors to gain a greater share of resources at the expense of subordinate competitors. Alternatively, competitive hierarchies could be weakened, or even reversed, if subordinate competitors perform better than dominant competitors within the remaining habitats (Caley and Munday 2003).

Despite the obvious potential for the degradation of coral reef habitat to alter or exacerbate competition among reef fishes, few studies have set out to test this. In one of the only experimental studies conducted to date, Boström-Einarsson et al. (2014) found that reduced habitat quality had such a profound effect on two coral-dwelling fishes (*Chrysiptera parasema* and *Dascyllus melanurus*) that it overwhelmed the effects of both intra- and interspecific competition. In another study, McCormick (2012) observed that mortality of a subordinate competitor, the damselfish *Pomacentrus moluccensis,* was higher on bleached and dead coral compared with healthy coral in the presence of a dominant damselfish competitor *P. amboinensis.* This suggests that habitat degradation intensified the effects of competition on the subordinate species. These two studies show that the effects of habitat loss on competitive interactions can be complex and counterintuitive and that more research is needed before reliable predictions can be made about the effect of habitat degradation on ecological processes in reef fish assemblages.

Climate change and ocean acidification could also have a direct effect on competitive interactions by altering the relative performance of different species in projected future environments. For example, if one species has a narrower thermal tolerance range and is living closer to its optimum temperature than a competitor, it may suffer a steeper decline in performance and thus become a less successful competitor. Sorensen et al. (2014) found that the thermal reaction norm of hypoxia tolerance differed between two competing species of coral-dwelling gobies, suggesting that the thermally tolerant species may gain a competitive advantage in surviving warmer ocean temperatures in the future. Even more surprisingly, McCormick et al. (2013) demonstrated that ocean acidification can completely reverse the competitive hierarchy between the damselfish *P. moluccensis* and *P. amboinensis,* leading to higher mortality in the species that is currently the competitive dominant and reducing mortality in the current-day subordinate. In this case the underlying cause of the switch in competitive dominance appears to relate to the sensitivity of the two species to neurological impairment caused by elevated levels of dissolved CO_2 (Nilsson et al. 2012). Projected future CO_2 levels have a greater effect on the behaviour of *P. amboinensis* compared with *P. moluccensis* (Ferrari et al. 2011), leading to a reversal in aggression and risk taking behaviour at higher CO_2 levels (McCormick et al. 2013). Such a dramatic shift in the outcome of competitive interactions could have far-reaching implications for the persistence of individual species and the structure of reef fish communities. To date, research on the effects of climate change and ocean acidification in marine ecosystems has tended to focus on individual performance (e.g. growth, survival, calcification) in single species, future studies will need to have a greater emphasis on the function of ecological processes, such as interspecific competition, if broadly applicable predictions are to be made about how these stressors will affect marine ecosystems (Gaylord et al. 2015).

2.10 Conclusions and future research directions

Our review of the literature highlights the wealth of experimental evidence in support of competition as a process that structures populations and communities of coral reef fishes. Intra- and interspecific competitors can alter patterns of distribution, abundance and resource use and also exert a significant influence on the demographic drivers that regulate populations. Clearly, it is time to move beyond the debates of the past about *whether* competition occurs and embrace the pluralistic notion that competition is one of the many factors that shape these communities. Other factors, such as predation, habitat variability and environmental change, will also play a role. The challenge ahead is to better understand the particular conditions in which competition will (or will not) exact its strongest influence. This review is concluded by highlighting some of the key avenues for future experimental research on this core ecological process.

1. Explore variation in the strength of competition across gradients in resource quality. Future experiments that simultaneously manipulate competitor density and resource quality on coral reefs will help to identify the specific resources that limit populations and understand how competitive interactions will change as resource quality declines. Calculation of effect sizes will aid in comparing the strength of competition across resource gradients within and between studies.

2. Explore temporal variation in the strength of competition. Most studies have measured variation in the strength of competition spatially, whereas very few have explored variation over time (e.g. Schmitt and Holbrook 2007, Forrester et al. 2008, Hixon et al. 2012). However it is temporal density dependence that stabilises populations and estimates of variation in the strength of competition over time are necessary to truly assess its role in regulating coral reef fish populations.

3. Expand research on competitive interaction networks. Most experimental research on competition among reef fishes has involved measuring pair-wise interactions, despite the fact that competitors are embedded within a community of interacting species. Future experiments that measure variation in the strength of competition among groups of species with similar resource requirements will provide greater insight into mechanisms of competitive coexistence in these diverse communities.

4. Extend competition research to important functional groups. Competition experiments have almost exclusively been conducted on small-bodied reef fish species (i.e. 80% of the experiments reviewed here involved damselfish, wrasse or gobies). As a result, our current knowledge of competition comes from a limited subset of the coral reef fish community and very little is still known about its effects on populations of larger-bodied coral reef herbivores and predators. Although experimental manipulations of the densities and resources of larger and more mobile species will be challenging, it is critical to expand knowledge on the processes regulating populations of fishes that play such an important role in the health and function of coral reef ecosystems.

Over the past 40 years, experiments have helped us to appreciate the importance of competition for resources in shaping coral reef fish communities. In an era of rapid environmental change and declining resources, continuing to expand our knowledge on this fundamental process has never been more imperative.

Chapter 3

What doesn’t kill you makes you stronger - increased condition of damselfishes following partial coral mortality

3.1 Abstract

Habitat loss continues to be a primary cause of biodiversity loss in numerous ecosystems across the globe. However, the response to disturbance is often complex and can depend on the extent of habitat loss, the degree of specialisation in resource use, and the intensity of competitive interactions over declining resources. In addition, conclusions about the impact on a species can vary depending on the demographic and life history parameters measured and the time-scale of the study. Here, I evaluated the consequences of partial habitat loss on the abundance, physical condition, and behaviour of a common coral-dwelling reef damselfish, *Pomacentrus moluccensis* in Kimbe Bay, Papua New Guinea. I experimentally induced partial mortality of colonies of *Acropora* coral and monitored the abundance and condition of resident *P. moluccensis* for four months. Throughout the experiment *P. moluccensis* showed a strong association with the live habitat portion over the dead portion of partially degraded colonies. Densities within this live habitat increased following the disturbance, but gradually dropped until they matched those of healthy colonies. This suggests that density dependent processes have regulated abundances of *P. moluccensis* on partially degraded colonies to a level that can be supported by the remnant habitat. Surprisingly, liver samples indicated that individuals on partially degraded colonies had a higher body condition than those living on healthy control colonies. Video analyses revealed *P. moluccensis* opportunistically feeding on the algal matrix covering degraded branches. These results indicate that successful competitors benefit by gaining access to a novel food source along the edge of prime

shelter space within live coral, which may facilitate recovery from moderate levels of disturbance. This study furthermore highlights the complex mechanisms underlying declines in abundance following habitat degradation.

3.2 Introduction

Habitat loss and degradation is a primary cause of population decline and loss of biodiversity in all disturbed ecosystems (Vitousek et al. 1997, Sala et al. 2000, Pereira et al. 2010). These negative responses are expected given that habitat loss leads to a decline in critical resources such as food, shelter and living space, all of which may limit the abundance of species. Increasing intensity of competitive interactions over declining resources, or an increase in susceptibility to predators in degraded habitats, may compound the problem (MacArthur and Levins 1964). However, the impact of habitat loss varies depending on numerous factors, such as the intensity of the disturbance (Schulze and Mooney 1994), flexibility in habitat use (Devictor et al. 2008) and the degree to which habitat loss alters the strength of biological interactions within and among species (Candolin and Wong 2012). Despite the pervasiveness of habitat degradation, the processes that underpin species declines and the demographic mechanisms involved remain poorly understood.

Perceptions as to the extent to which habitat loss detrimentally affects species can depend on the mechanisms involved and the temporal response. While habitat loss often has a direct impact on population densities (Brooks et al. 2002, Bender et al. 1998), the effects are not always immediate. Temporal monitoring of populations has demonstrated that habitat loss may initially increase population density in remnant habitats, followed by a gradual decline through time. For example, Schmiegelow et al. (1997) described a significant initial increase in the abundance of ten species of birds in remnant patches following the loss of forested landscapes. After two years this apparent positive effect of habitat loss on abundance had subsided and the authors suggest this may be due to density dependent factors like competition, predation, or nest parasitism. This short-term 'crowding effect' (Debinsky and Holt 2000) has also been observed in insect communities on grass lands (Collinge and Forman 1998) and alfalfa fields (Grez et al. 2004). These studies emphasise the importance of temporal monitoring in order to fully understand realised demographic consequences of habitat loss and the biological mechanisms responsible.

The perceived response of species may also depend on the parameters researchers choose to measure. The impacts of habitat loss are often measured in terms of numerical change (i.e. mortality rate, abundance, density), however an organism’s physiological fitness and behaviour are also likely to be altered. For example, Burton et al. (2006) followed wading birds after their primary foraging habitat was lost. Displaced birds migrated to adjacent habitat that already contained resident populations of conspecifics. The following year, mortality rates had increased by 44% amongst displaced birds while it remained the same in the population of prior residents. Similarly, the body condition of displaced birds was significantly lower than conspecific residents at the new foraging location. This suggests that displacement and subsequent crowding due to habitat loss can affect both numerical and individual performance parameters simultaneously. However, habitat loss may not always be detrimental for remnant populations. For example, saw-whet owls in areas with intermediate habitat loss had a higher body mass than owls in less disturbed areas, possibly because the prey generalist saw-whet owl benefits from higher levels of prey in a less homogeneous landscape (Hinam and Clair 2008). Indeed, it has been suggested that species with a degree of flexibility in their resource use are favoured in degraded environments as that flexibility allows them to extract some resource from an altered environment (Ries et al. 2004). This highlights the importance of measuring aspects of both fitness and behaviour to adequately understand the complexities in species responses to habitat loss. Furthermore, it suggests that sub-lethal effects and behavioural interactions may play an important part in the ultimate response to habitat loss.

Coral reef systems are threatened from a large suite of anthropogenic stressors and have experienced a global decline in hard coral cover (Gardner et al. 2003, Hughes et al. 2003, Bruno and Selig 2007). The coral matrix provides reef fishes with critical resources, such as food and shelter from predators. Given the importance of living corals it is likely that the loss of this habitat will influence ecological interactions between reef fishes. In particular, intraspecific competition is likely to be affected by habitat loss and degradation because displaced individuals may be forced to occupy the remaining habitats in higher densities. Habitat-associated reef fishes are particularly sensitive to increased densities of conspecifics, given their close association with spatially restricted coral colonies. For example, *Pomacentrus amboinensis,* a common damselfish*,* exhibit reduced growth and delayed maturation at high densities compared to less crowded conspecifics (Jones 1987 a,b, Jones 1991). Similarly, female *P. amboinensis* produce smaller offspring in crowded conditions, suggesting high density situations affect stress levels and metabolic output (McCormick 2006). While crowding can increase direct competition over food (e.g. Jones and McCormick 2002, Hixon and Jones 2005, Bonin et al. 2015) it has also been demonstrated that density dependent behaviours such as aggression may be an important indirect mechanism underpinning negative demographic effects (Forrester and Steele 2004, Forrester et al. 2006). Competition over finite resources in a high density environment is likely to lead to a range of numerical and fitness responses to habitat loss following an initial increase in densities in remnant habitat. However no study to date has investigated the density dependent mechanisms that may be operating during an ongoing degradation event.

The lemon damselfish, *Pomacentrus moluccensis,* is a coral-associated fish that rarely ventures far from the protective branches of the coral colony (Beukers et al. 1995, Brunton and Booth 2003). These fish have a close association with live coral, due to the shelter it provides, however they do not rely on the coral itself as a food source. Furthermore, the small scale of their home range (<1m, Booth 2016) makes them amenable to experimental manipulation and monitoring throughout the experiment. Thus, *P. moluccensis* is an ideal model species to study the consequences of crowding following habitat degradation. In this study I tested the effects of habitat loss on the abundance, behaviour, and condition of *P. moluccensis*. Habitat loss was experimentally induced and the abundance and behaviours of resident fish were recorded over a four month period on partially degraded coral colonies and non-degraded control colonies. In addition, I recorded the abundance of *P. moluccensis* in the surrounding area around each experimental colony to investigate local effects of habitat loss. At the end of the experiments body condition of surviving individuals in partially degraded habitat patches was compared to individuals from control habitats. I aimed to test: 1) how abundance and density of *P. moluccensis* in remnant live habitat is affected by partial habitat loss 2) and how observed effects change through time. I then 3) evaluate how the abundance of *P. moluccensis* in the local area surrounding experimental colonies was affected by the disturbance event. Finally, I aimed to 4) evaluate how aggression and feeding rates are affected by habitat loss and crowding and 5) measure individual condition after this series of events. I hypothesised that habitat degradation would increase aggressive interactions between individuals in crowded remnant habitat, and that this would lead to decreased feeding rates. I further expected that the combined effect of crowding and habitat degradation would lead to reduced body condition of individuals in remnant habitat patches.

3.3 Methods

Study location and experimental design

This study was conducted on the near-shore platform reefs in Kimbe Bay, Papua New Guinea (150°05'E, 5°25'S). This area has previously been disturbed by local outbreaks of the corallivorous crown of thorns starfish *Acanthaster planci* (Quinn and Korjis 1987, Jones et al. 2004), and this echinoderm is one of the foremost threats against live coral cover in the Indo-Pacific (Pratchett et al. 2014). To test for effects of habitat loss on fish densities, I transplanted *A. planci* to healthy coral colonies supporting natural aggregations of *Pomacentrus moluccensis* for a period long enough to induce partial coral mortality, while leaving a portion of the colony alive to provide remnant habitat. Thirty plating *Acropora* coral colonies were randomly selected on the exposed crest of three adjacent platform reefs. An open bottomed steel mesh cage containing two *Acanthaster planci* was placed on 20 colonies, to allow predation of live coral tissue. Cages covered approximately 60% of the total colony surface and were kept in place until all coral tissue beneath the cage had been consumed (Figure 3.1). An empty cage was placed on five colonies (cage control), and five were undisturbed (control). To simulate a natural outbreak of *A. planci*, resident *P. moluccensis* were not removed or manipulated during the experiment.

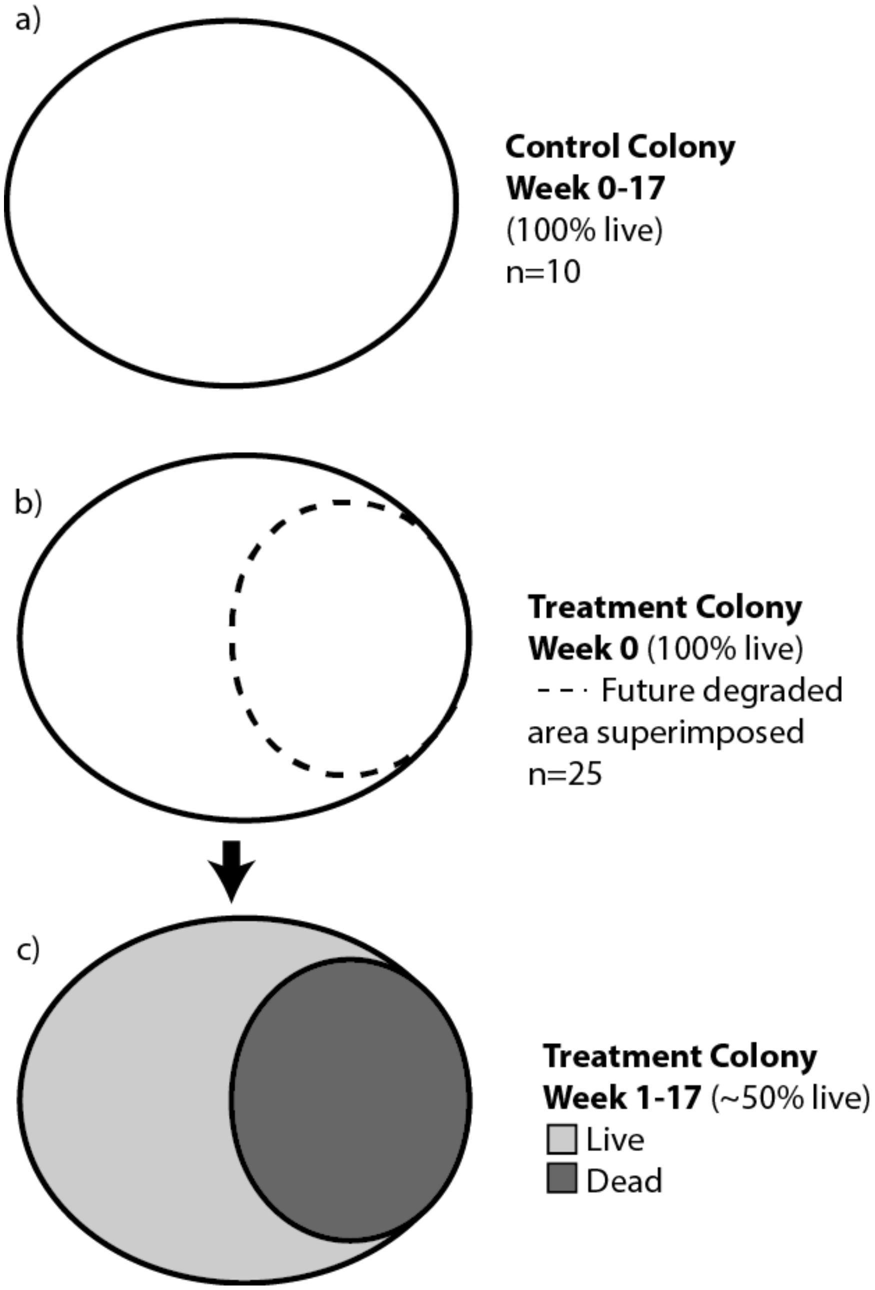

Figure 3.1: Experimental setup of the degradation experiment depicting a) control coral colonies b) treatment colony prior to disturbance at week 0, and c) treatment colonies post-disturbance, weeks 1-17. Colony b) illustrates how densities in 'live' and 'dead' habitat portions on the same coral colony can be superimposed on images of the colony prior to the disturbance event.

Coral colonies become overgrown with algae following mortality from crown of thorns starfish feeding. While it is not fully clear what resource(s) coral-associated fish gain from their association with live coral, the shelter space provided between branches appears important because variation in inter-branch spacing can affect survival and body condition (e.g. Noonan and Jones 2012). Inter-branch space was measured at the conclusion of the experiment as an estimate of the amount of shelter space lost following the death of the coral colony. Height (H), width (W) and depth (D) of these spaces were measured at 10 randomly selected locations on the surface of both the healthy and degraded coral colonies using Vernier callipers. The mean product of these three measurements (H × W × D) provided an estimate of the average total space available to fish hiding amongst the coral branches per colony. The dead portion of coral colonies had become overgrown by sponges and algae after four months reducing the available space between branches by 63% (Mean inter branch space= live (control): 19 $cm^3 \pm 1.26$ SEM, live portion (treatment colony): 19.7 $cm^3 \pm 1.24$, dead portion (treatment colony) 7.2$cm^3 \pm 0.44$. One way ANOVA $F_{(2,39)}=13.6$, $p<0.0001$). A Tukeys HSD post hoc test revealed that this was driven by a significant difference between the dead portion of treatment colonies compared to the live coral on both treatment and control colonies (Tukeys HSD, $p<0.001$ in both comparisons). However there was no significant differences in branch space between live coral on treatment colonies compared to control colonies (Tukeys HSD, $p=0.9$).

Abundance and density

Fish density in each habitat type was monitored through time to test for a crowding effect. I used digital images of each coral colony to evaluate abundance of *P. moluccensis* in each habitat type (Habitat type 1: Control colonies, type 2: degraded habitat on treatment colony, type 3: remnant live habitat on treatment colonies). Digital images of each colony were taken prior to disturbances (week 0), weekly for the first month (week 1-4) and at 4 months (week 17). Three images were taken at each monitoring event to accommodate for movement of individual fish. The total colony size and degraded patch size was calculated using an image processing program (ImageJ 1.46R, Schneider et al. 2012). The position of individual *P. moluccensis* were recorded on each colony to generate a mean density of individuals on each habitat type. I superimposed the area covered by dead coral post-disturbance on pre-disturbance images to ensure that the distribution of fish was uniform on colonies prior to the disturbance (Figure 3.1).

Linear mixed effects models (LME) were used to compare the overall density of *P. moluccensis* over time on degraded and control coral colonies. LME allows the inclusion of both fixed and random effects in a model and is particularly useful when repeated measurements are taken from the same statistical unit (longitudinal study) or where other violations of independence are present (Zuur et al. 2009). In addition, LME analyses readily handle unbalanced and missing data and allow all observational units to contribute information to the analysis (Pinheiro and Bates 2000).

I performed separate LME analyses to (1) compare the overall density of fish on partially degraded treatment colonies and control colonies and (2) compare densities of fish on the live and dead coral portion of treatment colonies, at different points in time following the disturbance. In the first analysis, damselfish density was modelled as a function of ‘colony type’ (fixed factor, 2 levels: Treatment/Control) and ‘week’ (fixed factor, 6 levels: 0, 1, 2, 3, 4, 17 weeks). In addition, the term ‘colony’ was included as a random factor in the model to account for the different initial starting densities on the individual colonies selected for the experiment. Modelling ‘colony’ as a random intercept effectively resolved the non-independence of repeated within-subject measurements (Zuur et al. 2009). The second analysis compared damselfish density on partially degraded coral colonies to densities on control colonies separately. *P. moluccensis* density was modelled as a function of habitat type (categorical factor, 3 levels: live portion (treatment colony)/dead portion (treatment colony) / Live (control)) and 'week', with 'colony' again included as a random factor. The full models were evaluated given the interest in how densities of *P. moluccensis* varied at different points in time after a disturbance (i.e. the interaction between weeks and colony or habitat type). LME analysis was conducted using the nlme package (Pinheiro et al. 2016) within the R environment (R Core Team, 2016). Data was log+1 transformed to improve the distribution of residuals. P-values were obtained through a restricted maximum likelihood approach (REML), which allows unbiased estimates of parameters by maximising the likelihood of fixed and residual random components simultaneously. REML removes assumptions of independence and homogeneity of variance, and therefore provides a flexible tool for analysing repeated measure through time.

Body condition

All remaining fish on each colony were collected at the conclusion of the experiment using a dilute clove oil solution. Total length (from tip of snout to end of caudal fin) was measured and livers dissected from the body and preserved in 10% formalin. The hepatosomatic index (HSI) was calculated using the ratio of (dry blotted) weight of livers to total length of fish. This index is a proxy for the physical condition of the fish, as heavier livers indicate a higher stored energy (lipid) content (Chellappa et al. 1995). The difference in HSI between treatment and control colonies was compared using a two-sample t-test. Because HSI is conventionally calculated as a ratio of liver weight to body weight (not length) I also validated the relationship between HSI and lipid content by quantifying the hepatocyte vacuolation on a subset of samples (n=10). Livers fixed in formalin were dehydrated in a graded ethanol series and embedded in paraffin wax. Wax blocks of livers were sectioned at 5 μm, and stained using Mayer's hematoxylin and eosin. A grid was superimposed on 40x magnification images using ImageJ (1.46R, Schneider et al. 2012), and was used to quantify the number of points (out of 234) that intersected hepatocyte vacuoles. Three estimates from three sections were recorded for each sample. The mean proportion of vacuoles in the liver was calculated and correlated with HSI index for each sample. A high level of correlation would indicate that HSI is a good proxy for lipid content in the livers of *P. moluccensis.*

Behavioural effects of habitat loss

To investigate if density dependent aggressive behaviour in crowded environments may be the underlying cause of a decline in density over time following degradation, I conducted behavioural monitoring throughout the duration of the experiment. Underwater video cameras (GoPro Hero 3) were used to monitor each colony at the same time periods as surveys of surrounding colonies (week 1, 4 and 17). Video recordings were used to compare the frequency of agonistic interactions and bite rates of *P. moluccensis* on control and treatment colonies. The first two minutes of each video were discarded to ensure behaviours recorded were unrelated to any disturbance caused by camera deployment. An agonistic interaction was defined as a nip or a chase between two *P. moluccensis* individuals within the coral colony area, and were recorded in a 10 minute period. The number of bites on either live or dead coral were also recorded during a 5 minute interval to investigate differences in feeding between control and treatment colonies. Both intraspecific agonistic interactions and bite rates were converted into per capita per minute rates. Mixed effects linear models were performed with habitat type (agonistic=2 levels: treatment and control; bite rates=3 levels: dead, live, control) and time (3 levels: Start, 1month, 4 months) as fixed categorical factors. Colony was included as random factor to accommodate the repeated measures of the same colony through time. P-values were obtained using REML as above.

Abundance patterns on surrounding colonies

While habitat loss will primarily affect the experimental colony and resident fish, it is known from previous studies that migration and recruitment external from the study site may also influence the outcome of disturbances. I therefore measured the density of *P. moluccensis* on surrounding colonies at three time points throughout the experiment; 1) immediately following disturbance, 2) 1 month post-disturbance and 3) 4-months post disturbance. All *P. moluccensis* within a 5 m radius from each experimental colony were recorded, as well as a record of unoccupied plating *Acropora* coral colonies. Linear mixed effects models were performed as for colony abundance estimates, using the abundance of adult *P. moluccensis* as response variable, experimental 'colony type' and 'week' as fixed factors, and 'colony' as random intercept.

3.4 Results

Abundance and density

There was an initial increase in densities of *P. moluccensis* on treatment colonies in the first 2 weeks after the start of the experiment, followed by a gradual decline over the following 15 weeks (Figure 3.2a, Table 3.1). Densities of *P. moluccensis* within the live portion of coral colonies increased immediately following the partial degradation of the colony (Figure 3.2b). The densities in the live portion of treatment colonies were significantly different from those on control colonies at week 3, 4, and 17 (Table 3.2). The initial high densities within the live coral portion gradually decreased over the four months with no signs of a plateau or reaching an equilibrium. Meanwhile, densities within the dead coral portion decreased over the course of the experiment (Figure 3.2b), although they were not significantly different to control colonies. Finally, there was no difference in densities of *P. moluccensis* on treatment colonies between the two sections of each coral colony prior to degradation (week 0, Table 3.1). Control colonies did not change significantly in densities throughout the time period (Figure 3.2b).

Body condition

The hepatosymatic index (HSI) of livers from fish on treatment colonies was 16% higher than those on control colonies (mean HSI ± SEM: control colony 0.38±0.02, treatment: 0.44±0.02). This indicates that the liver of fish on treatment colonies were significantly heavier than livers from control colonies in relation to body length (2-sample T-test, $t_{(1, 397)}$=2.7, p=0.007). There was a significant positive correlation between HSI and hepatocyte vacuolation (Linear regression t=5.5, df=6, p=0.002, R^2 0.83), indicating that HSI values are a good proxy for lipid content in *P. moluccensis* livers. The distribution of standard lengths within the group of surviving individuals on partially degraded treatment colonies was not significantly different from control colonies (Kolmogorov-Smirnov test D=0.09, p=0.35, Figure 3.3). Furthermore there was no overall difference in mean Standard Length of fish from treatment and control colonies (Mean size: Control 23.4 +/- SE mm SL, Treatment 24.6 +/-SE mm SL; Welch's t-test, t = -1.8155, df = 325.93, p-value = 0.07).

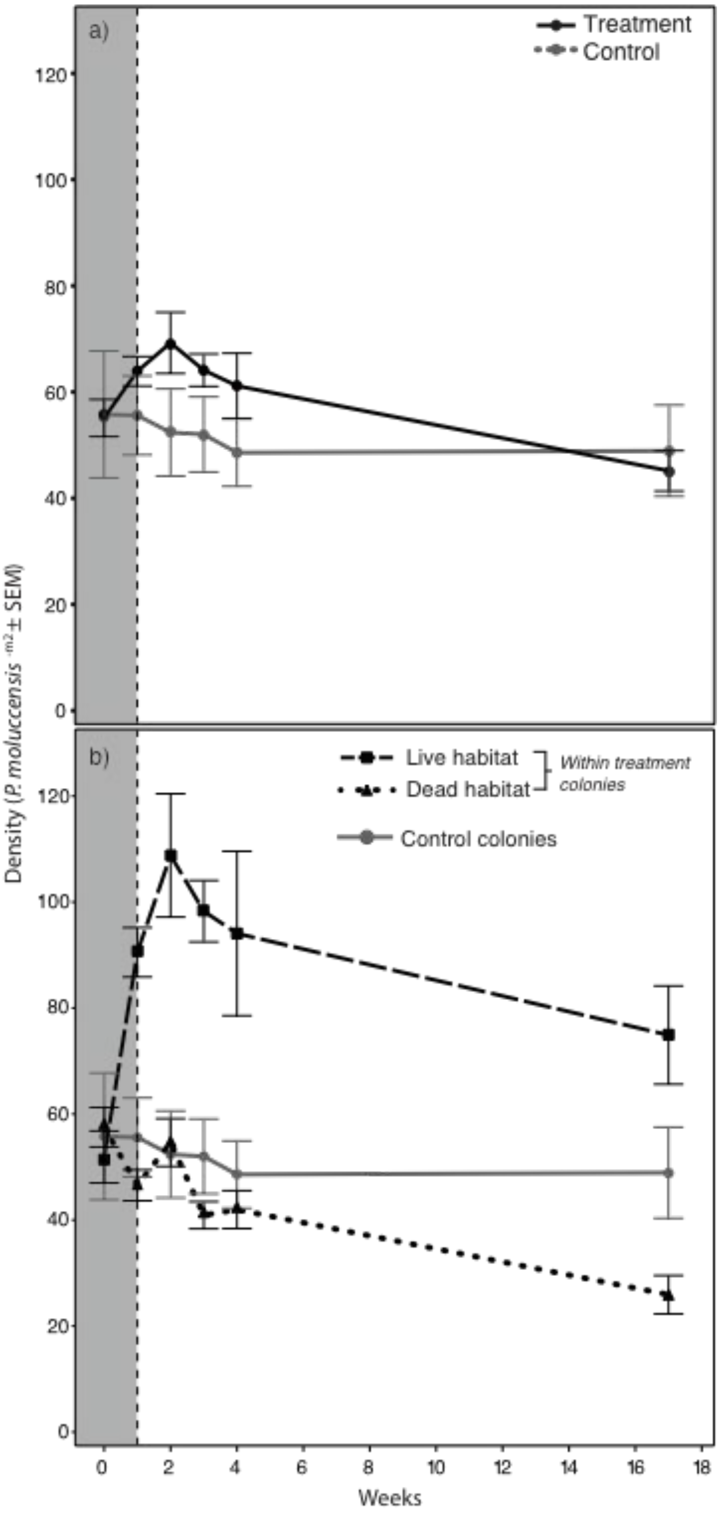

Figure 3.2: a) Overall average density of *P. moluccensis* on control and treatment colonies over the experimental period. b) Average density of *P. moluccensis* on the live and dead habitat section within treatment colonies compared to control colonies. Note that the live and dead habitat portion are part of the same treatment colony, (i.e. not independent) and are therefore only compared to densities on control colonies, not to each other. Shaded area denotes the degradation period when cages were present on colonies allowing the corallivorous crown-of-thorns starfish *Acanthaster planci* to consume the live coral tissue. At week 1, cages were removed and the experiment commenced. Error bars indicate standard errors.

Table 3.1: Results from Linear Mixed Effects model output comparing densities of *P. moluccensis* on treatment and control colonies (model 1). [model: log(density)~colony type*weeks, random=~1|colony]

Variable	**Value**	**SE**	**DF**	**t-value**	**p-value**
(Intercept)	1.638	0.104	607	15.815	0.000
Weeks (1)	-0.038	0.056	607	-0.671	0.503
Weeks (2)	-0.060	0.057	607	-1.061	0.289
Weeks (3)	-0.059	0.054	607	-1.089	0.277
Weeks (4)	-0.134	0.057	607	-2.349	0.019
Weeks (17)	-0.186	0.061	607	-3.043	0.002
Colony type x Weeks (week 0)	0.047	0.124	28	0.375	0.710
Colony type x Weeks (week 1)	0.064	0.062	607	1.047	0.296
Colony type x Weeks (week 2)	0.117	0.063	607	1.860	0.063
Colony type x Weeks (week 3)	0.099	0.060	607	1.669	0.096
Colony type x Weeks (week 4)	0.128	0.064	607	2.003	0.046
Colony type x Weeks (week 17)	0.144	0.069	607	-2.105	0.036

Table 3.2:) Linear mixed effects models output comparing densities of *P. moluccensis* on the live and dead portion of treatment colonies, to densities on control colonies through time. [model: log(density)~ habitat type * weeks +(1|colony)]

Variable	**Value**	**SE**	**DF**	**t-value**	**p-value**
(Intercept)	1.651	0.142	1132	11.587	0.000
Habitat Type (dead) Week 0	0.064	0.164	1132	0.391	0.696
Habitat Type (live) Week 0	-0.080	0.164	1132	-0.485	0.628
weeks1	-0.033	0.133	1132	-0.251	0.802
weeks2	-0.057	0.135	1132	-0.420	0.675
weeks3	-0.055	0.128	1132	-0.428	0.669
weeks4	-0.122	0.135	1132	-0.905	0.365
weeks17	-0.170	0.145	1132	-1.171	0.242
Habitat Type (dead) Week 1	-0.171	0.146	1132	-1.177	0.239
Habitat Type (live) Week 1	0.281	0.146	1132	1.929	0.054
Habitat Type (dead) Week 2	-0.055	0.149	1132	-0.370	0.712
Habitat Type (live) Week 2	0.279	0.149	1132	1.873	0.061
Habitat Type (dead) Week 3	-0.181	0.141	1132	-1.285	0.199
Habitat Type (live) Week 3	0.363	0.141	1132	2.573	0.010
Habitat Type (dead) Week 4	-0.133	0.151	1132	-0.876	0.381
Habitat Type (live) Week 4	0.303	0.151	1132	2.001	0.046

Habitat Type (dead) Week 17	-0.294	0.162	1132	-1.808	0.071
Habitat Type (live) Week 17	0.349	0.162	1132	2.151	0.032

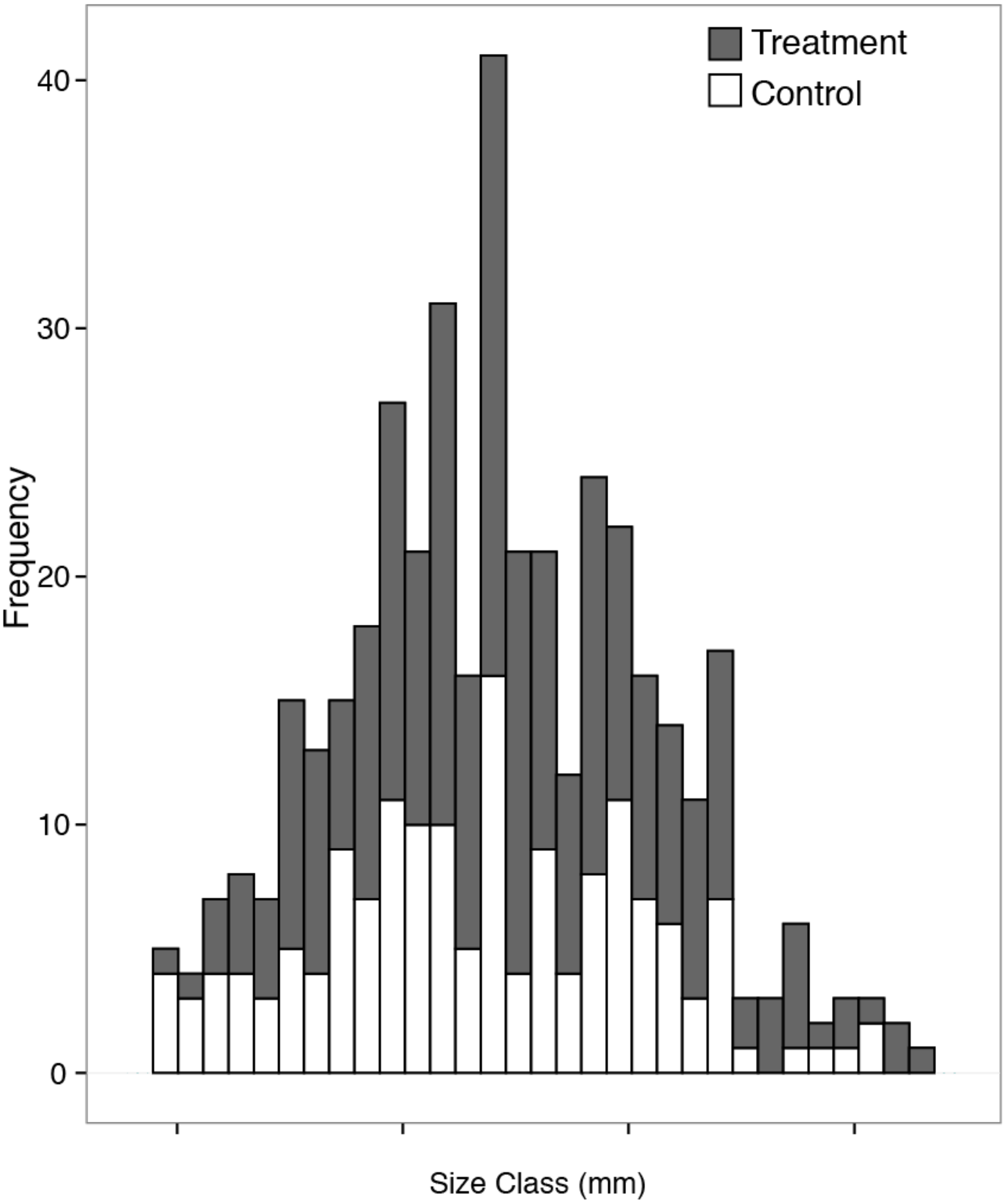

Figure 3.3: Frequency histogram of standard lengths (mm) of *P. moluccensis* on control and treatment colonies at the conclusion of the experiment (week 17).

Behavioural effects

There was a trend for increased levels of aggression experienced by each *P. moluccensis* on treatment colonies after one month (Figure 3.4a). However, due to a high degree of variability, there was no significant effect of either time of measurement or type of coral colony on the per

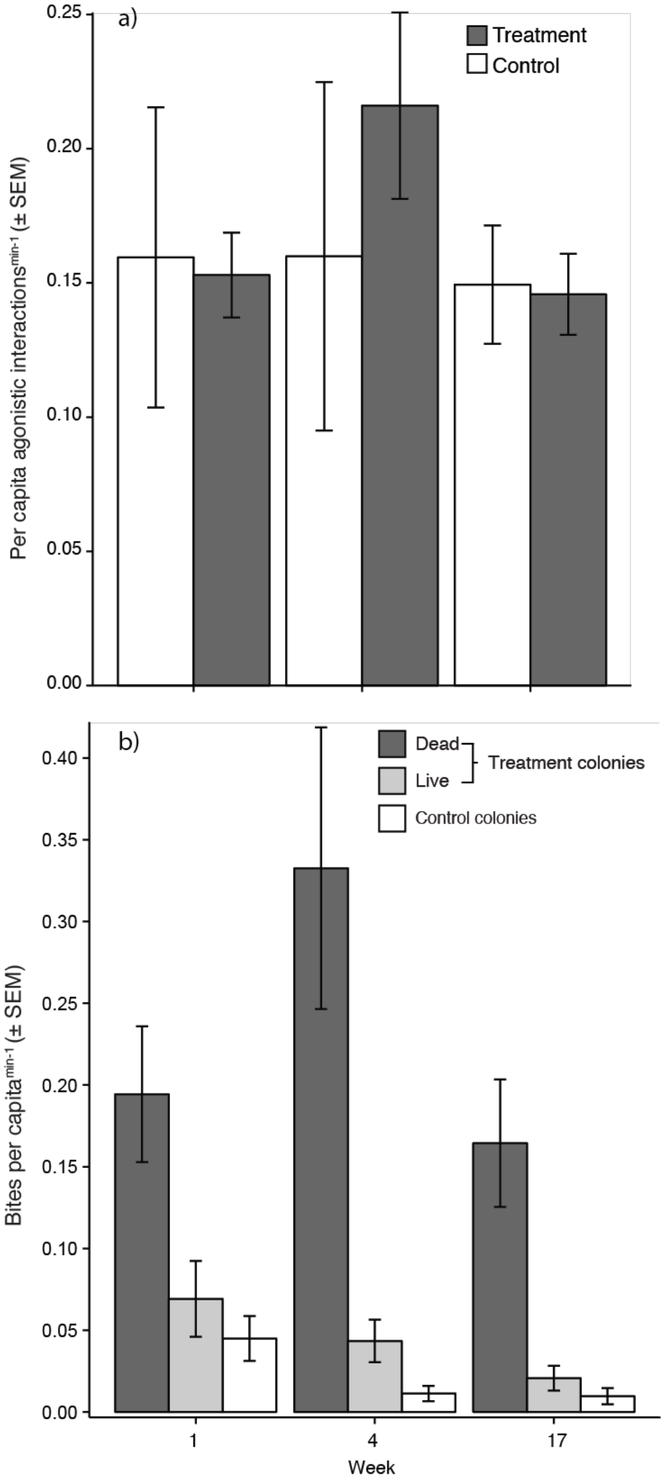

Figure 3.4: a) Per capita agonistic interactions experienced by *P. moluccensis* on treatment and control colonies at three time points of the experiment. Week 1 marks the start of the experiment, week 4 measures behaviours when density dependent behaviours are likely to be occurring due to crowding and week 17 marks the conclusion of the experiment. b) Feeding activity of *P. moluccensis* on coral colonies. The mean number of bites per capita on live and dead coral on the treatment colonies and bites on the live colony is compared across three time points.

capita agonistic interactions. The peak in agonistic activity coincided with the peak in densities within live coral portion on treatment colonies. *P. moluccensis* individuals took a significantly higher number of bites per capita from the degraded branches on coral colonies compared to healthy, throughout the study period (branch type: Chi-Square 40.1, df=2, p<0.001, time period: Chi-Square 3.23, df=2, p=0.20, interaction= Chi-Square 8.59, df=4, p=0.07,). There was no significant difference in number of feeding bites between live branches on treatment colonies or control colonies (Figure 3.4b).

Abundance patterns on surrounding colonies

The number of adult *P. moluccensis* in the areas adjacent to each experimental colony fluctuated significantly through time, but did not differ between control and treatment colonies (Figure 3.5). Furthermore, there was no interaction between the two main effects of time and colony type. While there was a lot of variability in the data, they suggest an increased number of fish in areas surrounding treatment colonies at the conclusion of the experiment (Figure 3.5).

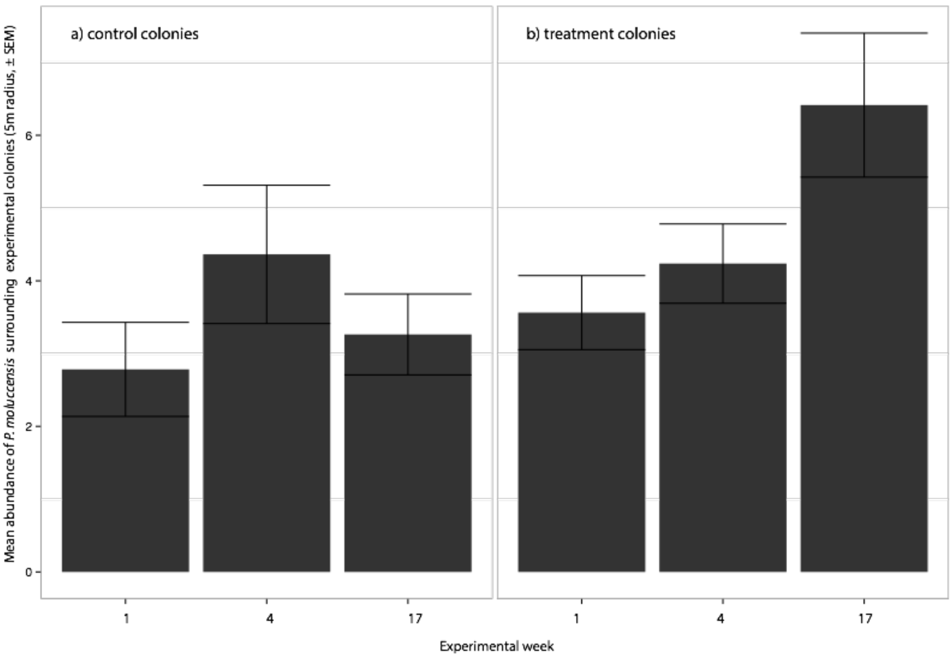

Figure 3.5: The mean abundance of *P. moluccensis* on colonies surrounding (<5m) each experimental colony at week 1 (start), week 4 and week 17 (end). Error bars represent standard errors.

3.5 Discussion

Habitat loss is recognised as one of the most pressing issues that will continue to threaten species persistence and biodiversity in the coming decades. An effective response to this problem requires greater understanding of the mechanisms involved and the overall impacts on species across a range of parameters. This study demonstrates that a partial habitat loss can result in a temporary increase in overall density of a common reef fish, *Pomacentrus moluccensis.* However, this increased density gradually subsided over a period of 17 weeks, at which point densities on treatment and control colonies were similar. Examining space use on degraded colonies revealed that this pattern was driven by a substantial increase in density within the remnant live coral portion immediately following the disturbance event. The subsequent decline in density over time suggests density dependent processes are regulating the abundance of *P.*

moluccensis within the remnant portion of healthy habitat. Indeed, I described a moderate peak in aggressive interactions between individuals in high density situations, coinciding in time with the decline in *P. moluccensis* abundance. Finally, I observed fish taking advantage of newly introduced foraging sites within the dead corals, reflected in an increased feeding rate of fish on disturbed colonies. This opportunistic feeding may underpin an increased hepatosomatic condition in surviving individuals in remnant live habitat compared to undisturbed control habitats. The results suggest that partial coral loss causes a range of responses, and although competitive interactions lead to a decline in abundance, the increased condition of survivors has the potential to aid in population recovery.

Following the loss of approximately 60% of the live habitat, I described a two-fold increase in density of individuals within the remnant healthy habitat of coral colonies. This crowding was transient in nature, and densities within the live coral portion gradually declined throughout the experiment. This pattern mimics that seen in birds in remnant live forest fragments following clear-cutting of surrounding boreal forests (Schmiegelow et al. 1997). The total abundance of birds increased in isolated remnants of live habitat in the first year following the loss of their surrounding habitat. This increase was however lost in the following year, when there were no differences between treatment and control patches. Similarly, insect densities more than doubled within isolated fragments of grassland following the mowing of adjacent habitat, but returned to pre-disturbance levels after five weeks (Collinge and Forman 1998). While a portion of the increase in densities on live habitat in this study could be explained by displaced individuals from the dead coral portion, the corresponding drop in densities on dead coral patches does not adequately explain the full increase. There was no change in densities immediately surrounding experimental colonies, which suggests that longer-distance migrants (i.e. > 5m) are the source of the influx in *P. moluccensis* in the first two weeks.

I expected the total number of *P. moluccensis* to decline following the disturbance event, however, there was no difference between the control and treatment colonies at the conclusion of the experiment. However, the downward trajectory of *P. moluccensis* densities on treatment colonies, compared to stable densities on undisturbed control colonies, indicates densities may have continued to fall if the experiment was allowed to continue past 17 weeks. The lack of an asymptote in densities on treatment colonies suggests I may have failed to capture the final density consequence in this study. This highlights the importance of timing when measuring consequences of habitat loss. Prior studies indicate that the timeframe to detect mortality-effects in coral-associated reef fishes following habitat degradation is highly variable (e.g. 2 months: Boström-Einarsson et al. 2014, 6 months: Lindahl 2001,1 year: Bouchon-Navaro 1985, 5 years: Pratchett 2004). Furthermore, these studies detail the effects of more profound declines in live habitat at the whole reef scale (Wilson et al. 2006). Due to moderate reductions in habitat in my study, remnant live habitat may have provided a buffer against severe declines in abundances following the disturbance event.

Given that habitat degradation alters the resources available in an ecosystem, it is likely to increase competition over limiting resources. Competitive interactions are an important structuring force in terrestrial (Begon 1986, Gurevitch 2000) and marine (Chapter 3) ecosystems, and are often manifested through density dependent behaviours (White et al. 2010). For example, shore-birds displaced by the loss of their primary foraging habitat often migrate into remnant live habitat. Crowding increases competition for resources, reduces food intake and ultimately increases winter mortality (Dolman and Sutherland

1995, Goss-Custard et al. 1995). In another example, human presence and development have increased interference competition over salmon (i.e. a high quality protein) within populations of North American brown bears and caused subordinate females and juveniles to switch to terrestrial protein sources and plant matter (lower energy yield) (Hilderbrand 1999). This dietary shift resulted in reduced body size and reproductive success, and ultimately declining population densities. In the current study, there was a peak in the number of aggressive interactions between fish on treatment colonies that coincides with the time period of greatest densities within the remnant live habitat. While density dependent interactions appear to be a likely mechanism of the decline in abundance, alternative processes like predator aggregation towards crowded colonies may also have contributed.

I expected that if density dependent processes like competition were regulating the size of the aggregations, this would also be reflected in the physiological condition of the surviving fishes at the conclusion of the experiment. A Hepatosomatic Index (HSI) was used as a proxy for physical condition, which has been demonstrated to be a reliable predictor of body condition in fishes in general (Chellappa et al. 1995) and is known to be reflection of diet quality in closely related reef fishes (McCormick 2003). Surprisingly, individuals on treatment colonies had a higher HSI than their control counterparts. This was unexpected given that reef fish often experience declines in condition following the loss of habitat (e.g. Pratchett et al. 2004, Berumen et al. 2005, Feary et al. 2009). Further analysis of behaviour revealed that *P. moluccensis* on treatment colonies were repeatedly biting on the dead coral branches at a rate of more than an order of magnitude higher than on live control colony branches. This suggests that individuals are supplementing their planktivorous diet with an alternate prey item living amongst the dead branches. I argue that the partial loss of live coral on treatment colonies created an opportunity wherein individuals gained access to a highly abundant food source in close proximity to adequate shelter from predators. The capacity of food augmentation to reverse negative effects of crowding has previously been demonstrated in zebrafish, where the addition of food pellets negated effects of high densities (Ramsay et al. 2006). This unanticipated consequence of habitat loss is an example of an edge effect due to complementary resource distribution in adjacent habitats along the edge (Ries et al. 2004, Ries and Sisk 2004), a process which is previously undescribed in the marine environment.

The unexpected results in this experiment highlight the complexity in impacts of habitat loss, which may include both negative and positive effects. In the case of *P. moluccensis*, which is primarily considered a planktivore, habitat degradation appears to have induced negative effects of crowding, while simultaneously improving food resources for the survivors. While this result is unexpected, it is not entirely unprecedented. Closely related damselfishes have previously been described to switch prey opportunistically (McCormick 2003) and species with the ability to utilise resources both within the remnant live habitat and recently disturbed habitat may be advantaged by a disturbance event (Debinski and Holt 2000). Although the food source accessed on the dead coral branches was not identified in this experiment, a recent study points to a valuable prey item within the dead branches. Kramer et al. (2014) has demonstrated three orders of magnitude higher abundance of crustacea on dead coral branches compared to live coral branches. Given that coral rubble maintains comparable quantities of small crustaceans it would suggest that this supplemental food source is permanently available in dead coral habitat. However, *P. moluccensis* is an extreme habitat specialist (Bonin 2012) that relies on live coral as shelter from predators, so individuals would only be able to benefit from this new food resource in dead coral if it was adjacent to suitable shelter amongst live coral branches. This type of edge effect has been extensively studied in forest ecosystems, and hinges on a degree of flexibility in the resource requirements of the affected species (Ethier and Fahrig 2011). While *P. moluccensis* may be a habitat specialist, it appears that they have more generalist feeding preferences, supporting the hypothesis that resource-generalist species benefit from their flexibility in resource use because it allows them to extract resources from an altered environment (Ries and Sisk 2004). It is crucial to note however that the dependence on live coral as a shelter suggests that these individuals are unlikely to be able to benefit from this advantage if whole coral colony mortality occurs.

Habitat loss and degradation is a pervasive issue in ecosystems globally, and it is becoming increasingly important to understand how organisms are affected by disturbances. Not only to document their decline, but also to be able to predict how they may respond to future disturbances. In this study I have described how the loss of 60% of live habitat on a coral colony generates a temporary increase in the total abundance of a common reef fish, *P. moluccensis* on coral colonies. I argue that the subsequent decline in densities is regulated by increased aggressive interactions on crowded treatment colonies. Contrary to my prediction I demonstrate that surviving individuals on treatment coral colonies have better body condition than their control counterparts. I suggest that this may be due to a complementary edge effect where the degradation event has introduced an easily accessible new food source within the degraded patches. These results highlight the complex nature of animal responses to habitat degradation and illustrate the importance of including multiple facets of organism fitness when evaluating consequences of habitat loss. Importantly however, the increased body condition described in surviving individuals suggests a level of resilience that may hint at a potential avenue for recovery from moderate disturbances in coral reef ecosystems.

Chapter 4

Loss of live coral, not shelter space, compromises sheltering behaviour in coral reef damselfish

4.1 Abstract

Tropical reefs have experienced an unprecedented loss of live coral in the past few decades and the biodiversity of coral-dependent species is under threat. Many reef fish species decline in abundance as coral cover is lost, yet the mechanisms responsible for these losses are largely unknown. A commonly hypothesised cause of fish decline is the loss of shelter space between branches as dead corals become overgrown by algae. This study aimed to test this hypothesis by quantifying changes in sheltering behaviour of a common damselfish, *Pomacentrus moluccensis*, following the death of their coral colony. Recently dead colonies of *Acropora* were allowed to accumulate algae and invertebrates over a period of five weeks. Groups of *P. moluccensis* were placed on either live or dead coral colonies, startled using a visual stimulus and their sheltering responses compared. *P. moluccensis* stopped sheltering amongst the coral branches immediately following the death of the coral, despite ample shelter. Instead, most individuals swam away from the dead coral into the surrounding water where they were exposed to predators. I argue that live coral is a necessary cue that elicits the appropriate behavioural response to potential predators. The disruption of this link poses a severe threat to coral-associated fishes on degrading reefs.

4.2 Introduction

Global ecosystems have been experiencing an unprecedented loss of habitat in the past century, primarily caused by human activity. Habitat loss can directly lead to population declines as a demographic response to the loss of critical resources, such as food or shelter (Vitousek et al. 1997). However, animal responses to altered environments are often first evident from changes in behaviour (Wong and Candolin 2015). Behavioural responses can be key factors underpinning the resilience of species to or recovery from environmental change (Van Buskirk 2012). Behaviour can ameliorate the effects of habitat degradation provided species have the capacity to respond in a way that improves their chances of survival. Unfortunately, an increasing number of studies have demonstrated that habitat loss and degradation alter key signals or cues used by animals in vital decision-making. In the most extreme scenarios, complete habitat destruction leads to the loss of both the cue and the habitat simultaneously, which in most cases would enable the animal to make accurate decisions about alternate habitat use (Pulliam and Danielson 1991). Anthropogenic disturbance and changes in land-use have also led to situations where altered or introduced environments mimic cues emitted by natural environments, which can elicit a maladaptive behavioural response ('ecological and evolutionary traps', Dwerrnychuk and Boag 1972, Schlaepfer et al. 2002). For example, many bird species are attracted to nest on agricultural pastures because they are structural similarity to native grasslands (Schlaepfer et al. 2002). Chicks in these nests have low survival rates compared to nests in native grasslands because mechanical harvesting of crops often occur before the chicks have fledged (Bollinger et al. 1990). Finally, habitat degradation can lead to the degradation, alteration or loss of the cue itself, without altering the quality of the resource provided by the habitat (Gilroy and Sutherland 2007). Despite the ubiquity of habitat degradation in global ecosystems, few studies have established mechanisms underpinning the threat to species, whether they are the direct effects of habitat loss on vital resources, a disruption of appropriate behavioural responses or a combination of these factors.

Coral reef ecosystems have been experiencing an unprecedented loss of hard-corals in recent decades, with an average 20% decline in live coral cover on reefs worldwide (Gardner et al. 2003, Bruno and Selig 2007, Wilkinson 2008, De'ath et al. 2012). Live corals provide the majority of structural complexity on coral reefs, and degradation of these biogenic habitats may negatively impact both the behaviour (McCormick 2009, 2012) and abundance (Garpe et al. 2006, Wilson et al. 2008) of fishes that rely on coral reef habitat. Typically there is an almost immediate decrease in the abundance of obligate coral-associated species, specifically coral-feeding (Bouchon-Navaro et al. 1985, Sano 2004) and coral-dwelling fishes (Jones et al. 2004), when live coral declines. For species that rely solely on live coral tissue as a food source, like many butterflyfishes (Chaetodontidae), declines in abundance appear to result from loss of food resources as the coral tissue dies (Williams 1986, Pratchett et al. 2004, 2006). However, although declines in these specialised corallivores are relatively well understood, there is limited understanding of the mechanisms causing a decline in live-coral dwellers. It is unknown whether these directly reflect increased mortality associated with declining resources, behavioural responses that follow from changing environmental cues, or a combination of these factors. First, live coral dwellers could be directly affected by habitat loss through increased competition for resources and elevated risk of predation (e.g. Boström-Einarsson 2014). Second, behavioural responses can be altered through the disruption of the appropriate cue (Schlaepfer 2002). Finally these alternate scenarios could both be impacting the affected species simultaneously. While these scenarios have been independently demonstrated in reef fishes, they are likely to occur simultaneously, however their interaction remains untested.

One possible explanation for the decline in coral-dwelling reef fish following habitat degradation could be the loss of shelter spaces among coral branches, which would leave these fish more vulnerable to predators (e.g. Garpe et al. 2006, Graham et al. 2006, Coker et al. 2009). Live corals, especially structurally complex species, provide critical shelter space from predators, and many habitat disturbances, (e.g. coral bleaching, crown-of-thorns seastar outbreaks, poor water quality) gradually degrade the quality of this shelter. Initially when the living coral tissue is lost, there is little change to the shelter available to coral-dwellers. In the months following tissue loss, structural degradation begins to occur through the settling of algae, sponges and invertebrates that overgrow the coral skeleton and reduce shelter spaces available between the branches. Eventually borers and grazers will contribute to the breaking down of the coral skeleton into rubble (Hutchings 1986). Given the importance of live coral as a shelter site from predators, it is not surprising that the effects of competitive interactions are exacerbated following coral mortality (McCormick 2012, Boström-Einarsson et al. 2014, Bonin et al. 2015). For example coral-dwelling reef fish compete for access to refuge between the branches, and suffer increased mortality through predation when this resource is limited (Holbrook and Smith 2002, Ford and Swearer 2013). Consequently, declines in shelter space due to colony overgrowth may increase predator-induced mortality and exacerbate competition for shelter, explaining the observed declines in coral-dwellers soon after disturbances that cause live coral loss.

While the ultimate reason for avoiding a dead coral may be a lack of shelter space, evidence suggests the live coral provides an important cue to inform behavioural decisions about habitat suitability. While a majority of reef fish recruit primarily to live corals (Jones et al. 2004, Coker et al. 2012a) adults often maintain a close association with living coral colonies. For example, the common reef fish *Chrysiptera arnazae* (previously *C. parasema*, Allen et al. 2010) migrated into remnant live portions of partially degraded coral colonies following habitat degradation (Boström-Einarsson et al. 2014). This occurred immediately following the loss of the living coral tissue when shelter space had not yet been reduced. Similarly a close congener, *P. amboinensis*, has been shown to vacate recently dead corals in search of healthy colonies nearby, but in contrast does not vacate colonies that are alive or bleached (Coker et al. 2012b). While our knowledge of the resource requirements for obligate corallivores forms a base for understanding the mechanisms responsible for their decline, despite more than half a century of research on coral reef fishes (Hixon 2011) we still do not fully understand what benefits many fish gain from their close association with live coral. However, this dichotomy of cues provided by the living coral tissue and the structure of the coral skeleton provides an excellent setting for testing how behaviour is affected by the loss of a presumed cue (living coral) when the benefit remains (shelter within branches).

Anthropogenic impacts on coral reefs are increasingly being traced to altered physiological processes that influence behaviour, which may occur prior to any loss of resources (Wong and Candolin 2015, Nagelkerken and Munday 2016). For example, changes in temperature (Biro and Stamps 2010), acidity (Domenici et al. 2012, Munday et al. 2012) and sediment loads (Wenger et al. 2012a, Wenger and McCormick 2013) are known to affect key behavioural decisions that negatively influence survival, including habitat selection (Munday et al. 2009, Wenger et al. 2011) and predator avoidance (Munday et al. 2010, Dixson et al. 2010a, Wenger et al. 2012b). Recent studies have suggested that the loss of live coral itself can independently influence the behaviour of reef fishes, altering the strength of aggressive interactions (e.g. McCormick and Weaver 2012, Boström-Einarsson et al. 2014) and risk assessment (Lönnstedt et al. 2013). A declining amount of live coral habitat may furthermore induce high levels of intraspecific competition, as individuals within the same species are likely to have similar resource requirements (Bonin et al. 2015). Given the wealth of evidence that reef fish behaviour may be affected by habitat degradation, and the importance of shelter space provided by coral colonies it is surprising that no study to date has evaluated how sheltering behaviour is affected by coral mortality.

The aim of this study was to test how the sheltering behaviour of a common reef damselfish, *Pomacentrus moluccensis*, is affected by the degradation of their coral colony host. By focusing on how behaviour changes at different stages of habitat degradation I could test the link between changes in behaviour, loss of coral tissue, and ultimate changes to shelter availability. To address these questions I performed a startle experiment, where groups of *P. moluccensis* on coral colonies were exposed to a darting object and subsequent sheltering behaviour was recorded. The trials were conducted over the course of seven weeks to capture a gradient of habitat quality from healthy coral at the start, to dead but with shelter space unchanged (week 0) and through a progressive overgrowth of the colony by the accumulation of algae and invertebrates (week 1-5 post disturbance). To test whether there were intercohort size-based differences in response to shelter I included fish from two size groups; recently settled recruits and adults. Because outcomes of competitive interactions are generally mediated through size, where larger individuals or species are competitively dominant to smaller competitors (Robertson 1995, 1998), I hypothesised that smaller fish may be excluded from shelter by larger individuals.

4.3 Methods

Study species

The lemon damsel, *Pomacentrus moluccensis*, is an obligate coral-dwelling damselfish (Pomacentridae) often found in dense aggregations on plating *Acropora* coral colonies on shallow reefs. They are known to retreat into the branches of their coral colony hosts to escape predators or other perceived threats (Beukers and Jones 1998). Given that competitive dominance is primarily size dependent (Robertson 1998) I size matched fish into groups of large and small fish to evaluate whether there is a intercohort difference in access to shelter. I collected *P. moluccensis* in two size classes: 10-15mm (mean 13.4 mm ±0.04 SEM), representing recently settled fish (< 1 week post settlement) and 20-25mm (mean 22.6 mm ±0.07 SEM) representing young adults with a close association to individual coral colonies. Fish were collected using a dilute solution of clove oil (a light anaesthetic) and hand nets, and placed in a plastic bag. Individuals were allowed to recover from handling stress in the plastic bag for a minimum of one hour with frequent water changes.

Experimental protocols

I used an underwater "startle" experiment to test how sheltering behaviour of *P. moluccensis* was affected by the degradation of their coral habitat over a seven week period. Coral colonies were degraded and the behaviour of groups of *P. moluccensis* was recorded through time as colonies gradually accumulated algae and invertebrates. Thirty corymbose *Acropora* colonies were collected from the exposed reef crest of platform reefs in Kimbe Bay, Papua New Guinea (150°05'E, 5°25'S) and transported to the study reefs. Colonies were of similar size and branch morphology (mean size 754 cm^2, ± 32.9 SEM). Two cages were constructed of PVC pipes (90cmWxHxD) covered in a thin mesh that allowed flow of water in and out of the cage. The cages served multiple purposes by protecting the fish from predators and restricting external visual disturbances. Cages were placed on flat sandy bottom in ~3 m of water, approximately 1 meter apart. Two opposing sides had entry and exit holes for a startle device to pass through. A 20cm black torpedo-shaped object was rapidly pulled through the cage to startle the fish. The shape and size of the object resembled a potential predator.

Coral colonies were placed inside experimental cages on a small rubble base and groups of six *P. moluccensis,* (three small and three large) were placed on colonies. Fish were allowed to habituate to their new surroundings for 20 minutes. The startle device would then be pulled through the cage once, and the fish removed from the cage. Each group of fish was only tested once to avoid learning from previous trials. Each startle trial was recorded using two video cameras mounted directly above and to the side of the coral colony. Recordings were played back in slow motion and sheltering behaviour was recorded. Sheltering behaviour was scored in three mutually exclusive and exhaustive categories: 1) retreat amongst coral branches, 2) shelter on base of colony, and 3) swimming off the colony into the surrounding water (unprotected). The size and position of each fish was recorded when the startle object was immediately above the coral colony. The intercohort test will investigate whether there are any differences in access to shelter between large and small fishes. However, because I did not complete the reciprocal experiment where equal densities of a single size fish were startled I cannot exclude innate differences in behaviour between juvenile and adult fish. Finally, to analyse habitat association I recorded the number of fish within a 5 cm distance of the coral colony immediately before the startle device entered the cage.

After the first set of trials were conducted, 25 colonies were placed in cages on the reef containing multiple individuals of the corallivorous crown-of-thorns starfish *Acanthaster planci.* The starfish were allowed to consume 100% of the live coral tissue of these treatment colonies (~3 days). The colonies were thereafter placed in a shallow (~1.5-2 m deep) reef flat area where they were allowed to accumulate algae and settling invertebrates for the duration of the experiment (Figure 4.1). The remaining five colonies were placed in cages without *A. planci* for three days to control for handling stress and were thereafter placed in the same shallow location as treatment colonies. I recorded no mortality, injury or disease in control colonies throughout the experiment. Trials were thereafter conducted weekly for a total duration of 7 weeks (before degradation, day of degradation and week 1-5 post-degradation). 24 trials were conducted each week (9 control trials and 15 treatment trials), using a random subset of 5 treatment and 3 control colonies. Each colony was used for three sequential trials using a different group of fish.

Branch space

The space available between branches was evaluated weekly by measuring the mean inter branch space on control and treatment colonies. Height (H), width (W) and depth (D) was measured of 10 randomly selected inter branch spaces using Vernier calipers. The product of these three measurements (H × W × D) gives an estimate of the total space available to fish hiding amongst the coral branches. Furthermore, a subset of five colonies (three treatment, two control) was photographed using standard photogrammetry (structure from motion) methods for development of three-dimensional models (e.g. Burns et al 2015, Lavi et al 2015). I expected to measure a reduction in volume of space available between the branches from a series of three-dimensional models of the coral colony through time. Dense cloud mesh and textured models were produced using

PhotoScanPro. Unfortunately both of these methods failed at producing reliable estimates of shelter space available and are therefore not discussed further.

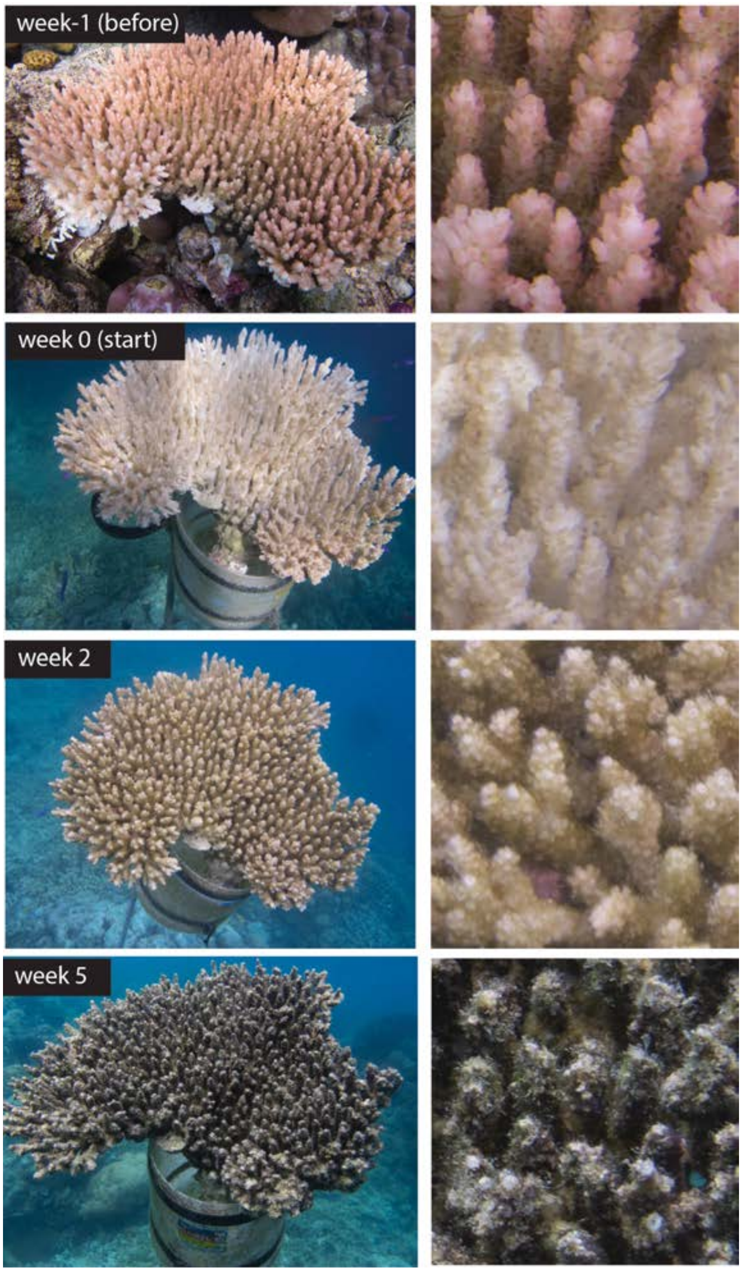

Figure 4.1 The progression of a treatment colony from live (week-1), immediately after degradation by COTS was complete (Week 0),followed by the accumulation of a thin layer of algae (week 2) through to a dense turf algae growing on the branches (Week 5). Right hand pictures depicts an area approximately 50mmx50mm (HxW).

Statistical analysis

I analysed whether the choice of sheltering position (i.e. sheltering among the branches, on the base or off the colony) differed between control (live) and treatment (increasingly degraded) using a log-linear analysis. The model included thee factors: sheltering positions (3 categories: sheltering among the branches, on the base or off the colony), colony type (2 categories: control and degraded) and trial week (7 categories: before, start and week 1-5 post disturbance). The saturated model analyses the frequency (i.e. sum of *P. moluccensis* from each replicate trial) in each possible combination of the three factors and their interactions.

Model selection was achieved by backwards elimination of terms in the model, and goodness-of-fit assessed using likelihood ratios. A signifiant Chi-square test between a reduced and full model indicates that the elimination of the excluded factor in the reduced model is not warranted. The most parsimonious model (i.e. the least complex model that best accounts for the variances in the observed frequencies) was then selected based on goodness-of-fit results. The use of a time factor does not necessitate a repeated measures analytical method given that I used a new group of fish during each trial event, and randomly picked a colony each trial from a larger set of possible colonies. No analyses violated assumptions of expected frequencies of >5 in 80% and >1 in 100% of categories for log-linear analyses. All statistical analyses were conducted within the R-environment (R Core Team, 2016). A second log-linear analysis was performed to evaluate whether habitat association differed between control and treatment colonies over the trial period. I analysed whether the number of *P. moluccensis* present immediately prior to the startle event differed between colony types (2 categories: control and treatment colonies) over time (7 categories: categorical factor, 7 levels), and the interaction between the two main factors. Finally, a third log-linear analysis was performed to evaluate any size based differences in the number of fish with access to shelter space between the branches of the coral colony. The count of *P. moluccensis* sheltering amongst branches could then be evaluated for differences in body size (2 categories: large, small), trial week (7 categories) and colony type (2 categories: control and treatment).

Effect sizes were calculated for all analyses (sheltering position, size effects and numbers present pre-startle) as partial eta-squared (η_P^2) which can be interpreted as the unexplained variation in the dependent variable, plus the variation explained by the factor in question. This allows comparisons across different studies (i.e. meta-analyses), which may contain additional factors or covariates. Assumptions of independence and normality of residuals were examined visually. Tukeys HSD pairwise posthoc tests were used to investigate underlying patterns in the data.

4.4 Results

Sheltering position

*P. moluccens*is were much more likely to shelter amongst the branches of live colonies, compared with the dead colonies (average number of *P. moluccensis* sheltering in between branches on live colony 5.2±0.16 SEM, dead colony 1.4±0.2). The majority of individuals stopped sheltering in corals that were recently dead, instead choosing to move off colony. *P. moluccensis* was more likely to move off the dead coral colonies in response to the stimulus, compared to live colonies (Treatment colony 3.9±0.23 SEM, control colony 0.7±0.14). Finally, few individuals chose to shelter on the base of the colony in either control or treatment colonies (control colony 0.1±0.06 SEM, treatment colony 10.6±0.12). The saturated model was the most appropriate model to compare the frequency of *P. moluccensis* in each category. A significant three-way interaction between all main factors (colony type, sheltering position and trial week) influenced the frequency of *P. moluccensis* in each category (Table 4.1). This suggests that the number of *P. moluccensis* sheltering in each position (branch, base or off colony) varies between colony types, over the trial period. The three-way interaction was driven by a decline in fish sheltering between the branches on treatment colonies, concomitant with an increase in individuals that exhibited no sheltering behaviour. A majority of fish sheltered amongst branches when the colony was healthy and this behaviour persisted through time (Figure 4.2a). However, the number of fish sheltering amongst branches declined drastically immediately following the degradation of the colony on treatment colonies (Figure 4.2a). In contrast, few fish avoided sheltering altogether on control colonies, while numbers outside of shelter increase through time on treatment colonies (Figure 4. 2b). Finally, fish were unlikely to seek shelter at the base of the colony at any time, with little variation over the course of the experiment (Figure 4.2c)

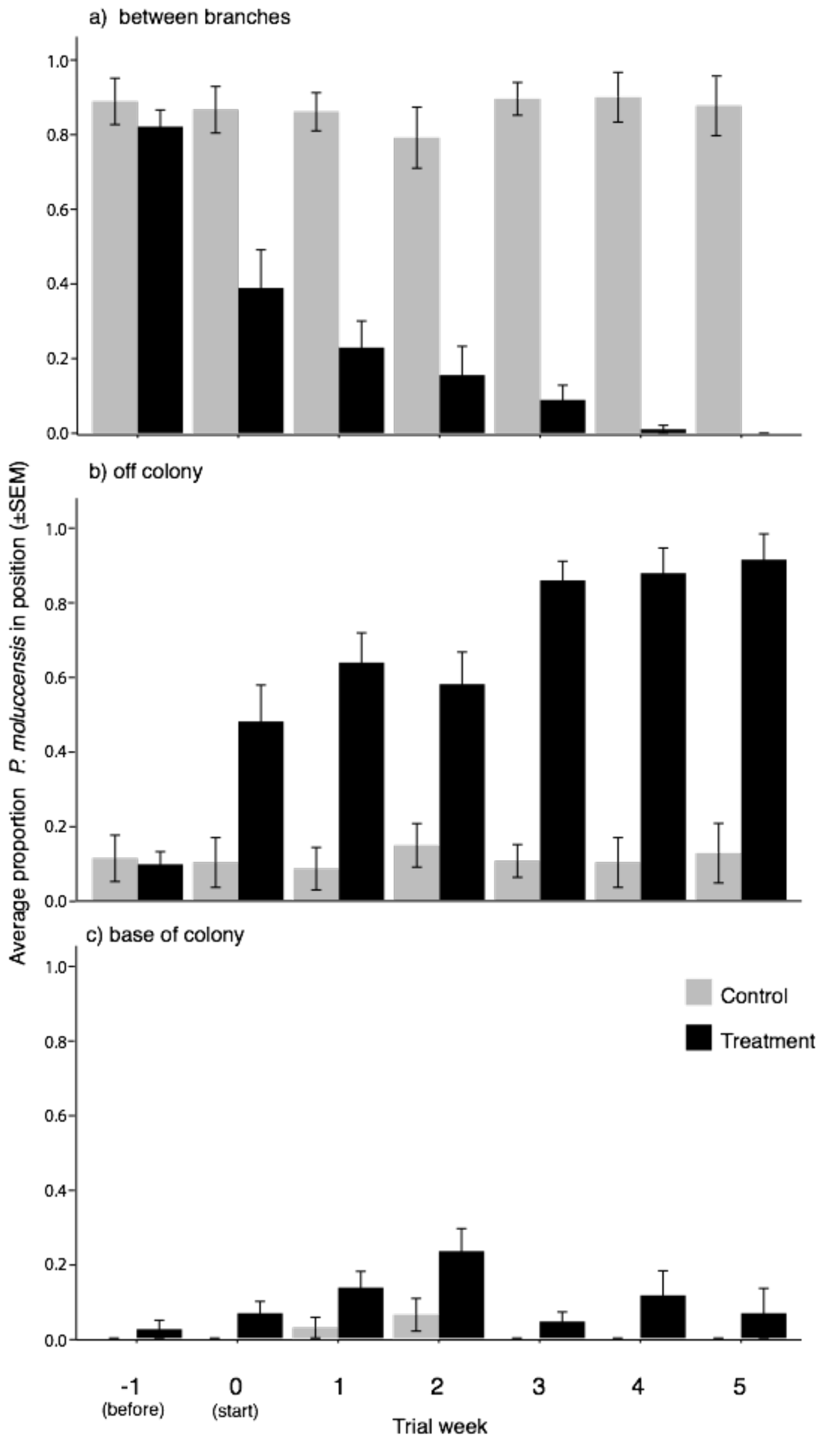

Figure 4.2: Average proportion of *Pomacentrus moluccensis* recorded either (a) sheltering between coral branches, (b) swimming off the coral colony (i.e not sheltering), and (c) at the base of the colony following a visual startle. Trials were conducted on either control (100% live) colonies (grey bars) or treatment colonies (black bars). Treatment colonies were 100% live in week -1, tissue recently dead (same day) in week 0, and with gradually accumulating algae and settling invertebrates in week 1-5. Each trial tested 6 *P. moluccensis* in a group, with 9 control and 15 treatment trials each week. Error bars indicates SEM.

Table 4.1: Log-linear analysis of sheltering position (three levels: sheltering amongst branches, on the base of the colony or off the colony) of *P. moluccensis* in a startle experiment using two types of colonies (degraded and control), over 7 trial weeks. The level of degradation through overgrowth by algae and invertebrates increased on treatment colonies over time, while control colonies remained 100% live throughout the experiment.

	Df	Deviance	Residual df	Residual Deviance	Chis-quare p- value
NULL			41	1110.01	
Colony type	1	141.42	40	968.59	<0.001
Sheltering position	2	332.23	38	636.36	<0.001
Trial Week	6	4.89	32	631.46	0.56
Colony type × sheltering position	2	316.64	30	314.83	<0.001
Colony type × Trial week	6	18.51	24	296.32	<0.01
Sheltering position × Trial Week	12	227.62	12	68.7	<0.001
Sheltering position × Colony type × Trial Week	12	68.7	0	0	<0.001

Pre-Startle position

A majority of *P. moluccensis* individuals were present on control colonies prior to the startle event, while association with the coral colony was more varied on treatment colonies (Figure 4.3). There was a significant interaction between trial week and colony type (Table 4.2) indicating that the effect of colony type on the number of *P. moluccensis* present on the colony prior to the startle event varied throughout the trial weeks.

Inter-cohort differences

There was no evidence of a size-based or intercohort difference in the fish that accessed prime shelter habitat amongst the branches of the coral colony. This was reflected in a lack of significance of any interactions containing the size factor (2-way interactions with trial week and colony type, and the 3 way interaction containing all factors). In addition, the main factor of size was not significant in the reduced model (log-linear analysis, **Chi-square** =363.1, df=299, p=0.239). Remaining factors (Main factors trial week and colony type, and the interaction between the two) were all significant, reflecting the changes in sheltering position described above. A large proportion of categories had expected frequencies below 5, therefore violating the assumptions of log-linear analysis. This results in a loss of statistical power, however visual analysis of the data do not indicate any differences between large and small fish in their access to sheltering space amongst the branches (Figure 4.4).

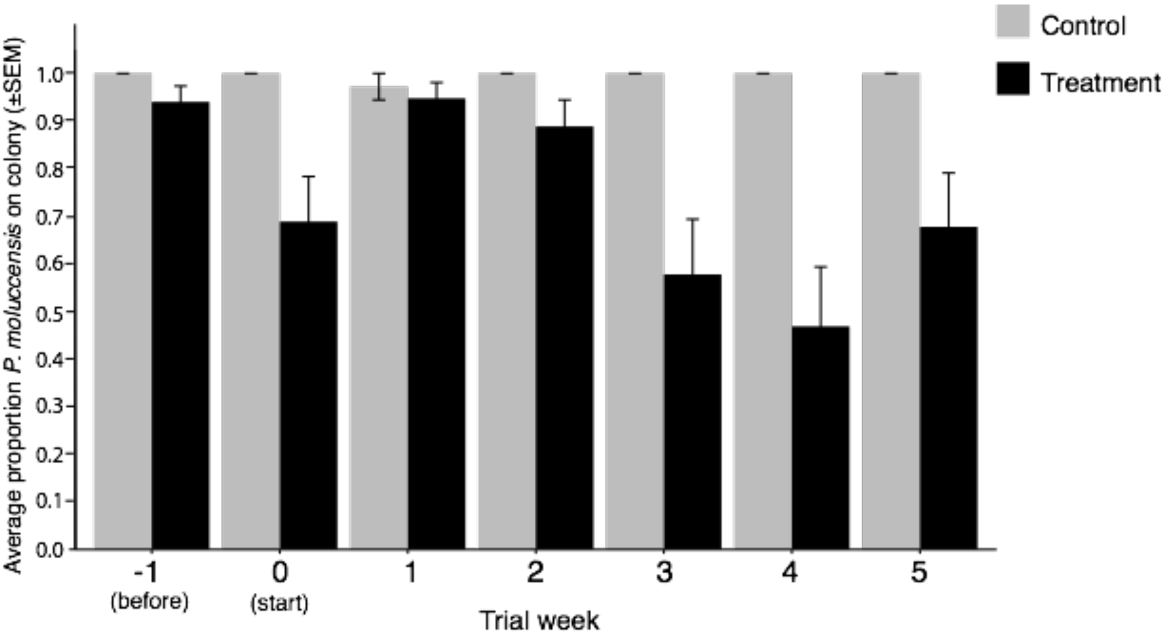

Figure 4.3. The average proportion of *P. moluccensis* present on the control (grey bars) and treatment colonies (black bars) immediately before the startle event occurred over the 7 week trial period. Each trial tested 6 *P. moluccensis* in a group, with 9 control and 15 treatment trials each week. Error bars indicate SEM.

Table 4.2: Log-linear analysis of colony association prior to startle trial. Frequency of *P. moluccensis* present prior to startle depending on colony type (degraded and control), over the course of the experiment (Trial week: 7 levels). The level of degradation through overgrowth by algae and invertebrates increased on treatment colonies over time, while control colonies remained 100% live throughout the experiment.

	Df	Deviance	Residual df	Residual Deviance	Chi-square p- value
NULL			13	100.836	
Colony type	1	55.365	12	45.471	<0.001
Trial Week	6	31.038	6	14.433	<0.001
Colony type × Trial week	6	14.433	0	0	0.025

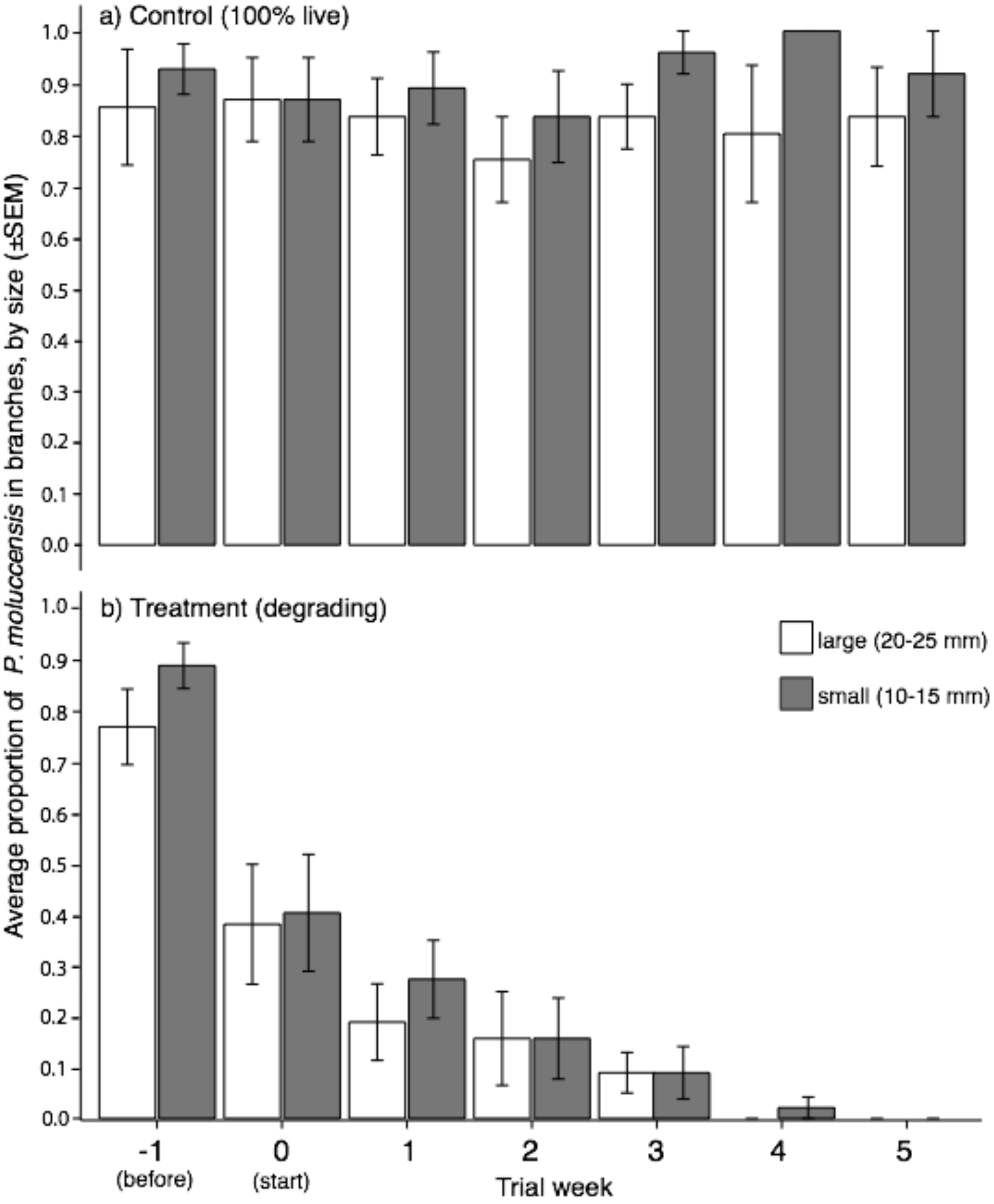

Figure 4.4: Comparison of the average proportion (out of 3 in each size class per trial) of large (20-25mm, white bars) and small (10-15mm, grey bars) *P. moluccensis* sheltering within the coral branches on control (a, live) and treatment (b, degraded) over seven trial weeks. Treatment colonies gradually accumulated algae, sponges and settling invertebrates during the five weeks following the death of 100% of the colony tissue. Error bars indicate SEM.

4.5 Discussion

This study has demonstrated that sheltering behaviour of *Pomacentrus moluccensis* is fundamentally and rapidly altered by coral mortality. Following the degradation of their colony, a majority of individuals stopped sheltering altogether and instead moved to high-risk locations off the colony. In contrast, most fish on control colonies sheltered between coral branches when startled. Given that behavioural changes occurred immediately following the degradation event, I argue that this is not a result of declining shelter space available between degrading branches, but rather a direct reaction to the loss of live coral tissue. This presence of live tissue appears to be necessary to elicit the coral-shelter seeking behavioural response, independently of any change in the quality of the shelter *per se*. The disruption of this critically important behaviour suggests a potential mechanism underlying the loss of reef fishes following habitat degradation.

The loss of live coral from coral bleaching, diseases and outbreaks of coral predators tend to leave the structure of the coral skeleton intact, only removing the living coral tissue. This initial degradation of the reef habitat is often followed by a rapid decline in fish species that either feed on live coral tissue (Bouchon-Navaro et al. 1985, Pratchett et al. 2006, Wilson et al. 2006) or have little redundancy in their resource requirements (Munday 2004b, Munday et al. 2008). A second stage of degradation occurs as space between the branches of coral colonies is lost within weeks of the degradation event, due to settling of algae and invertebrates. Finally the reef is reduced to rubble in a process expedited by invertebrate borers and storms over an estimated time-span of 4-10 years (Sano et al. 1987, Sheppard et al. 2002). The second and third degradation stage are often hypothesised to be the reason for a gradual decline in coral-dwelling fishes, because refuges from predators are lost as the structural complexity of the coral habitat is lost (Pratchett et al. 2008, Bonin et al. 2009a, Graham et al. 2009). While this hypothesis is ubiquitous in the coral reef fish literature, it has not previously been tested. Here I show it may be more linked to the loss of coral tissue, rather than the longer-term loss of shelter.

In this study I demonstrate that changes in the sheltering behaviour of a small bodied damselfish start occurring prior to any changes in the amount of space available. After only one week, at which stage the coral branches are only covered in a thin layer of algae, a majority of *P. moluccensis* were not seeking shelter in between coral branches in response to a threat, but were exposed off the colony. The startle experiment indicated that this was due to a decreased association with the habitat even prior to the startle event. This suggests *P. moluccensis* no longer received the appropriate cue from the dead coral habitat, and therefore failed to behave appropriately, i.e shelter amongst the branches from the approaching threat. This is similar to the concept of "evolutionary traps", where a cue prompts a behaviour that has been rendered maladaptive by environmental change. Prior to disturbances organisms respond to cues in a way that is adaptive in their natural environment (Sih et al. 2011) but environmental change can decouple the cue-response relationship such that the response is now maladaptive (Schlaepfer 2002, 2010). While superficially similar, this study describe a corollary to evolutionary traps, where the cue has been altered, but the benefit from acting on the cue remains. If living coral is the cue to indicate a suitable shelter space, then the death of the colony prevents the appropriate behaviour (ie sheltering within branches) despite there still being space available for refuge. Gilroy and Sutherland (2007) proposed that this kind of scenario would be common almost decade ago, yet it remains undescribed in the literature. They hypothesised that minor changes to habitat may render it less attractive to animals, while the underlying habitat quality remains unaltered. A dead coral may not fit into the description of an ‘undervalued resource’ for very long, however this work highlights the complex flow-on effects of habitat degradation and loss on ecological communities.

While the nature of the cue provided by corals may not be fully understood this study suggests that the absence of live coral tissue fails to elicit the correct behavioural response to a potentially life threatening risk. This begs the question; which cue-response relationship would cause individuals swim past perfectly suitable habitat in favour of riskier locations, and fail to shelter from predators? Currently, there are three potential reasons offered in the literature: loss of camouflage from predators and changes to the visual and olfactory perception of habitat. A recently dead coral colony may leave reef fish vulnerable to predators as the bright white coral skeleton provides inadequate camouflage to the brightly coloured fish (McCormick 2009). This suggests that the visual cue of a live-coral signals a safe place to hide from predators. Indeed this has been demonstrated in aquaria where fish on bleached corals were twice as likely to be attacked by a predator compared to live corals (Coker et al. 2009). This does however not appear to translate in the natural environment. A study conducted during a natural degradation event of a large reef area demonstrated that survival trajectories of fish on bleached (coral tissue still alive but lacking pigmentation) and dead (coral tissue dead, only white skeleton remaining) are significantly different (Bonin et al. 2009a). In fact the fish on bleached corals did not suffer higher mortality than their counterparts on live corals. Similarly fish on live and bleached corals show the same level of fidelity to their coral habitat while individuals on dead corals are inclined to migrate in search for higher quality habitat (Coker et al. 2012b). These emigrations increase vulnerability to predation as fish are forced to leave the shelter of coral hosts. Combined, these studies suggest that changes in behaviour in relation to dead coral habitat are not camouflage related, but rather responses to a cue used to identify suitable habitat.

Avoidance of dead coral may occur because it does not look like coral anymore to the fish, however no studies to date have directly investigated visual effects of habitat degradation to reef fishes. If the lack of pigmentation affects the visual assessment of dead coral colonies, then reactions should be similar between bleached and recently dead corals that have both lost their symbiotic algae and pigments (Brown 1997). In aquarium trials *P. moluccensis* selects live coral over bleached and dead coral when allowed to use visual cues only (McCormick et al. 2010) however such a cafeteria-style array may not be available in a reef environment. Indeed, during an ongoing bleaching event Bonin et al. (2009a) did not record any difference in *P. moluccensis* recruitment or persistence on bleached and live colonies. This suggests that while fish favour live coral when given the choice in a side-by-side comparison, they are unlikely to detect a difference between live or bleached coral on the reef. Importantly, the literature suggests that this misidentification does not translate into a demographic consequence.

Reef fish behaviour is often mediated by olfactory stimuli such as the smell emitted by a predator and injured conspecifics (e.g. Atema et al. 2002, Dixson et al. 2010b, Holmes and McCormick 2010, Vail and McCormick 2011). A third hypothesis on why reef fish may avoid dead corals is that the chemical cocktail emitted by a dead coral may hinder the detection of predators (McCormick 2009). The smell of a dead coral colony, even when heavily diluted, is strong enough to obstruct alarm cues and cause congener *Pomacentrus amboinensis* to cease predator-avoidance behaviour (Lönnstedt et al. 2013, McCormick and Lönnstedt 2016). Perhaps the different olfactory signal of a dead coral colony is enough to deter *P. moluccensis* from seeking refuge amongst the colony branches.

While the exact reason why the fish avoid dead coral colonies remains unclear, this experiment suggests that they have lost the association with the habitat as a potential refuge site. A loss in association with degraded habitat has previously been described in *P. moluccensis* (Booth and Beretta 2002, McCormick et al. 2010, Coker et al. 2012b) and for closely related damselfishes (Boström-Einarsson et al. 2013, 2014) however this is the first time it has been demonstrated that this behaviour persists during predator evasion. The similarities in habitat use between large and small fish suggests that the absence of sheltering behaviour itself is not due to resource limitation or competitive interactions. If the number of shelter sites were limited I would expect larger fish to dominate intraspecific interactions and gain preferential access to shelter (Robertson 1998, Poulos and McCormick 2015).

Changes in sheltering behaviour of *P. moluccensis* described in this study indicate that the decline in coral-dwelling fishes following habitat degradation may be due to a proximate and an ultimate cause. By teasing apart effects of loss of live coral itself from the loss in structural integrity this study has demonstrated that it is the absence of live coral tissue that is the proximate factor in the decline of *P. moluccensis* following habitat degradation. Cues received from live coral tissue may signal a suitable place to hide from predators, and the absence of these cues stops *P. moluccensis* from using the refuge despite it still being available. In a sense, the available shelter space between recently dead coral branches is an ‘undervalued resource’ (sensu Gilroy and Sutherland 2007), albeit temporarily. While the ultimate cause may be increased mortality due to a lack of shelter space, the proximate cause is the loss of the behavioural cue that elicits the correct predator evasion strategy.

In conclusion, this study has revealed the early disruption of sheltering behaviour in reef fish following the death of branching corals, likely leading to immediate predation-induced mortality following habitat degradation. This is the first study to evaluate sheltering behaviour of reef fishes for a biological disturbance such as crown-of-thorns outbreaks or coral bleaching. The early onset of behavioural change highlights the importance of live coral tissue itself, and how the loss of this live tissue fundamentally alters escape responses. The absence of sheltering behaviour offers a potential pathway to understanding the decline in reef fish (other than corallivores) following habitat degradation. In the context of evolutionary traps, this work highlights the consequences of anthropogenic disturbance on critical behavioural cues in the marine environment. The study adds to the growing body of work demonstrating that the disruption of natural behavioural processes may be more important than the direct loss of resources.

Chapter 5

Density dependent habitat selection in response to habitat loss in a coral reef fish

5.1 Abstract

Habitat loss and the associated declines in resource availability have far-reaching effects on ecological communities. In the early stages of habitat loss, individuals are often forced to crowd into the remnant high quality patches. However, the redistribution of individuals following disturbance may be governed by density dependent habitat selection, where the decision to join crowded populations in high quality patches or sparsely populated low quality patches depends on the relative fitness costs. Reef fishes are increasingly subject to declining availability of coral habitat, but the consequences of crowding and the potential for density dependent habitat selection in coral-associated fishes have not been examined. In this study I investigate whether habitat loss leads to crowding and experimentally test the role of density dependent habitat selection on the spatial distribution of a common coral reef fish, *Pomacentrus moluccensis*. Firstly, I identified reefs with a range of live and dead coral habitat, and recorded local densities of *P. moluccensis* on live and dead coral colonies. I found that *P. moluccensis* adults only used dead coral colonies when the average density of fish on live coral colonies were elevated, which only occurred on reefs where >50% of colonies were dead. I hypothesised that the loss of habitat causes crowding on remnant live coral until some fish are forced to occupy less preferred dead colonies. I then conducted a choice experiment to investigate if density dependent habitat selection was the mechanism underlying this pattern. When presented with the choice of two colonies, fish were more likely to choose a near empty alternate colony when the other colony was severely crowded with conspecifics (~317 fish

m^{-2}). Once adults begin using dead coral, conspecific attraction may secondarily contribute to high numbers of fish choosing low quality habitat. I argue that a scarcity of preferred live coral habitat and density dependent habitat selection explain the redistribution of fish on disturbed reefs, and may ultimately provide one explanation for population declines following habitat loss on coral reefs.

5.2 Introduction

A fundamental tenet of ecological theory is that the spatial distribution of individuals within a landscape is governed by the availability of resources. The theoretical model describing this pattern, the 'Ideal Free Distribution' (Fretwell and Lucas 1969), predicts that individuals will be distributed within a landscape to maximise their fitness (Morris 1987). In this model, individuals select a habitat based on the quality of that habitat, and distribution patterns reflect the quality and quantity of resources provided by habitat patches (Fretwell 1972). However, the value of a habitat will decline with increasing density, such that the more individuals access a certain habitat patch, the lower the quality of that habitat to each individual. Intraspecific competition within a patch reduces the amount of resources available *per capita*, causing individuals to choose the less crowded, lower quality patches once per capita resource availability becomes higher in those patches (MacArthur and Levins 1964). Through this process of 'density dependent habitat selection', individuals distributed according to the Ideal Free Distribution can access equal resources from habitat patches of unequal quality. There is increasing empirical evidence that habitat quality (e.g. Milinski 1979, Dreisig 1995, Mobæk et al. 2009, Bradbury et al. 2015) and density dependent habitat selection (e.g. Parker 1970, Bergman et al. 2007) play a major role in determining the distribution of species in heterogeneous landscapes. These processes may also be strongly implicated in species responses to habitat loss and fragmentation that is happening in almost all ecosystems.

Habitat loss and degradation are one of the most pressing threats to global species diversity and the persistence of threatened species (Vitousek et al. 1997, Brooks et al. 2002). These disturbances impact on species by causing a decline in and altering the spatial arrangement of critical resources. Habitat loss has the potential to influence the distribution of species towards a new ideal free distribution equilibrium in two stages. First, individuals who suffer the direct loss of their habitat are likely to migrate towards and crowd into remnant habitat patches (eg Chapter 3). Secondly, increased competition in remnant habitat patches reduces the quality of these patches to individuals, prompting them to choose alternate remnant habitat, or habitat of lower quality (density dependent habitat selection). While this sequence of events is predicted in models based on the Ideal Free Distribution (Pulliam and Danielson 1991), its role in determining responses to habitat degradation has never been explicitly tested.

In theory, density dependent habitat selection maximises the fitness of species in a heterogeneous landscape by ensuring that each individual gains the maximum resource available per capita (Rosenzweig 1991). However, this may only occur if degraded habitats are still providing sufficient resources to sustain individuals, albeit at a lower density. Density dependent habitat selection following habitat loss may become maladaptive if it forces individuals to incorrectly select an alternate habitat that ultimately is unable to provide the resources required for survival (Delibes et al. 2001, Kristan and William 2003). Modelling this scenario suggests that populations may be able to persist if lower quality habitat is lost, but can ultimately go extinct if high quality habitat is lost and the lower quality habitat is unable to sustain the population (Pulliam and Danielson 1991). These studies suggest that the persistence of populations following habitat loss will ultimately depend on the magnitude of the disturbance and the quality of remaining habitat.

Coral reef fishes are being increasingly subject to the loss and degradation of coral reef habitat through a range of anthropogenic processes. The majority of fish species on coral reefs are reliant on the structure provided by the hard coral matrix at some stage in their life cycle, either during recruitment as larvae (Jones et al. 2004, Coker et al 2013), as a food source (Cole et al. 2008, Pratchett 2004) or to seek refuge from predators (Holbrook and Schmitt 2002). There is increasing evidence that loss of corals is linked to declining reef fish biodiversity and reduced abundance of many coral-associated species (Graham et al. 2006, Jones et al. 2004, Wilson et al. 2006). However, the behavioural responses to declining coral cover and increasing spatial heterogeneity of reef habitats are poorly understood. In particular, the roles of crowding and density dependent habitat selection have not been investigated.

Small bodied reef fishes, such as the lemon damselfish, *Pomacentrus moluccensis* recruit as larvae to live coral, and spend the majority of their life in close association with living coral colonies (Bonin 2012). They use a combination of senses, including vision, smell and hearing, to identify suitable habitat (Atema et al. 2002, Tolimieri et al. 2000, Lecchini et al. 2005). Juvenile fish use these highly attuned senses to judge habitat quality, and have been shown to preferentially select coral habitats that are already inhabited by conspecific adults (Sweatman 1983, Booth, 1995). Moreover, both juvenile and adult *P. moluccensis* have been shown to preferentially select live corals over those that are dying or dead (Öhman et al. 1998, Feary et al. 2007). Coral-associated reef fishes, such as *P. moluccensis*, have the capacity to judge habitat quality and select particular habitats using cues from the environment, but their capacity to assess habitat quality based on conspecific density, and the consequences of such decisions for their distributions in degraded reef environments, remain unknown.

The aim of this study was to investigate whether habitat degradation leads to crowding and density dependent habitat selection in a common coral-associated reef fish species, *P. moluccensus*. I first analyse how the distribution and habitat use of *P. moluccensis* is affected by a large scale habitat degradation event and quantify the extent to which population density increases in remnant coral patches with increasing levels of disturbance. Secondly, I conduct a controlled choice experiment to test how habitat selection in juvenile *P. moluccensis* is influenced by both increasing conspecific density and the quality of the alternative habitat.

5.3 Methods

Study site and species

The two parts of this study, 1) documenting levels of crowding in response to coral loss and 2) the experimental test of density dependent habitat selection, were both conducted on shallow platform reefs in Kimbe Bay, Papua New Guinea (150°05'E, 5°25'S). Shallow reefs in the area have been under high pressure from the coral-reef eating crown-of-thorns seastar *Acanthaster planci* (COTS), one of the foremost threats to live coral cover in the Indo-Pacific region (Bruno and Selig 2007, De’ath et al. 2012, Pratchett et al. 2014). At the time of this study, in April 2013, an outbreak of COTS was underway on reefs in Kimbe Bay, with an overall average density of 2.6 starfish per 200 m^2 ± 0.34 SEM, far exceeding values typically used to describe an outbreak (0.3 starfish per 200m^2, Moran et al. 1992, 0.8 starfish per 200 m^{-2}; Pratchett 2005). Because *A. planci* consumes only the living coral tissue and leaves the colony skeleton intact, outbreaks of the starfish typically reduce live coral cover dramatically but leave the underlying structure of the habitat intact. Furthermore, COTS preferentially consume certain coral taxa (e.g *Acropora*) and avoid certain growth morphologies (e.g massive corals) over others (De'ath and Moran 1998, Pratchett 2010, Pratchett et al. 2014), resulting in a mosaic of dead and live corals. The Kimbe outbreak was characteristically patchy in nature, with densities reaching 46 COTS per 200 m^2 on the most severely affected reef areas, while some areas were only mildly affected. This patchiness in habitat disturbance created a gradient that I utilised in this study to explore the influence of habitat degradation on distribution patterns and habitat use by *P. moluccensis*.

The lemon damselfish *P. moluccensis*, is a common coral-associated reef fish. These fish recruit exclusively to live coral, and show strong selectivity towards corymbose and plating *Acropora* growth morphologies (Bonin 2012). They are highly sedentary and site-attached with typical home ranges rarely exceeding 1m (Booth 2016). This makes them highly amenable to experimental manipulation and also reduces their ability to relocate long distance if their local habitat is disturbed. They have previously been demonstrated to crowd into remnant live habitat following habitat partial loss of live coral (Chapter 3), and are therefore ideal candidates to test density dependent habitat selection.

Distribution and local density across a gradient of habitat damage

The local distribution of *P. moluccensis* across its primary habitat (i.e. plating *Acropora* colonies) was investigated during an outbreak of crown-of-thorns starfish. All available plating and corymbose *Acropora* colonies were surveyed within 50 × 2m (100 m^2) belt-transects (n = 49) along the exposed reef crest of 12 shallow platform reefs that varied in their degree of impact to the live coral habitat. The start of each transect was marked using a GPS, and transects were separated from each other by a minimum of 5 meters. Coral colonies were classed into four categories based on presence of *P. moluccensis* (occupied/unoccupied) and health of coral (live/dead). A number of coral colonies had sustained patchy damage, where parts of the colony remained live (21 out of a total 379 surveyed colonies). Given that *P. moluccensis* have been demonstrated to persist on coral colonies with ~60% dead coral (Chapter 3) those with >80% dead coral were scored as 'dead' while remaining colonies were scored as live. For occupied colonies, the number of resident damselfish were counted, with recruits identified based on their size (< 10 mm) and paler body colouration and counted separately from adults. Digital photographs were then taken directly above the surface of the colony (with ruler for scale) in order to estimate total fish density on each colony. Approximately 12 months after the initial surveys, I returned to each transect using GPS locations and conducted repeat counts of all *P. moluccensis* present. This allowed me to compare how the overall abundance of *P. moluccensis* was affected by the crown-of-thorns outbreak.

The proportion of dead colonies out of the total colonies on each transect varied substantially (i.e. from 0 to 92%) across the survey sites. Transects were therefore grouped into five categories that represented varying degrees of local habitat degradation for *P. moluccensis*: <10% dead coral (n=10 transects), 10-25% (n=7), 25-50% (n=6), 50-75% (n=18) and >75% dead coral (n=8). I then conducted a log-linear analysis to investigate whether the use of live versus dead colonies by *P. moluccensis* was influenced by the proportion of dead coral in the local area. To achieve this, all colonies used by *P. moluccensis* were categorised by colony type (2 levels: live or dead) and also the proportion of dead colonies at a transect level (5 levels: <10%, 10-25%, 25-50%, 50-75%, >75%). All expected cell counts exceeded five, and therefore satisfied assumptions of log-linear analysis. This resulted in a model evaluating differences in the number of occupied coral colonies depending on coral colony type, and proportion dead coral in the surrounding area, and the interaction between the two categories. Model selection was achieved by backwards elimination of terms in the model, and goodness-of-fit assessed using likelihood ratios.

The surface area of each colony was calculated using ImageJ (Schneider et al. 2012) in order to calculate a total density of *P. moluccensis* on each occupied colony. To evaluate whether the density of *P. moluccensis* that were using live coral colonies changed across locations that varied in the degree of habitat degradation in the local area, I compared the mean density of *P. moluccensis* on live corals across locations with <10%, 10-25%, 25-50%, 50-75% and >75% dead coral using a Kruskal-Wallis test. This non-parametric test was used to accommodate heteroscadicity that could not be resolved through transformations. Dunn's postdoc tests using the Benjamini-Hochberg correction were used to further investigate differences between categories (Benjamini and Hochberg 1995, Quinn and Keogh 2009). Finally, I was interested in whether habitat choices by adults would influence recruitment patterns of juveniles. To test this I pooled all counts of recruiting juveniles in to a 2 x 2 contingency table with two categories, colony type (2 levels: live and dead) and adult presence (2 levels, adult present/absent). I used a Pearson's Chi-squared test to analyse whether the frequency of recruiting juveniles on the two types of coral colonies (live and dead) was dependent on whether there was an adult present (2 levels, adult present/absent). Finally I compared the mean overall abundance of *P. moluccensis* at the study location at two points in time; April 2013 (start of outbreak), and April 2014 (12 months later*)* using a Students t-test.

Density dependent habitat selection

To experimentally test for density dependent habitat selection in *P. moluccensis* recruits I performed a habitat choice experiment in underwater enclosures. *P. moluccensis* recruits were allowed to choose between a 100% live coral colony with an established group of conspecifics of varying densities, and an alternate colony that had a very low density of conspecifics (i.e. two individuals) and was either alive or dead. By increasing the density of conspecifics on the live coral colony I aimed to determine the point where individuals choose the alternate colony over crowded conditions on the established colony. I used five density levels (~142, 165, 186, 326 and 663 fish m$^{-2,}$) ranging from those normally encountered on healthy reefs (140 individuals m$^{-2,}$ personal observation) to extreme levels above those normally experienced in the reef environment (663 m^{-2}). Using levels that exceed those found in nature allowed me to effectively measure and detect density dependent effects (Inouye 2001, Forrester 2006). Because *P. moluccensis* are known to recruit to conspecifics (Öhman et al. 1998) I placed two adult fish on the alternate colony. This ensured that choices made by juveniles were strictly related to the density of conspecifics of the established colony and the quality of the alternate colony, and not confounded by avoidance of empty colonies by this aggregative species. I then tested whether the propensity to choose the alternate colony was affected by its quality by repeating the trials using a dead colony as the alternate. *P. moluccensis* recruits are readily distinguished from older conspecifics based on lighter coloration and smaller size, and individuals that had settled the previous night could therefore be collected by patrolling the same area of the reef every morning. Recruits were collected using dilute clove oil and hand nets, and placed in clip seal bags. Fish used in the established colonies were collected from existing groups so that social dynamics and hierarchies were already established.

Four replicate cages were placed in a shallow sandy area (approximately 3 m depths). Cages were 1×1m squares, with internal dividers (Figure 5.1). External walls, roof and colony divider were constructed of wire and plastic mesh (mesh size <5mm) so that water could pass through, yet prohibiting movement of fish. The cages contained three chambers; the main chamber and two colony chambers containing the established and alternate colonies. A fine aluminium mesh divided the main chamber from the two colony chambers and prohibited larger resident fish from escaping while allowing the test fish (new recruit) to pass through to the chosen colony.

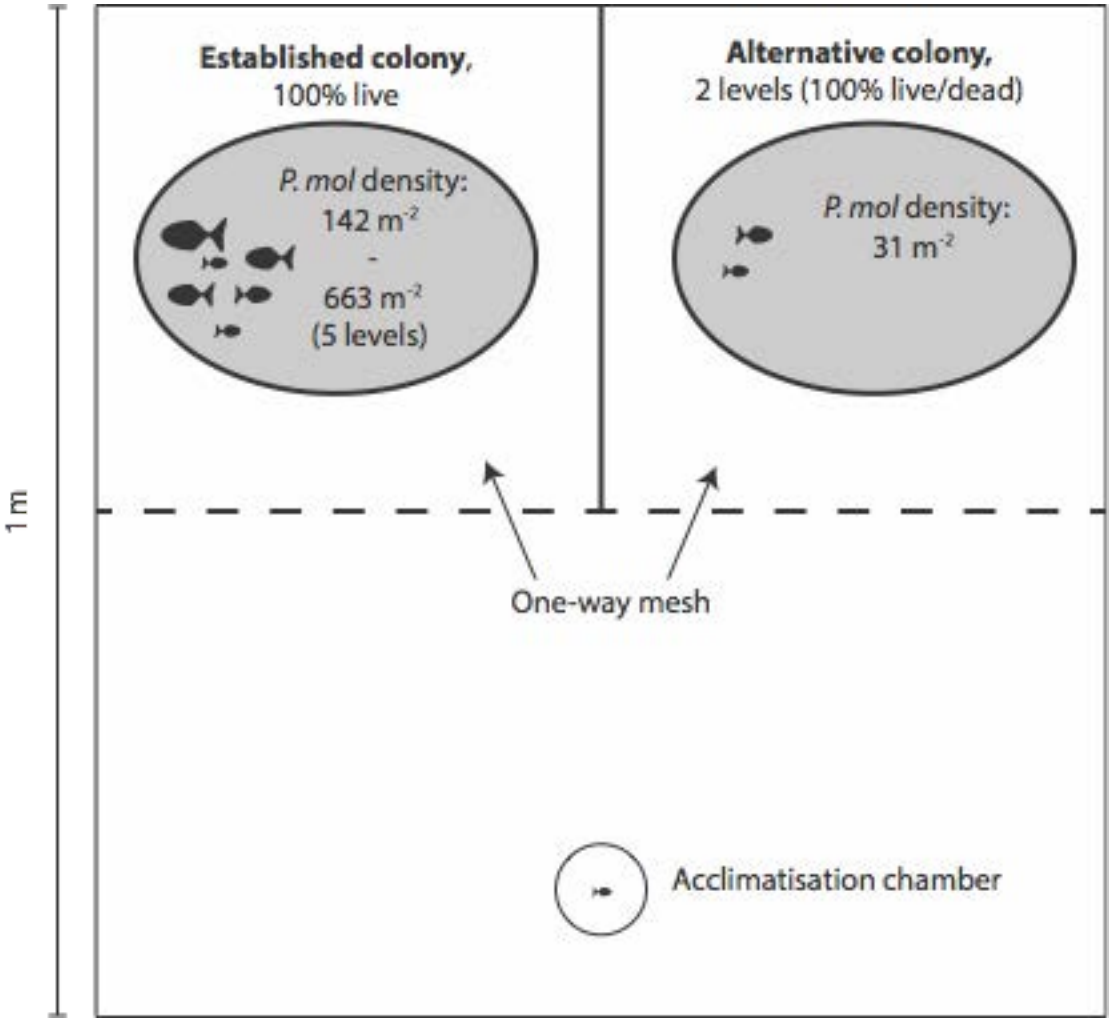

Figure 5.1: Experimental setup of choice chamber. The **established colony** consisted of a live corymbose coral colony, stocked with five different density levels of *P. moluccensis* (between 142-663 per m^2). The **alternative colony** consisted of either a live or dead corymbose *Acropora* colony and was stocked with two *P. moluccensis.* The one-way mesh allowed the small recruiting *P. moluccensis* to pass through but prohibited the larger adults and subadults from leaving their colonies.

Collected recruits were placed in an acclimatisation tube (PVC pipe 75 mm diameter with mesh lid) in the main chamber for 30 minutes. After the acclimatisation period a diver removed the tube by pulling an attached string. This ensured that the diver was at a minimum of 2 m distance from the cage, reducing disturbance to the fish. Each choice trial was started between 16:00 and 17:00 in the afternoon, allowing the recruit to make a choice overnight. Given that *P. moluccensis* settle at night this mimics conditions of habitat choice on the reef. A diver recorded the chosen colony in the morning, by visually inspecting the cages between 7:00-8:00. Given that it has previously been demonstrated that habitat choice during the night tends to persist throughout the day (Öhman et al. 1998, Feary et al. 2007), this method was likely to reflect the initial choice of the recruit. Choice tests were replicated 10 times at each of the five density levels for both alternate colony types (i.e. live or dead), resulting in 100 total tests. A new recruit was used in each choice trial to ensure that individuals were naïve to the experimental system and choices were not affected by prior learning.

The effect of colony quality and density of the established colony on the habitat choice of a juvenile *P. moluccensis* was compared using a logistic regression. The logistic regression modelled the colony choice of a *P. moluccensis* recruit (established colony=0, alternate colony=1) as a function of the density of resident *P. moluccensis* on the established colony (between 130 and 662 individuals per m^2) and the identity of the alternate colony (live or dead). Akaike's information criterion (AIC) were used to select a model that provided the best fit to the data using the fewest possible predictor variables. The fit of the selected model was evaluated using a likelihood ratio test, and the significance of each term in the reduced model was evaluated using a Wald Chi-Square test. A significant effect of density would indicate that the colony choice by the *P. moluccensis* recruit is altered by the density on the established colony. A significant effect of colony identity or an interaction between the two would indicate that this response differs depending on the quality of the alternate colony. Regression coefficients (β) provide an indication of relative effect size for each term in the model.

5.4 Results

Distribution and local density across a gradient of habitat damage

Overall I surveyed the habitat use of *P. moluccensis* on 379 coral colonies on 49 transects ranging from 0 to 91% dead coral. Habitat use by *P. moluccensis* varied depending on the amount of dead coral in the immediate vicinity. A significant two-way interaction indicated that the frequency of occupancy of live and dead coral colonies was influenced by the proportion dead coral surrounding each colony (saturated log-linear model retained, $p< 0.001$). When there was only low level of habitat degradation in the local area (i.e. < 25% dead colonies), *P. moluccensis* exclusively occupied live coral colonies (Figure 5.2a). In contrast, when approximately half of coral colonies were dead in the local area, *P. moluccensis* started using a small proportion of dead habitat. Finally, when more than three quarters of coral colonies are degraded, *P. moluccensis* occupied an equal number of dead and live coral colonies (Figure 5.2a).

The average density of adult *P. moluccensis* on live coral colonies increased as the amount of dead coral in the immediate surroundings increased. This was expressed as a significant difference in the mean density of *P. moluccensis* per colony between the five categories of proportion dead coral (Kruskal-Wallis Chi-Square test df =4, p=<0.001). When comparing transects with <10% dead coral, to those with >75% dead coral there was a more than two-fold increase in the average density of *P. moluccensis* per colony (mean density 34.8±3.3 SEM, and 97.0±31.2, respectively) and a substantial increase in variability.

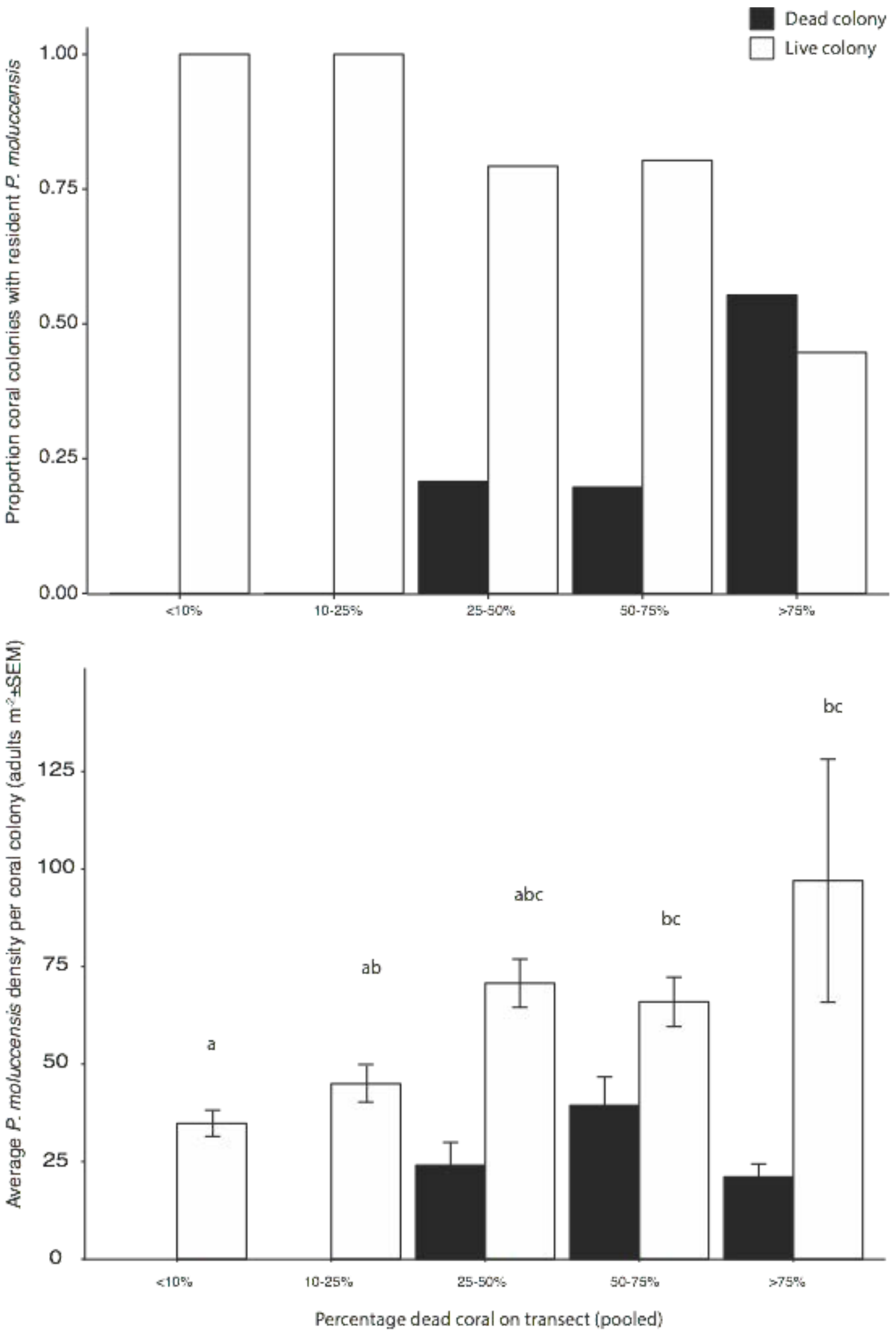

Figure 5.2: a) The proportion of dead (black) and live (white) coral colonies occupied by *P. moluccensis* at transects with a varying proportion dead coral colonies. Transects were pooled into five categories to satisfy assumption of log-linear analysis. b) The average density of *P. moluccensis* aggregations on coral colonies at transects with a varying proportion dead coral colonies. Error bars indicate SEM, letter signify significant groupings from post-hoc testing.

Juvenile *P. moluccensis* were more likely to recruit to a dead coral if there was an adult present, indicated by a significant interaction between colony type and adult presence (Pearson's Chi-square test: Chi-square =8.3, p=0.004, Figure 5.3a). This was driven by colonies on transects with more than 50% dead coral, as no *P. moluccensis* recruited to dead coral colonies on transects with lower levels of damage (Figure 5.3b). However, on transects with higher levels of degradation, more *P. moluccensis* recruited to dead corals with adults on them than to live corals (38 and 23 juveniles respectively, Figure 5.3c).

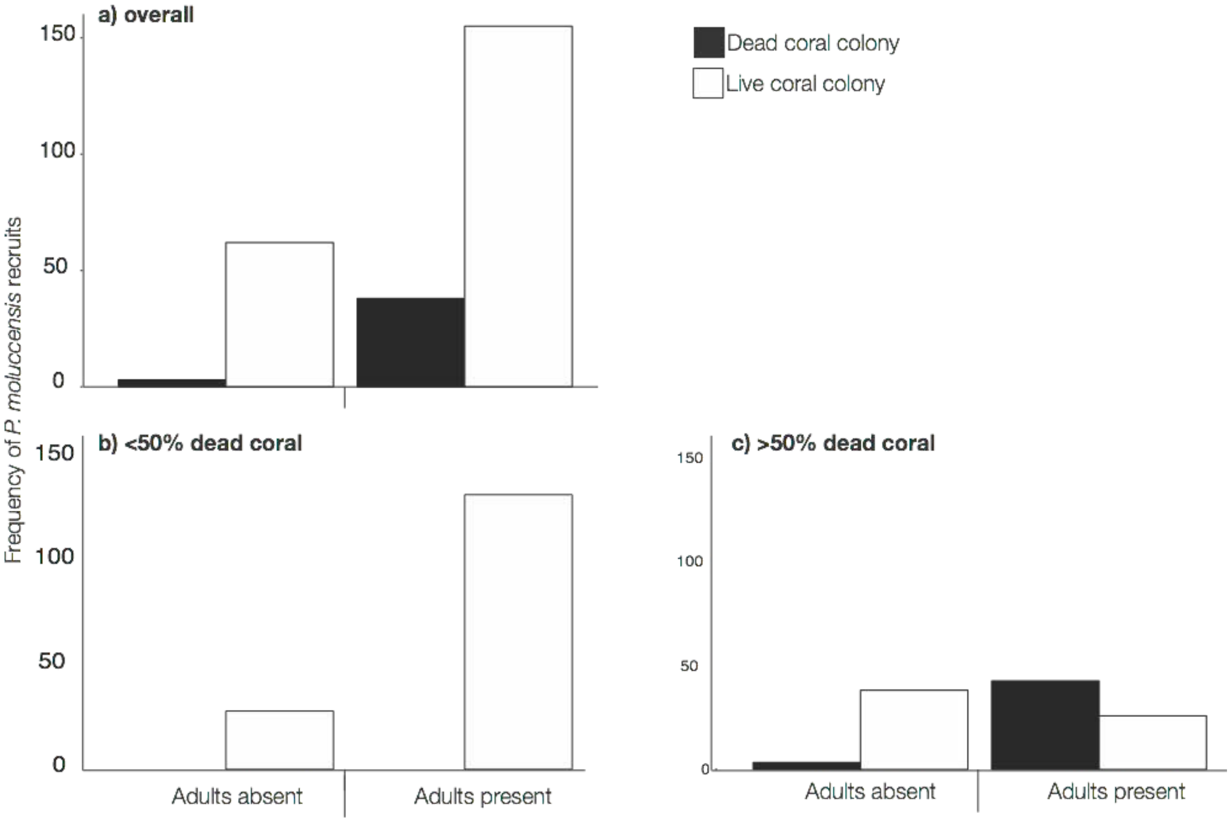

Figure 5.3. The frequency of P. moluccensis larvae that recruited to live (white) and dead (black bars) coral colonies depending on the presence and absence of conspecific adults. Panel a) depicts the overall frequency across 49 transects, while b) includes transects with <50% dead coral, and c) includes only transects with >50% dead coral.

There was an overall decline in the abundance of *P. moluccensis* between the first and second survey time (Students T-test, $t_{(1,96)}$=2.4, p=0.02). At the start of the disturbance event the average density per transect was 0.45 individuals m^{-2} (±0.05 SEM). After 12 months, this had dropped by 38%, to 0.28 individuals m^{-2} (±0.05 SEM).

Density dependent habitat selection

The choice experiment revealed clear density dependent habitat choice. The most appropriate model in evaluating habitat choice in recruiting *P. moluccensis* did not include the interaction between the two factors density and alternate colony quality. The density of the established colony had a significant effect on the habitat choice of *P. moluccensis* recruits (Table 5.1) wherein recruits were more likely to choose the alternate colony when the density of prior residents was high (Figure 5.3). There was no significant difference in choice between the healthy and dead coral colony (Table 5.1), although there was a suggestion that fish were more reluctant to choose the dead coral colony than the live (Figure 5.3). For example, when the alternative colony was live the model

Table 5.1. Logistic regression of colony choice by recruiting *P. moluccensis. Fish were allowed to choose between a colony with an established group of conspecifics (5 density levels of aggregation) and an alternate colony (live or dead).*

Factors	beta	SE - beta	Chi-square	df	p
Constant	-5.07	0.97			
Density (est. colony)	0.01	0.003	20.7	1	<0.0001
Alt. colony type	-0.87	0.69	1.6	1	0.2
Likelihood ratio test (full model)			62.7	2	<0.0001

Notes: The established colony was stocked with a range of densities of P. moluccensis, while the alternate colony type was either healthy (dummy coded 1) or dead (2). The Wald Chi-square test evaluates the importance of each term in the model (Colony Choice~Established colony density+Alternative colony type), while the likelihood ratio test evaluates the fit of the whole model against a simple null model. β is the regression coefficient and provides an indication of effect size.

predicts that more than 50% of the fish will choose it over the established colony if densities were above 317±70.5 (95%CI) fish m^{-2}. If the alternative colony was degraded however, the equivalent density on the established colony was 412±103 fish m^{-2}.

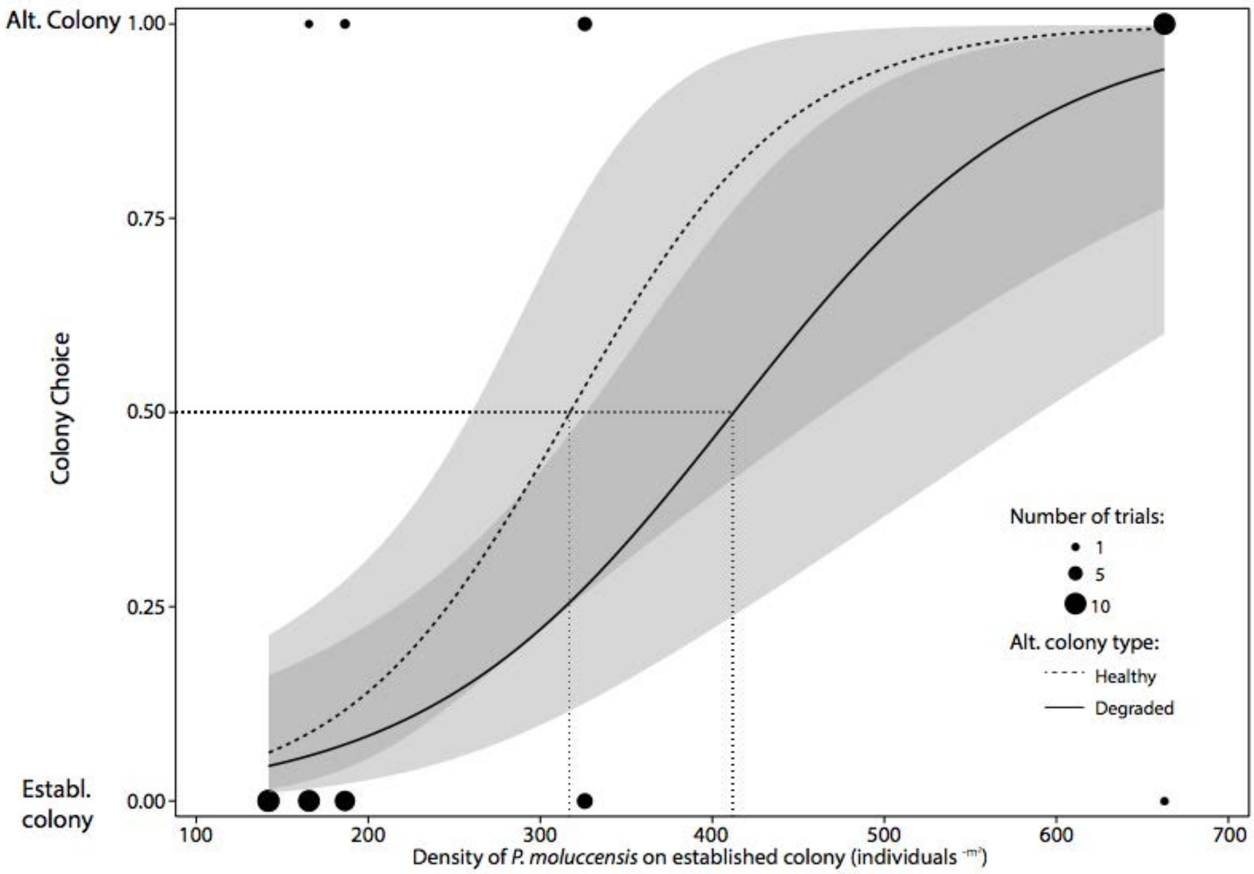

Figure 5.4. Logistic regression of colony choice of recruit *P. moluccensis.* Established colony (colony choice=0) was occupied by an aggregation of *P. moluccensis* adults and sub-adults in densities ranging from 142-663 individuals m^{-2} (x-axis). The alternate colony (colony choice=1) was occupied by 2 adult *P. moluccensis* and was either live or dead. Dotted lines indicate the densities above which 50% of the recruits are likely to choose the alternate colony (Alternate colony = Healthy: 317± 70 individuals m^{-2} (95% CI); degraded: 412 ± 103 m^{-2}). 10 trials were conducted at each density (n=5) per colony type (n=2) combination (grand total trials n=100). Size of point indicates number of trials with that outcome. Shaded bands indicate 95% confidence intervals around model prediction.

5.5 Discussion

Density dependent habitat selection is a fundamental mechanism governing the distribution of species in patchy landscapes. Because habitat loss alters the abundance and arrangement of resources it is likely to lead to crowding and subsequent density dependent habitat selection. In this study I described changes in the distribution patterns and habitat use of a common coral reef fish at differing levels of degradation through an ongoing crown-of-thorns outbreak. The lemon damsel, *Pomacentrus moluccensis* started utilising dead coral habitat when densities within aggregations on remnant live coral colonies colonies were higher than under natural conditions. I hypothesise that increased densities on live coral colonies were caused by displaced individuals from recently dead colonies in the surrounding area. Crowded conditions may force some individuals to choose an alternate habitat nearby, like a dead coral colony. In addition, the surveys revealed that *P. moluccensis* recruits were more likely to recruit to a dead coral colony with an adult present than those without an adult. Finally, a behavioural choice experiment showed that *P. moluccensis* recruits display density dependent habitat selection, choosing preferred occupied habitat up to a threshold density, above which they select alternate unoccupied habitats. These results illustrate how habitat disturbances are likely to influence the distribution and abundance of reef fishes through behavioural processes.

The habitat use of *P. moluccensis* adults was affected by the proportion of dead coral on each transect. On reefs where the damage from crown-of-thorns starfish was low, *P. moluccensis* adults exclusively used live coral. In contrast, adults started occupying dead coral colonies when the surrounding reef contained a high proportion of dead coral per transect. To my knowledge, there are no prior studies documenting *P. moluccensis* occupying significant proportions of dead coral habitat under natural conditions, suggesting that this behaviour is unusual for this species. This behaviour may only occur during periods of habitat disturbance when the abundance of suitable live coral habitat drops below a level where it can sustain the resident population of fish. These live coral specialists preferentially select branching and corymbose *Acropora* colonies when they recruit to the reef, which is reflected in the distribution of both adults and juveniles on the reef (Bonin 2012). Furthermore, when faced with the choice between a live and a dead coral in an experimental setting, *P. moluccensis* consistently choose live coral (e.g Öhman et al. 1998, Feary 2007). These studies suggests that *P. moluccensis* have the capacity to assess the quality of a habitat, and their selectivity for live coral suggests it confers benefits or provide resources not available from dead coral.

One explanation for the shift in habitat use and distribution of *P. moluccensis* onto dead coral colonies on reef with a high proportion of dead coral is through density dependent habitat selection. This process occurs in two stages; 1) individuals leave dead habitat in search of remnant live habitat which becomes crowded with displaced individuals and prior residents and 2) crowded conditions forces some individuals to choose alternate habitat. Mobile animals are known to relocate to remnant live habitat following habitat loss. For example, Oystercatchers feeding on mussels have been consistently demonstrated to leave disturbed feeding grounds in favour of remnant habitat patches following habitat loss (Goss-Custard 1977, Goss-Custard et al. 2006). Similarly, *P. moluccensis* has previously been shown to vacate dead coral colonies in search of live habitat nearby (Coker 2012a). Displaced individuals from ‘source’ aggregations naturally increase the densities of organisms in ‘sink’ aggregations (Pulliam and Danielson 1991). For example, remnant live patches of coral in Chapter 3 experienced a temporary increase in *P. moluccensis* following a partial loss in live coral. In the present study, the average density of *P. moluccensis* per live coral colony more than doubled between transects with high (>75%) and low (<10%) proportion dead coral. However, crowded conditions are known to lead to competition over resources in reef fishes. Density dependent interactions like competition (Ward et al. 2006) and aggression (Boström-Einarsson et al. 2014) has been demonstrated to lead to both lethal (Brunton and Booth 2003) and sub-lethal outcomes (Booth 1995) in coral reef fishes, suggesting that competition for resources on live corals is an important regulating mechanisms. Crowded conditions on remnant live habitat can therefore encourage individuals to choose alternate habitat nearby (i.e density dependent habitat selection), where competition for resources is lower.

Alternatively, late-arriving individuals to remnant colonies may be faced with priority effects, where prior residents are competitively dominant by virtue of their timing of arrival. While priority effects have been well-documented for recruiting reef fishes (e.g Almany 2004, Geange and Stier 2009, Poulos and McCormick 2014) less is known about how adult movement may be affected by prior residents. In one of the few studies to investigate this, Coker et al. (2013b) described how adults of the humbug damselfish (*Dascyllus aruanus*) placed on a dead coral colony were unlikely to successfully enter a group of unfamiliar conspecifics on a live coral colony placed nearby. In contrast, when group members were removed from the group and placed on coral rubble they were immediately allowed access to the group. Based on distributions alone it is impossible to decipher which one of these scenarios are true; whether fish *selected alternate habitat* (i.e. density dependent habitat selection) or were *prevented to use remnant live habitat* by dominant conspecifics (i.e. priority effect). While distribution alone is not sufficient to understand changes in habitat use, the behavioural experiment demonstrates that *P. moluccensis* engages in density dependent habitat selection. When choosing between a coral colony with an established group of conspecifics and an alternate colony with a pair of conspecifics, recently recruited *P. moluccensis* consistently chose the established coral colony, as long as the densities remained relatively low. However, when densities increased above those regularly observed on undisturbed reefs, the recruit was more likely to choose the alternate colony. The model predicted that 50% (or more) of recruits chose the alternate colony when the density on the established colony was over 317±70.5 (95%CI) individuals m^{-2}. This density of conspecifics per coral colony was recorded on the reef only on transects with more than 50% dead coral per transect. While the majority of coral colonies on the reef did not display such extreme densities, this suggests that a lack of available colonies with low densities of conspecifics is sufficient to cause density dependent habitat selection in juveniles.

Density dependent habitat selection has been described in a wide variety of taxa and ecosystems (e.g. birds in forests: Krebs 1971, freshwater fish: Milinski 1979, ducks in lakes: Harper 1982, sheep on grasslands: Mobæk et al. 2009), and interactions with habitat loss has been explored using modelling (Pulliam and Danielson 1991), but this is one of the first studies to investigate how the loss of live habitat can trigger a chain of events leading to density dependent habitat selection. Density dependent habitat selection can be beneficial in a heterogeneous ecosystem, because it maximises the resources extracted from each habitat. In theory, this ensures that each individual in a population achieves maximum fitness (Morris 1987) by optimising their spatial distribution and use of resources. However, this study suggests that during a habitat degradation event, when adequate alternate habitat may not be available, this process leads to individuals choosing a habitat they rarely select otherwise. This begs the question, are there consequences for *P. moluccensis* of theses changes in habitat choice?

In species where individuals select habitat based primarily on the presence of conspecifics, rather than based on habitat quality directly, there is a higher risk of aggregating in suboptimal habitat (e.g. Tiainen 1983, Mihoub et al. 2009, Serrano and Tella 2007). Previous work has indicated that *P. moluccensis* is highly selective for conspecifics (Öhman et al. 1998). In this study I observed that juvenile damselfish used dead coral more often when the colonies had resident adults. If conspecific presence is no longer a reliable indicator of habitat quality, which might be the case if adults are forced out of preferred habitat due to habitat loss and subsequent overcrowding, conspecific attraction can therefore become maladaptive. This suggests that species that rely on conspecific presence to judge habitat quality are at a higher risk of selecting suboptimal habitat following habitat loss and highlights an interesting area for future work.

Coral-dwelling specialists like *P. moluccensis* often experience negative effects of living on dead coral, such as reduced growth (Feary et al. 2009) and higher mortality (e.g. Bonin et al. 2009, Lönnstedt and McCormick 2014). Given that the ultimate cause of mortality in coral reef fishes is almost exclusively predation (Hixon and Carr 1997), and prior research has demonstrated that *P. moluccensis* cease anti-predator behaviour on dead coral (Chapter 4) the chances of survival are low for individuals on dead coral colonies. This suggests that density dependent habitat selection during a habitat degradation event is a maladaptive behaviour, because the alternate habitat is unlikely to provide sufficient resources to maintain the population. This has been demonstrated in bird communities, where individuals suffer detrimental consequences from displacement into suboptimal habitat. For example, shorebirds relocate to remnant live habitat following the loss of their primary foraging habitat, but competition over food with prior residents at the alternate habitat reduces the survival rate of displaced individuals (Burton et al. 2006). Individual effects are likely to translate into population level effects, and descriptive studies have suggested that a majority (60-75%) of reef fish species decline in abundance following coral mortality (Jones et al. 2004, Wilson et al. 2006). Indeed, in my study location there was a 38% reduction in the abundance of *P. moluccensis* in the 12 months following the peak of the crown-of-thorns outbreak. One mechanism responsible for this decline may be density dependent habitat selection due to habitat loss.

Density dependent habitat selection is a fundamental concept in ecology that has been demonstrated in many taxa and ecosystems. Results from this study suggest that adults crowd into remnant live habitat, which encourages some individuals to use suboptimal habitat in which they are unlikely to persist. Juvenile habitat use suggests that adult presence on dead coral colonies attracts recruiting juveniles into settling on dead coral habitat that they would otherwise rarely select. Despite the ubiquity of habitat loss in almost all global ecosystems, this study is one of the first to evaluate how habitat loss influences density dependent habitat selection. These results provide insight into how habitat loss interacts with density dependent habitat selection with potential consequences at the population level. The findings furthermore highlight the complexity in underlying mechanisms and animal responses to habitat loss.

Chapter 6

General Discussion

Coral reef fishes have a complex but vital relationship with coral reefs, yet despite six decades of research into coral reef ecology we still do not fully understand what resources many fish gain from their close association with live coral. Certainly, the abundance and quality of resources is one of the primary drivers shaping ecological communities, defining species' interactions and governing their distribution in space. When these resources are depleted, competition over remaining resources is likely to intensify, altering vital behaviours like foraging and predator avoidance, and ultimately affecting key demographic traits. The nature and availability of resources will thus affect the abundance and diversity of species supported by the habitat. While the loss of coral reef habitat has been linked to declines in reef fish abundance and species diversity, the mechanisms underpinning this decline remain largely unknown.

In this thesis I have provided insight into how reef fishes interact with degraded habitat, how critical behavioural processes are influenced by habitat loss, and how shifts in habitat use and distribution can have unexpected consequences. These findings highlight the complex ways in which reef fishes respond to disturbances. Chapter 2 synthesised the current knowledge on resource competition in reef fishes and highlighted the scarcity of studies which have considered the effects of habitat loss on competitive interactions. In Chapter 3 I explored the effects of partial habitat loss on densities of the lemon damselfish *Pomacentrus moluccensis*, and demonstrate a crowding effect on remnant live habitat. Chapter 4 tested how the response to threat in this species was influenced by the loss of live coral and the reduction of shelter space. Finally, in Chapter 5 I investigated whether complete coral mortality would lead to density dependent habitat selection during an ongoing disturbance event, both in situ and under experimental conditions. These chapters provide compelling evidence of the importance of living coral to reef fishes, not just for the structure they provide, but also because they may drive patterns of habitat use, govern distributions, and act as a cue to elicit appropriate behaviour.

6.1 The importance of live coral to reef fishes

Habitat loss is well-documented to have negative effects on reef fish communities (Graham et al. 2006, Jones et al. 2004, Wilson et al. 2006), however the mechanisms underlying this decline are mostly unknown. To fully understand the biological processes underlying demographic effects of habitat loss we need to understand what resources fish gain from their close association with live corals. While corallivorous fish are likely to suffer increased mortality following habitat loss because they have lost their primary food source (Cole et al. 2008, Graham et al. 2009, Pratchett and Berumen 2008), the resource requirements for many coral dwelling species are comparatively poorly understood. While the resource is not always known, Chapter 2 demonstrated that competition over finite resources is an important ecological process structuring and regulating reef fish populations. A common assumption has been that the loss of structural complexity on dead reefs leaves fishes exposed to predators (e.g. Garpe et al. 2006, Graham et al. 2006, Coker et al. 2009), however this assumption has never been experimentally tested.

The results from this thesis suggests that the live coral tissue itself is of critical importance to reef fishes, independent of the loss in structural integrity that occurs as coral colonies erode. When the live tissue of coral colonies was experimentally removed (Chapter 3), reef fishes that inhabit these colonies immediately left the dead portion of the colony. Even though the shelter space among colonies remained, fish no longer utilised this portion of the colony, crowding into remnant live habitat instead. The timing of these changes in habitat use suggest that this was not a response to a loss in shelter space, but rather to the loss of living tissue itself. This distinction between the effects of the loss of live tissue, (i.e. coral mortality from a non-destructive process like bleaching or crown-of-thorns starfish) as opposed to the effects of the loss of three-dimensional structure (through storms or gradual erosion of the coral skeleton) has previously been suggested in multiple studies of natural disturbance events (Booth and Beretta 2002, Wilson et al. 2006, Graham et al. 2009). However, Chapter 4 provided the first experimental evidence in situ, demonstrating that changes in sheltering behaviour occurred immediately following the death of the coral tissue, independently of any reductions in space between the coral branches. While structural complexity is important to coral-dwelling reef fishes, it may be secondary, both in importance and in timing, to the loss of the living coral tissue itself.

Chapter 5 demonstrated that the loss of living corals can also affect the distribution and habitat use of reef fishes on coral colonies. I recorded a two-fold increase in fish densities on remnant live coral colonies on heavily degraded reefs compared to reefs with limited coral mortality. These crowded aggregations within remnant live habitat are a testament to the importance of live coral to P. moluccensis. However, when crowding reached a threshold level and despite their high level of live coral specialisation under natural conditions (e.g. Bonin 2012), P. moluccensis started occupying dead coral habitat. While changes in towards lower quality habitat can have demographic consequences to reef fishes (discussed below) it may also impact competitive hierarchies maintaining biodiversity of coral reef ecosystems. It is well documented that interspecific interactions can increase the complexity of response to habitat loss (Banks et al., 2007, Brown, 2007, Debinski and Holt, 2000, Nee and May, 1992). Ecologists seeking to understand the maintenance of biodiversity on coral reefs first applied terrestrial niche theories (MacArthur and Levins 1967), whereby competitive coexistence of species relies on a fine-scale division of resources provided by the coral reef matrix (Smith and Tyler 1972). While this theory has been somewhat tempered and replaced by alternate theories over time (Sale 1976, 1977, Victor 1983, Doherty 1983), Chapter 2 has illustrated that competition over resources is indeed an important structuring mechanism in coral reefs ecosystems. It follows that changes to resource availability that encourages altered habitat use and distribution has the potential to disrupt established ecological niches, competitive hierarchies, and food webs (Buchman et al. 2013, Duffy et al. 2007, Melián and Bascompte 2002, Nee and May 1992, Tilman et al. 1997). A shift in habitat use can therefore have profound indirect effects on ecological systems, and highlights the complexity of responses to the loss of live coral in reef fish communities.

6.2 Demographic consequences of habitat loss on coral reefs

The consequences of coral loss on the abundance and density of reef fishes are well documented (Jones et al. 2004, Graham et al. 2006, Wilson et al. 2006) but results from this thesis suggest that the response of reef fish to habitat loss are more complex. Despite the partial degradation of coral colonies in Chapter 3 and the initial crowding of surviving fish, individuals had a higher body condition than conspecifics on control colonies. I hypothesised that these observations were due to a complimentary edge effect where surviving individuals benefited from abutting foraging (in dead coral) and sheltering (in live coral) habitats created by the degradation event. Because body condition in reef fishes is linked to increased reproductive output (Donelson et al. 2008), competitive dominance (Booth and Beretta 2004) and growth (Kerrigan 1994), these surviving individuals could provide an avenue for recovery after moderate disturbances. Indeed, while the overall abundance of P. moluccensis on disturbed colonies was not substantially lower than on control colonies at the conclusion of the experiment. It is important to remember however that this experiment tested the effects of partial coral mortality, which allowed the fish to maintain access to remnant live habitat on the coral colony.

In Chapter 4 I explored the consequences of complete mortality of individual coral colonies on reefs with a gradient of overall damage. Reef fish whose colony died appeared to migrate into remnant live habitat, and this redistribution of fish has at least three potential demographic consequences. First, leaving the safety of the protective coral branches is fraught with danger for small-bodied reef fish. Roving predators are likely to increase the mortality in displaced fishes (Hixon 1991, Hixon and Beets 1994). Second, fish that successfully enter remnant live coral are likely to suffer demographic effects of crowding (Hixon and Webster 2002), like reduced survival (Hixon and Jones 2005, Booth 1995, Forrester 1995), growth (Jones 1987a, b, Jones and McCormick 2002), and reproductive output (Booth 1995, Jones 1987b). And finally, fish that are forced to inhabit dead coral are likely to suffer similar negative consequences of inhabiting this suboptimal habitat. The effects of coral loss on the survival (e.g. Bonin et al. 2009, Lönnstedt and McCormick 2014) and growth (Feary et al. 2009) of reef fish have previously been demonstrated. I observed a 38% decline in the overall abundance of P. moluccensis in the study area in the 12 months following a major crown-of-thorns outbreak. While it was not possible to attribute which mechanisms were responsible for this population decline, it is likely that habitat loss was a primary contributor.

6.3 Altered behaviours due to habitat loss on coral reefs

There has been an increasing awareness that changes in individual animal behaviour frequently represent the first response to habitat loss and degradation, and often underpin subsequent demographic impacts on populations and ecosystems (Candolin and Wong 2012, Wong and Candolin 2015). Indeed, results from this thesis provide evidence that this may also be the case in coral reef ecosystems. Chapter 4 demonstrated that sheltering behaviour of reef fishes can be fundamentally and rapidly altered by coral mortality. Following the degradation of their colony, a majority of *P. moluccensis* stopped sheltering altogether and instead moved to high-risk locations away from their colony. In contrast, most fish on control colonies sheltered between coral branches when startled. Given that behavioural changes occurred immediately following the degradation event, this does not appear to be a result of declining shelter space available between degrading branches, but rather a direct reaction to the loss of live coral tissue. This can be regarded as a special case of an undervalued resource (Gilroy and Sutherland 2007), a proposed versions of an evolutionary trap, where the cue used to assess habitat quality (in this case the live coral tissue) is lost while the quality of the resource remains (shelter space between branches).

Similarly, recruiting juveniles in Chapter 4 may be trapped by evolutionary adaptive behaviours rendered maladaptive by environmental change. Animals frequently recruit to the presence of conspecifics (Booth, 1995, Muller et al. 1997, Sweatman 1983), presumably because the presence of conspecifics indicates a high quality habitat. This behaviour may however become maladaptive when conspecifics have altered their habitat use as a consequence of habitat loss. The distribution and habitat use patterns from the observational study as well as the outcome of the behavioural experiment in Chapter 4 suggests that the presence of adults on dead coral colonies is encouraging juveniles to recruit to dead coral habitat. They are unlikely to persist on these colonies given that they do not have access to refuges in remnant live coral on the same colony (like fish in Chapter 3) and are known to cease critical anti-predator behaviour on dead coral habitat (Chapter 4).

Previous studies investigating changes in behaviour during habitat degradation events in the marine environments have focused on the detection of chemical cues dispersed in the water column. For example, the close congener *P. amboinensis* ceased anti-predator responses to a chemical alarm cue when their coral colony was surrounded by dead coral (McCormick et al. 2016, McCormick and Lönnstedt 2016). The correct response to a predator presumably occurs in two stages. In stage one, the animal has to correctly identify and detect the presence of a threat, and in stage two they respond in a manner appropriate based on their environment. While the authors concluded that the important behavioural change of *P. amboinensis* was due to a loss in the ability to detect alarm cues in degraded environments, the results from this thesis present an alternate theory. Chapter 4 indicates that the change in behaviour is linked to a perceived lack of suitable places to hide (i.e. e. coral mortality affects stage two) rather than their ability to detect the threat (i.e. stage one). The use of a visual startle device avoids the confounding effect of altering both the threat (chemical alarm cues that can be masked by the dead coral environment) and the sheltering environment (dead versus live coral colony) simultaneously. I argue that changes in anti-predator response are likely due to an inability to recognise the dead coral as a suitable place to shelter, rather than a loss in the ability to detect threats. In the context of evolutionary traps, this work highlights the consequences of anthropogenic disturbance on critical behavioural cues in the marine environment. These findings add to the growing body of work demonstrating that the disruption of natural behavioural processes may be more important than the direct loss of resources.

6.4 Future research and concluding remarks

The outcomes of this thesis have demonstrated the complex nature of reef fishes' response to habitat loss, and suggest several key areas for future research. First and foremost, several chapters have highlighted the importance of the living coral tissue to reef fish, and not just the structure it provides. A preoccupation with viewing corals solely as a three-dimensional structure for non-corallivorous reef fishes may hinder our understanding of reef fish responses to habitat loss. However, despite 60 years of research into coral reef fish ecology (Hixon 2011), we still do not fully understand what resources fish gain from their close association with live coral. While a resolution to this knowledge gap has proved elusive, it remains critical to effectively manage and mitigate effects from future disturbances on coral reefs. Second, while there has been a growing understanding in terrestrial ecology that changes in individual behaviour may be the first response to habitat loss and degradation (Candolin and Wong 2012, Wong and Candolin 2015), marine ecologists appear to be lagging behind. Evolutionary guided behaviour may offer a glimmer of hope in uncertain times of environmental change if individuals are capable of adapting to changing conditions. Conversely, species can get caught in 'evolutionary traps' as the cues they use to assess habitat quality are no longer indicative of a high quality habitat (Schlaepfer et a 2002). An increased understanding of how the behaviour of marine species is affected by habitat loss is therefore important to understand impacts of anthropogenic activities on coral reefs. Finally, this thesis has provided a first preliminary insight into how density dependent habitat selection may affect habitat use and distribution of reef fishes. A more thorough and comprehensive investigation of how habitat use, spatial distributions and space use in reef fishes are affected by the loss of critical resources provided by the habitat will aid our understanding of how disturbances affect, not just individuals, but whole communities of reef fishes. Data collected in the course of this thesis may allow some of these questions to be investigated further. The large outbreak of crown-of-thorn starfish at my study sites and subsequent coral decline, allowed me to collect a long-term data set mapping benthic cover, and reef fish habitat use prior, during and post-disturbance. While the timing of the outbreak did not allow the inclusion of this data set as a chapter in the thesis, I expect that this immense data set, once fully analysed, will provide a unique insight into how spatial distributions and habitat use change during an ongoing degradation event.

In summary, this thesis has investigated effects of habitat degradation on key ecological processes determining the distribution of reef fishes, competition for resources and their interaction with the coral reef habitat. Combined, the results from this thesis suggest that reef fish response to habitat disturbance will depend on the magnitude of disturbances (Chapter 3), the quality of remaining resources (Chapter 5), their flexibility in resource use (Chapter 3), and whether critical behaviours are altered by the loss of live coral (Chapter 4). It showed complex fitness responses to coral loss and established that live coral tissue is critical, not just the structure they provide, but also for eliciting adaptive behavioural responses to the threat of predation. It provided the first demonstration of the crowding hypothesis in the marine environment and is the first to investigate how density dependent habitat selection is affected by habitat degradation.The outcomes of this thesis highlight the importance of living corals in the ecology and behaviour of coral reef fishes, and their complex responses to coral reef loss and degradation.

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Wong MYL, Munday PL, Buston PM, Jones GP. 2008. Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. Behavioral Ecology 19:353–361.

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York, NY: Springer New York.

Appendix 1

Publications

Chapter 2 has been published at the time of submission of this thesis:

- Bonin MC, Boström-Einarsson L, Munday PL, Jones GP. 2015. The Prevalence and Importance of Competition Among Coral Reef Fishes. Annu. Rev. Ecol. Evol. Syst. 46:169–190.

During this dissertation the following papers (not relating directly to chapters in the thesis) have been published:

- Boström-Einarsson L, Rivera-Posada J. 2016. Controlling outbreaks of the coral-eating crown-of-thorns starfish using a single injection of common household vinegar. Coral Reefs 35:223–228.
- Boström-Einarsson LE, Bonin MC, Munday PL, Jones GP. 2014. Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. Ecology 95:3056–3067.
- Boström-Einarsson L, Bonin MC, Munday PL, Jones GP. 2013. Strong intraspecific competition and habitat selectivity influence abundance of a coral-dwelling damselfish. Journal of Experimental Marine Biology and Ecology 448:85–92.

Appendix 2

Supplemental figure 2.1

Spreadsheet with all publications included in Chapter 2, outlining experimental type, outcome, study species etc. can be viewed on the following pages.

In addition, an interactive figure that allows you to visually explore the data can be found via the journal webpage. Competition experiments can be filtered by design, response variable, experimental outcome, focal family, and/or life stage. Details of the corresponding original publications are also listed for each filter or combination of filters.

PUBLICATION DETAILS					EXPERIMENT DETAILS						RESPONSE VARIABLES TESTED					
Year	**Full Reference**	**Family**	**Species 1 (focal)**	**Species 2**	**Type of Experiment**	**intra or inter?**	**Juv or adult competitors?**	**Experimental setting**	**Resource inferred by author**	**What resource manipulated?**	**Survival**	**Growth**	**Reproductive fitness**	**Recruitment**	**Distribution/ Resource Use**	**Abundance**
1976	Sale, P.F., 1976. the effect of territorial adult pomacentrid fishes on the recruitment and survival of juveniles on patches of coral rubble. Journal of Experimental Marine Biology and Ecology 24, 297–306.	Pomacentridae	*Pomacentrus wardi*	*Pomacentrus apicalis*	Competitor density manipulation	inter	juv vs. adult	natural patch reef	**space**	**none**	no	no	no	YES	no	YES
1976	Sale, P.F., 1976. the effect of territorial adult pomacentrid fishes on the recruitment and survival of juveniles on patches of coral rubble. Journal of Experimental Marine Biology and Ecology 24, 297–306.	Pomacentridae	*Pomacentrus wardi*	n/a	Competitor density manipulation	intra	among juv	natural patch reef	**space**	**none**	no	no	no	YES	no	YES
1979	Robertson, D.R., Sheldon, J.M., 1979. competitive interactions and the availability of sleeping sites for a diurnal coral-reef fish. Journal of Experimental Marine Biology and Ecology 40, 285–298.	Labridae	*Thalassoma bifasciatum*	n/a	Competitor density manipulation	intra	among adults	natural reef	**shelter**	**shelter holes**	no	no	no	no	YES	no
1979	Robertson, D.R., Sheldon, J.M., 1979. competitive interactions and the availability of sleeping sites for a diurnal coral-reef fish. Journal of Experimental Marine Biology and Ecology 40, 285–298.	Labridae	*Thalassoma bifasciatum*	n/a	Resource manipulation	intra	among adults	natural reef	**shelter**	**shelter holes**	YES	no	no	no	no	no
1980	Coates, D., 1980. prey-size intake in humbug damselfish, dascyllus-aruanus (pisces, pomacentridae) living within social-groups. The Journal of Animal Ecology 49, 335–340.	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density manipulation	intra	juv vs. adult	natural reef	**food**	**none**	no	no	no	no	YES	no
1981	Robertson, D.R., Hoffman, S.G., Sheldon, J.M., 1981. availibility of space for the territorial caribbean damselfish eupomacentrus planifrons. Ecology 62, 1162–1169.	Pomacentridae	*Eupomacentrus planifrons*	n/a	Resource manipulation	intra	among adults	natural reef	**food, shelter**	**food, shelter**	no	YES	YES	YES	YES	no
1982	Doherty, P.J., 1982. some effects of density on the juveniles of two species of tropical, territorial damselfish. Journal of Experimental Marine Biology and Ecology 65, 249–261.	Pomacentridae	*Pomacentrus flavicauda*	*Pomacentrus wardi*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
1982	Doherty, P.J., 1982. some effects of density on the juveniles of two species of tropical, territorial damselfish. Journal of Experimental Marine Biology and Ecology 65, 249–261.	Pomacentridae	*Pomacentrus wardi*	*Pomacentrus flavicauda*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
1982	Doherty, P.J., 1982. some effects of density on the juveniles of two species of tropical, territorial damselfish. Journal of Experimental Marine Biology and Ecology 65, 249–261.	Pomacentridae	*Pomacentrus wardi*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**space**	**none**	YES	YES	no	no	no	no
1982	Doherty, P.J., 1982. some effects of density on the juveniles of two species of tropical, territorial damselfish. Journal of Experimental Marine Biology and Ecology 65, 249–261.	Pomacentridae	*Pomacentrus flavicauda*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
1983	Doherty, P.J., 1983. tropical territorial damselfishes - is density limited by aggression or recruitment. Ecology 64, 176–190.	Pomacentridae	*Pomacentrus flavicauda*	*Pomacentrus wardi*	Competitor density manipulation	inter	juv vs. adult	natural patch reef	**none**	**none**	YES	no	no	YES	no	no
1983	Doherty, P.J., 1983. tropical territorial damselfishes - is density limited by aggression or recruitment. Ecology 64, 176–190.	Pomacentridae	*Pomacentrus wardi*	n/a	Competitor density manipulation	intra	juv vs. adult	natural patch reef	**none**	**none**	YES	YES	no	YES	no	no
1985	Doherty, P.J., 1983. tropical territorial damselfishes - is density limited by aggression or recruitment. Ecology 64, 176–190.	Pomacentridae	*Eupomacentrus leucostictus*	*Eupomacentrus planifrons*	Dominance experiment	inter	among adults	aquarium	**shelter**	**shelter holes**	no	no	no	no	YES	no
1985	Ebersole, J.P., 1985. niche separation of 2 damselfish species by aggression and differential microhabitat utilization. Ecology 66, 14–20.	Pomacentridae	*Eupomacentrus planifrons*	*Eupomacentrus leucostictus*	Dominance experiment	inter	among adults	aquarium	**shelter**	**shelter holes**	no	no	no	no	YES	no
1985	Sweatman, H., 1985. the influence of adults of some coral-reef fishes on larval recruitment. Ecol. Monogr. 55, 469–485.	*assemblage*	*assemblage*	*Dascyllus spp.*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**none**	**none**	no	no	no	YES	no	no
1985	Sweatman, H., 1985. the influence of adults of some coral-reef fishes on larval recruitment. Ecol. Monogr. 55, 469–485.	Pomacentridae	*Chromis caerulea*	n/a	Competitor density manipulation	intra	juv vs. adult	experimental patch reef	**none**	**none**	no	no	no	YES	no	no

		EFFECT DETECTED?								SUMMARY		
Behaviour	**Which behaviour(s)?**	**Survival**	**Growth**	**Reproductive fitness**	**Recruitment**	**Distribution/ Resource Use**	**Abundance**	**Behaviour**	**Details of competitive effect on focal sp.**	**Overall - Competitive effect detected?**	**Author conclusion (study overall)**	**Year**
no	no	n/a	n/a	n/a	NEGATIVE	n/a	YES	n/a	Presence of adults reduce recruitment and abundance of juveniles	**YES**	Recruitment is limited by available space, competition over space with adults stops recruits from accessing space that is not vacant	1976
no	no	n/a	n/a	n/a	NO	n/a	NO	n/a	No effect of resident juveniles on recruitment or abundance of other juveniles	**NO**	Recruitment is limited by available space, competition over space with adults stops recruits from accessing space that is not vacant	1976
no	n/a	n/a	n/a	n/a	n/a	NO	n/a	n/a	When individuals were removed, vacated sites not taken over by conspecifics	**NO**	Resource not limited, limited evidence for competition	1979
YES	aggression, search activity, time to shelter	NO	n/a	n/a	n/a	n/a	n/a	YES	No effect of reducing the availability of shelter holes on survival of wrasse. Some behaviours affected i.e. longer search time for shelter holes, entered holes later than usual, but no increased aggression from conspecifics	**NO**	Resource not limited, limited evidence for competition	1979
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	When larger fish removed, smaller fish ate larger prey. Larger fish in groups exclude smaller fish from accessing larger prey items, and smaller fish shift their resource use in presence of larger fish.	**YES**	Rank determines access to preferred prey size	1980
no	n/a	n/a	NO	NO	NO	NO	n/a	n/a	In reefs with half algal mats removed, densities increased in remaining half, while full removals resulted in relocation of algal mats. Increased densities did not have a negative growth/reproductive/recruitment effect	**NO**	*E. planifrons* population is not limited by habitat availability	1981
no	n/a	NO	n/a	n/a	n/a	n/a	n/a	n/a	Competitor presence did not influence survival	**NO**	Limited evidence for competition, populations regulated by recruitment limitation	1982
no	n/a	NO	n/a	n/a	n/a	n/a	n/a	n/a	Competitor presence did not influence survival	**NO**	Limited evidence for competition, populations regulated by recruitment limitation	1982
no	n/a	NO	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Increasing conspecific density reduced growth but not survival	**NO**	Limited evidence for competition, populations regulated by recruitment limitation	1982
no	n/a	NO	n/a	n/a	n/a	n/a	n/a	n/a	No effect of increasing conspecific density on survival	**NO**	Limited evidence for competition, populations regulated by recruitment limitation	1982
no	n/a	NO	n/a	n/a	NO	n/a	n/a	n/a	Adult heterospecific prior residents did not reduce recruitment or survival	**NO**	Competition not important, recruitment limitation structures reef fish communities	1983
no	n/a	NO	NEGATIVE	n/a	NO	n/a	n/a	n/a	Presence of adult conspecific prior residents reduced growth but did not influence recruitment or survival	**NO**	Competition not important, recruitment limitation structures reef fish communities	1983
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	On complex coral heads, interspecific competitor *E. planifrons* won aggressive interactions and dominated habitat	**YES**	Competitive dominance can vary with habitat structure, interference competition responsible for evolution of habitat preferences	1985
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	On simple coral heads, interspecific competitor *E. leucostictus* won aggressive interactions and dominated habitat	**YES**	Competitive dominance can vary with habitat structure, interference competition responsible for evolution of habitat preferences	1985
no	n/a	n/a	n/a	n/a	NEGATIVE	n/a	n/a	n/a	Increased densities of resident *D. aruanus* and *D. reticulatus* reduced the abundance and diversity of heterospecific recruits	**YES**	Priority effects are both negative and positive. Positive effect of conspecifics likely due to habitat selection, while negative effects of *Dascyllus* residents unlikely to be related to resource availability.	1985
no	n/a	n/a	n/a	n/a	POSITIVE	n/a	n/a	n/a	Positive effect of resident conspecific density on recruitment	**NO**	Priority effects are both negative and positive. Positive effect of conspecifics likely due to habitat selection, while negative effects of *Dascyllus* residents unlikely to be related to resource availability.	1985

1985	Sweatman, H., 1985. the influence of adults of some coral-reef fishes on larval recruitment. Ecol. Monogr. 55, 469–485.	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density manipulation	intra	juv vs. adult	experimental patch reef	**none**	**none**	no	no	no	YES	no	no
1985	Sweatman, H., 1985. the influence of adults of some coral-reef fishes on larval recruitment. Ecol. Monogr. 55, 469–485.	Pomacentridae	*Dascyllus reticulatus*	n/a	Competitor density manipulation	intra	juv vs. adult	experimental patch reef	**none**	**none**	no	no	no	YES	no	no
1985	Sweatman, H., 1985. the influence of adults of some coral-reef fishes on larval recruitment. Ecol. Monogr. 55, 469–485.	Pomacentridae	*Pomacentrus popei*	n/a	Competitor density manipulation	intra	juv vs. adult	experimental patch reef	**none**	**none**	no	no	no	YES	no	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus leucosternon*	*Acanthurus lineatus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus leucosternon*	*Zebrasoma scopas*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus leucosternon*	*Acanthurus nigrofuscus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus leucosternon*	*Acanthurus triostegus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus lineatus*	*Acanthurus nigrofuscus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus lineatus*	*Zebrasoma scopas*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus lineatus*	*Acanthurus triostegus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus lineatus*	*Acanthurus leucosternon*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus nigrofuscus*	*Acanthurus lineatus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus nigrofuscus*	*Acanthurus leucosternon*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus nigrofuscus*	*Zebrasoma scopas*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus nigrofuscus*	*Acanthurus triostegus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus triostegus*	*Acanthurus lineatus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus triostegus*	*Acanthurus leucosternon*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus triostegus*	*Zebrasoma scopas*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no

no	n/a	n/a	n/a	n/a	POSITIVE	n/a	n/a	n/a	Positive effect of resident conspecific density on recruitment	**NO**	Priority effects are both negative and positive. Positive effect of conspecifics likely due to habitat selection, while negative effects of *Dascyllus* residents unlikely to be related to resource availability.	1985
no	n/a	n/a	n/a	n/a	POSITIVE	n/a	n/a	n/a	Positive effect of resident conspecific density on recruitment	**NO**	Priority effects are both negative and positive. Positive effect of conspecifics likely due to habitat selection, while negative effects of *Dascyllus* residents unlikely to be related to resource availability.	1985
no	n/a	n/a	n/a	n/a	NO	n/a	n/a	n/a	Low settlement so data lacking power to detect an effect	**NO**	Competitive dominance can vary with habitat structure, interference competition responsible for evolution of habitat preferences	1985
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	A. leucosternon took over territory when *A. lineatus* removed. No clear dominance in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	YES	No change in distribution of when *Z.scopas* removed. No clear dominance in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO - ASYMMETRIC	No change in distribution when subordinate *A. nigrofuscus* removed. *A. leucosternon* dominated in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO - ASYMMETRIC	No change in *A. leucosternon* distribution when subordinate *A. triostegus* removed. *A.leucosternon* dominated in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO - ASYMMETRIC	No change in *A. lineatus* distribution when subordinate *A. nigrofuscus* removed. *A. lineatus* dominated in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO - ASYMMETRIC	No change in *A. lineatus* distribution when subordinate *Z. scopas* removed. *A. lineatus* dominated in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO - ASYMMETRIC	No change in *A. lineatus* distribution when subordinate *A. triostegus* removed. *A. lineatus* dominated in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	YES	No change in *A. lineatus* distribution when subordinate *A. leucosternon* removed. No clear dominance in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Subordinate *A. nigrofuscus* took over territory when dominant *A. lineatus* removed. *A. lineatus* dominated in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Subordinate *A. nigrofuscus* took over territory when dominant *A. leucosternon* removed. *A. leucosternon* dominated in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	*A. nigrofuscus* took over territory when *Z. scopas* removed. *Z. scopas* dominant in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO - ASYMMETRIC	No change in *A. nigrofuscus* distribution when subordinate *A. triostegus* removed. *A. nigrofuscus* dominated in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Subordinate *A. triostegus* took over territory when dominant *A. lineatus* removed. *A. lineatus* dominated in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Subordinate *A. triostegus* took over territory when dominant *A. leucosternon* removed. *A. leucosternon* dominated in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Subordinate *A. triostegus* took over territory when dominant *Z. scopas* removed. *Z. scopas* dominated in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986

1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Acanthurus triostegus*	*Acanthurus nigrofuscus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Zebrasoma scopas*	*Acanthurus lineatus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Zebrasoma scopas*	*Acanthurus leucosternon*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Zebrasoma scopas*	*Acanthurus nigrofuscus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1986	Robertson, D.R., Gaines, S.D., 1986. interference competition structures habitat use in a local assemblage of coral-reef surgeonfishes. Ecology 67, 1372–1383.	Acanthuridae	*Zebrasoma scopas*	*Acanthurus triostegus*	Competitor density manipulation	inter	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
1987	Jones, G.P., 1987. some interactions between residents and recruits in two coral reef fishes. Journal of Experimental Marine Biology and Ecology 114, 169–182.	Pomacentridae	*Pomacentrus amboinensis*	*Dascyllus aruanus*	Competitor density manipulation	inter	among juv	experimental patch reef	**none**	**none**	YES	YES	no	no	no	no
1987	Jones, G.P., 1987. some interactions between residents and recruits in two coral reef fishes. Journal of Experimental Marine Biology and Ecology 114, 169–182.	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**none**	**none**	YES	YES	no	no	no	no
1987	Jones, G.P., 1987. some interactions between residents and recruits in two coral reef fishes. Journal of Experimental Marine Biology and Ecology 114, 169–182.	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**none**	**none**	YES	YES	no	no	no	no
1987	Jones, G.P., 1987. competitive interactions among adults and juveniles in a coral-reef fish. Ecology 68, 1534–1547.	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**none**	**none**	YES	YES	YES	no	no	no
1987	Jones, G.P., 1987. competitive interactions among adults and juveniles in a coral-reef fish. Ecology 68, 1534–1547.	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	intra	juv vs. adult	experimental patch reef	**none**	**none**	YES	YES	YES	no	no	no
1987	Jones, G.P., 1987. competitive interactions among adults and juveniles in a coral-reef fish. Ecology 68, 1534–1547.	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**none**	**none**	YES	YES	YES	no	no	no
1987	Jones, G.P., 1987. competitive interactions among adults and juveniles in a coral-reef fish. Ecology 68, 1534–1547.	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	intra	juv vs. adult	experimental patch reef	**none**	**none**	YES	YES	YES	no	no	no
1988	Jones, G.P., 1988. experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of 2 coral-reef fishes. Journal of Experimental Marine Biology and Ecology 123, 115–126.	Pomacentridae	*Dascyllus aruanus*	*Pomacentrus amboinensis*	Competitor density manipulation	inter	among juv	experimental patch reef	**habitat**	**habitat type**	YES	YES	no	no	no	no
1988	Jones, G.P., 1988. experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of 2 coral-reef fishes. Journal of Experimental Marine Biology and Ecology 123, 115–126.	Pomacentridae	*Pomacentrus amboinensis*	*Dascyllus aruanus*	Competitor density manipulation	inter	among juv	experimental patch reef	**habitat**	**habitat type**	YES	YES	no	no	no	no
1988	Jones, G.P., 1988. experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of 2 coral-reef fishes. Journal of Experimental Marine Biology and Ecology 123, 115–126.	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**habitat**	**habitat type**	YES	YES	no	no	no	no
1988	Jones, G.P., 1988. experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of 2 coral-reef fishes. Journal of Experimental Marine Biology and Ecology 123, 115–126.	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**habitat**	**habitat type**	YES	YES	no	no	no	no
1989	Clarke RD. 1989. Population Fluctuation, Competition and Microhabitat Distribution of Two Species of Tube Blennies, Acanthemblemaria (Teleostei: Chaenopsidae). B Mar Sci. 44(3):1174–85	Blenniidae	*Aacanthemblemaria aspera*	*Acanthemblemaria spinosa*	Competitor density manipulation	inter	among adults	experimental patch reef	**habitat**	**shelter holes**	no	no	no	no	YES	no
1989	Clarke RD. 1989. Population Fluctuation, Competition and Microhabitat Distribution of Two Species of Tube Blennies, Acanthemblemaria (Teleostei: Chaenopsidae). B Mar Sci. 44(3):1174–85	Blenniidae	*Aacanthemblemaria aspera*	n/a	Competitor density manipulation	intra	among adults	natural reef	**habitat**	**shelter holes**	no	no	no	no	YES	no

YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Subordinate *A. triostegus* took over territory when dominant *A. nigrofuscus* removed. *A. nigrofuscus* dominated in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Subordinate *Z. scopas* took over territory when dominant *A. lineatus* removed. *A. lineatus* dominated in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	*Z. scopas* took over territory when *A. leucosternon* removed. No clear dominance in aggressive encounters.	**YES**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO	No change in distribution of *Z. scopas* when *A. nigrofuscus* removed. *Z. scopas* dominant in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
YES	aggression	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO	No change in *Z. scopas* distribution when subordinate *A. triostegus* removed. *Z. scopas* dominated in aggressive encounters.	**NO**	Interference competition promotes habitat partitioning among food competitors. Dominance is often not strongly asymmetrical.	1986
no	n/a	NO	NO	n/a	n/a	n/a	n/a	n/a	No effect of interspecific competitor presence on survival or growth of P. amboinensis	**NO**	Competitive effects are species-specific, intraspecific effects stronger than those between species	1987
no	n/a	NEGATIVE	NO	n/a	n/a	n/a	n/a	n/a	Survival decreased with density both in presence and absence of conspecific prior residents	**YES**	Competitive effects are species-specific, intraspecific effects stronger than those between species	1987
no	n/a	NO	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Increased conspecific density reduced growth, but no effect of density or prior residents on survival	**YES**	Competitive effects are species-specific, intraspecific effects stronger than those between species	1987
no	n/a	NO	NEGATIVE	NO	n/a	n/a	n/a	n/a	0+ years (focal): Growth decreased with juv density in first 8 months,	**YES**	Post-recruitment competitive processes restrict adult population size through delayed maturation	1987
no	n/a	NO	NO	NEGATIVE	n/a	n/a	n/a	n/a	0+ years (focal): Growth not affected by adult presence, but maturation delayed	**YES**	Post-recruitment competitive processes restrict adult population size through delayed maturation	1987
no	n/a	NO	NO	NO	n/a	n/a	n/a	n/a	1+ years (focal): No effects of initial juvenile density on survival, growth or maturation on 1+ years.	**NO**	Post-recruitment competitive processes restrict adult population size through delayed maturation	1987
no	n/a	NO	NEGATIVE	NEGATIVE	n/a	n/a	n/a	n/a	1+ years (focal): 1+ yr growth and age of maturation decreased in presence of adults	**YES**	Post-recruitment competitive processes restrict adult population size through delayed maturation	1987
no	n/a	NO	NO	n/a	n/a	n/a	n/a	n/a	No effect of interspecific competitor on growth or survival	**NO**	Coral substratum type has stronger effect than competitor density on survival. Competitive effects are species-specific.	1988
no	n/a	NO	NO	n/a	n/a	n/a	n/a	n/a	Weak positive effect of *D. aruanus* density on survival, but no effect on growth	**YES**	Coral substratum type has stronger effect than competitor density on survival. Competitive effects are species-specific.	1988
no	n/a	NEGATIVE	NO	n/a	n/a	n/a	n/a	n/a	Negative effect of conspecific density on survival but not growth.	**NO**	Coral substratum type has stronger effect than competitor density on survival. Competitive effects are species-specific.	1988
no	n/a	POSITIVE	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Positive effect of conspecific density on survival, but negative effect on growth.	**YES**	Coral substratum type has stronger effect than competitor density on survival. Competitive effects are species-specific.	1988
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Both species prefer higher position in habitat, but when they co-occur *A. spinosa* excludes *A. aspera*	**YES**	Evidence of strong intra- and interspecific competition over mutually preferred resource. **Competition can occur below carrying capacity of habitat, as it is likely to be variation resource quality that individuals are competing over.**	1989
no	n/a	n/a	n/a	n/a	n/a	NO	n/a	n/a	*A. aspera* shelter holes generally not reoccupied after removal of conspecifics	**NO**	Evidence of strong intra- and interspecific competition over mutually preferred resource. **Competition can occur below carrying capacity of habitat, as it is likely to be variation resource quality that individuals are competing over.**	1989

1989	Clarke RD. 1989. Population Fluctuation, Competition and Microhabitat Distribution of Two Species of Tube Blennies, Acanthemblemaria (Teleostei: Chaenopsidae). B Mar Sci. 44(3):1174–85	Blenniidae	*Acanthemblemaria spinosa*	n/a	Competitor density manipulation	intra	among adults	natural reef	**habitat**	**shelter holes**	no	no	no	no	YES	no
1990	Forrester GE. 1990. Factors Influencing the Juvenile Demography of a Coral-Reef Fish. Ecology. 71(5):1666–81	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density + resource manipulation	intra	among juv	experimental patch reef	**food**	**food**	YES	YES	YES	no	no	no
1990	Forrester GE. 1990. Factors Influencing the Juvenile Demography of a Coral-Reef Fish. Ecology. 71(5):1666–81	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density + resource manipulation	intra	juv vs. adult	experimental patch reef	**food**	**food**	YES	YES	YES	no	no	no
1990	Jones GP. 1990. The Importance of Recruitment to the Dynamics of a Coral-Reef Fish Population. Ecology. 71(5):1691–98	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	intra	juv vs. adult	natural patch reef	**none**	**none**	no	no	no	no	no	YES
1991	Forrester GE. 1991. Social Rank, Individual Size and Group Composition as Determinants of Food-Consumption by Humbug Damselfish, Dascyllus-Aruanus. Animal Behaviour. 42:701–11	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density manipulation	intra	juv vs. adult	natural reef	**food**	**none**	no	no	no	no	YES	no
1992	Buchheim JR, Hixon MA. 1992. Competition for Shelter Holes in the Coral-Reef Fish Acanthemblemaria spinosa Metzelaar. Journal of Experimental Marine Biology and Ecology. 164(1):45–54	Blenniidae	*Acanthemblemaria spinosa*	n/a	Competitor density + resource manipulation	intra	among adults	natural reef	**shelter**	**shelter holes**	YES	no	no	no	YES	no
1992	Clarke RD. 1992. Effects of Microhabitat and Metabolic-Rate on Food-Intake, Growth and Fecundity of 2 Competing Coral-Reef Fishes. Coral Reefs. 11(4):199–205	Blenniidae	*Aacanthemblemaria aspera*	*Acanthemblemaria spinosa*	Resource manipulation	inter	among adults	experimental patch reef	**food**	**position above substrate**	no	YES	YES	no	no	no
1995	Booth DJ. 1995. Juvenile Groups in a Coral-Reef Damselfish - Density-Dependent Effects on Individual Fitness and Population Demography. Ecology. 76(1):91–106	Pomacentridae	*Dascyllus albisella*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**none**	**none**	no	YES	no	no	no	no
1995	Booth DJ. 1995. Juvenile Groups in a Coral-Reef Damselfish - density-dependent effects on individual fitness and population demography. Ecology. 76(1):91–106	Pomacentridae	*Dascyllus albisella*	n/a	Competitor density manipulation	intra	among juv	natural patch reef	**none**	**none**	YES	YES	YES	no	no	no
1995	Forrester GE. 1995. Strong density-dependent survival and recruitment regulate the abundance of a coral-reef fish. Oecologia. 103(3):275–82	Gobiidae	*Coryphopterus glaucofraenum*	n/a	Competitor density manipulation	intra	among adults	experimental patch reef	**shelter**	**none**	YES	YES	no	YES	no	no
1995	Robertson DR. 1995. Competitive ability and the potential for lotteries among territorial reef fishes. Oecologia. 103(2):180–90	Pomacentridae	*Stegastes diencaeus*	*Stegastes dorsopunicans*	Competitor density manipulation	inter	among adults	natural reef	**space**	**none**	no	no	no	no	YES	no
1995	Robertson DR. 1995. Competitive ability and the potential for lotteries among territorial reef fishes. Oecologia. 103(2):180–90	Pomacentridae	*Stegastes diencaeus*	*Stegastes dorsopunicans*	Resource manipulation	inter	among adults	natural reef	**space**	**territory size**	no	no	no	no	YES	no
1995	Robertson DR. 1995. Competitive ability and the potential for lotteries among territorial reef fishes. Oecologia. 103(2):180–90	Pomacentridae	*Stegastes dorsopunicans*	*Stegastes diencaeus*	Competitor density manipulation	inter	among adults	natural reef	**space**	**none**	no	no	no	no	YES	no
1995	Robertson DR. 1995. Competitive ability and the potential for lotteries among territorial reef fishes. Oecologia. 103(2):180–90	Pomacentridae	*Stegastes dorsopunicans*	*Stegastes diencaeus*	Resource manipulation	inter	among adults	natural reef	**space**	**territory size**	no	no	no	no	YES	no
1996	Robertson DR. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology. 77(3):885–99	Pomacentridae	*Stegastes diencaeus*	*Stegastes planifrons*	Competitor density manipulation	inter	among adults	natural patch reef	**habitat**	**none**	no	no	no	no	no	YES
1996	Robertson DR. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology. 77(3):885–99	Pomacentridae	*Stegastes leucostictus*	*Stegastes planifrons*	Competitor density manipulation	inter	among adults	natural patch reef	**habitat**	**none**	no	no	no	no	no	YES
1996	Robertson DR. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology. 77(3):885–99	Pomacentridae	*Stegastes partitus*	*Stegastes planifrons*	Competitor density manipulation	inter	among adults	natural patch reef	**habitat**	**none**	no	no	no	no	no	YES
1996	Robertson DR. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology. 77(3):885–99	Pomacentridae	*Stegastes planifrons*	*Stegastes partitus*	Competitor density manipulation	inter	among adults	natural patch reef	**habitat**	**none**	no	no	no	no	no	YES

no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Most *A. spinosa* holes were reoccupied quickly when conspecifics removed	**YES**	Evidence of strong intra- and interspecific competition over mutually preferred resource. **Competition can occur below carrying capacity of habitat, as it is likely to be variation resource quality that individuals are competing over.**	1989
no	n/a	NEGATIVE	NEGATIVE	NEGATIVE	n/a	n/a	n/a	n/a	Growth increased with feeding but negatively density dependent. Survival decreases with recruit density. Maturation increased with feeding, but had no relationship to initial recruit densities.	**YES**	Food limitation may regulate populations indirectly by affecting growth rates	1990
no	n/a	POSITIVE	NEGATIVE	NEGATIVE	n/a	n/a	n/a	n/a	Presence of adults enhanced survival of recruits, but depressed growth and therefore maturation	**YES**	Food limitation may regulate populations indirectly by affecting growth rates	1990
no	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	Positive density dependent relationship between recruit and adult densities, until asymptote	**NO**	Populations can be both recruitment limited and regulated by density dependent processes, depending on recruitments success	1990
YES	feeding rate	n/a	n/a	n/a	n/a	YES	n/a	YES	The size of prey consumed decreased as group size increased. Fish also fed farther upstream as group size increased. Larger and higher ranked fish within a group consumed larger prey items compared to smaller fish and fed upstream from them.	**YES**	Social rank determines priority access to food	1991
no	n/a	NEGATIVE	n/a	n/a	n/a	YES	n/a	n/a	Large mortality when no shelter holes present, lower when shelter holes added.	**YES**	Shelter holes limited resource for blennies	1992
YES	feeding rate	n/a	NEGATIVE	NEGATIVE	n/a	n/a	n/a	YES	Fitness consequence of interspecific competition. Both species have higher growth, fecundity, and feeding rate at higher position in microhabitat, but *A. spinosa* excludes *A. aspera* from accessing the high position. Subordinate competitor *A. aspera* has lower oxygen consumption and metabolic activity so it is able to cope with lower feeding	**YES**	Lower metabolic rates of allows coexistence as it can persist in lower quality microhabitat	1992
no	n/a	n/a	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Growth decreases in larger groups, and may increase with social rank	**YES**	Fitness effects of group living highly variable between years, complex interactions	1995
YES	aggression	POSITIVE	NEGATIVE	NEGATIVE	n/a	n/a	n/a	YES	Survivorship, aggression and time to maturity increase with group size, while growth decreased with increasing density	**YES**	Fitness effects of group living highly variable between years, complex interactions	1995
no	n/a	NEGATIVE	NO	n/a	NEGATIVE	n/a	n/a	n/a	Density dependent adult mortality, no effect on growth, strong density dependent recruitment	**YES**	Density dependent mortality of adults and density dependent recruitment of juveniles together regulate blennie populations	1995
no	n/a	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	n/a	Distribution does not change upon removal of interspecific competitor	**NO**	Refutes lottery hypothesis - *S. diencaeus* competitively dominant over *S. dorsopunicans* due to size advantage throughout most of life	1995
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	When territory size is reduced, *S. diencaeus* uses aggression to take over living space of smaller (but not larger) conspecific and *S. dorsopunicans* neighbours.	**YES**	Refutes lottery hypothesis - *S. diencaeus* competitively dominant over *S. dorsopunicans* due to size advantage throughout most of life	1995
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Subordinate species takes over territory when dominant *S. diencaeus* is removed	**YES**	Refutes lottery hypothesis - *S. diencaeus* competitively dominant over *S. dorsopunicans* due to size advantage throughout most of life	1995
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	When territory size is reduced, *S. dorsopunicans* uses aggression to take over living space of smaller (but not larger) conspecific and neighbours.	**YES**	Refutes lottery hypothesis - *S. diencaeus* competitively dominant over *S. dorsopunicans* due to size advantage throughout most of life	1995
no	n/a	n/a	n/a	n/a	n/a	n/a	NO	n/a	No change in population abundance following removal of *S. planifrons*	**NO**	Asymmetric competition among congeneric species can influence population size and habitat use.	1996
no	n/a	n/a	n/a	n/a	n/a	n/a	NO	n/a	No change in population abundance following removal of *S. leucostictus*	**NO**	Asymmetric competition among congeneric species can influence population size and habitat use.	1996
no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Population abundance of *S. partitus* doubled after removal of competitively dominant *S. planifrons*	**YES**	Asymmetric competition among congeneric species can influence population size and habitat use.	1996
no	n/a	n/a	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	No change in population abundance following removal of *S. partitus*	**NO**	Asymmetric competition among congeneric species can influence population size and habitat use.	1996

1996	Robertson DR. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology. 77(3):885–99	Pomacentridae	*Stegastes variabilis*	*Stegastes planifrons*	Competitor density manipulation	inter	among adults	natural patch reef	**habitat**	**none**	no	no	no	no	no	YES
1996	Robertson DR. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology. 77(3):885–99	Pomacentridae	*Stegastes variabilis*	*Stegastes partitus*	Competitor density manipulation	inter	among adults	natural patch reef	**habitat**	**none**	no	no	no	no	no	YES
1999	Caselle JE. 1999. Early post-settlement mortality in a coral reef fish and its effect on local population size. Ecol. Monogr. 69(2):177–94	Labridae	*Thalassoma bifasciatum*	n/a	Competitor density manipulation	intra	among juv	natural patch reef	**none**	**none**	YES	no	no	no	no	no
1999	Forrester G. 1999. The influence of adult density an larval settlement in a coral reef fish, *Coryphopterus glaucofraenum*. Coral Reefs. 18(1):85–89	Gobiidae	*Coryphopterus glaucofraenum*	n/a	Competitor density manipulation	intra	juv vs. adult	experimental patch reef	**none**	**none**	no	no	no	YES	no	no
1999	Schmitt RJ, Holbrook SJ. 1999. Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. Oecologia. 118(1):76–86	Pomacentridae	*Dascyllus aruanus*	*Dascyllus flavicaudus*	Competitor density manipulation	inter	among juv	experimental patch reef	**shelter**	**none**	no	no	no	no	no	YES
1999	Schmitt RJ, Holbrook SJ. 1999. Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. Oecologia. 118(1):76–86	Pomacentridae	*Dascyllus flavicaudus*	*Dascyllus aruanus*	Competitor density manipulation	inter	among juv	experimental patch reef	**shelter**	**none**	no	no	no	no	no	YES
1999	Schmitt RJ, Holbrook SJ. 1999. Mortality of juvenile damselfish: implications for assessing processes that determine abundance. Ecology. 80(1):35–50	Pomacentridae	*Dascyllus trimaculatus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**space, shelter**	**none**	YES	no	no	no	no	no
1999	Srinivasan M, Jones GP, Caley MJ. 1999. Experimental evaluation of the roles of habitat selection and interspecific competition in determining patterns of host use by two anemonefishes. Mar. Ecol. Prog. Ser. 186:283–92	Pomacentridae	*Amphiprion melanopus*	*Premnas biaculeatus*	Dominance experiment	inter	among adults	aquarium	**habitat**	**habitat type**	no	no	no	no	YES	no
2000	Forrester GE, Steele MA. 2000. Variation in the presence and cause of density-dependent mortality in three species of reef fishes. Ecology. 81(9):2416–27	Gobiidae	*Coryphopterus nicholsii*	n/a	Competitor density manipulation	intra	among adults	experimental patch reef	**shelter, food, parasitism, disease**	**none**	YES	no	no	no	no	no
2000	Forrester GE, Steele MA. 2000. Variation in the presence and cause of density-dependent mortality in three species of reef fishes. Ecology. 81(9):2416–27	Gobiidae	*Lythrypnus dalli*	n/a	Competitor density manipulation	intra	among adults	experimental patch reef	**space, shelter from predators**	**none**	YES	no	no	no	no	no
2000	Schmitt RJ, Holbrook SJ. 2000. Habitat-limited recruitment of coral reef damselfish. Ecology. 81(12):3479–94	Pomacentridae	*Dascyllus trimaculatus*	*Amphiprion chrysopterus*	Competitor density + resource manipulation	inter	juv vs. adult	experimental patch reef	**habitat**	**anemone cover**	no	no	no	YES	no	no
2000	Schmitt RJ, Holbrook SJ. 2000. Habitat-limited recruitment of coral reef damselfish. Ecology. 81(12):3479–94	Pomacentridae	*Dascyllus flavicaudus*	n/a	Competitor density + resource manipulation	intra	juv vs. adult	experimental patch reef	**habitat**	**coral cover**	no	no	no	YES	no	no
2000	Schmitt RJ, Holbrook SJ. 2000. Habitat-limited recruitment of coral reef damselfish. Ecology. 81(12):3479–94	Pomacentridae	*Dascyllus trimaculatus*	n/a	Competitor density + resource manipulation	intra	juv vs. adult	experimental patch reef	**habitat**	**anemone cover**	no	no	no	YES	no	no
2000	Webster MS, Hixon MA. 2000. Mechanisms and individual consequences of intraspecific competition in a coral-reef fish. Mar. Ecol. Prog. Ser. 196:187–94	Grammatidae	*Gramma loreto*	n/a	Competitor density manipulation	intra	juv vs. adult	natural reef	**food**	**none**	no	no	no	no	YES	no
2001	Munday PL. 2001. Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia. 128(4):585–93	Gobiidae	*Gobiodon brochus*	*Gobiodon histrio*	Resource manipulation	inter	among juv	natural reef	**habitat**	**habitat type**	YES	YES	no	no	no	no
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon axillaris*	*Gobiodon histrio*	Competitor density manipulation	inter	among adults	natural reef	**space**	**none**	no	no	no	no	no	YES
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon axillaris*	*Gobiodon histrio*	Dominance experiment	inter	among adults	aquarium	**habitat**	**none**	no	no	no	no	YES	no
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon brochus*	*Gobiodon histrio*	Competitor density manipulation	inter	among adults	natural reef	**space**	**none**	no	no	no	no	no	YES

no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Population abundance of *S. varibilis* doubled after removal of competitively dominant *S. planifrons*	**YES**	Asymmetric competition among congeneric species can influence population size and habitat use.	1996
no	n/a	n/a	n/a	n/a	n/a	n/a	NO	n/a	No change in population abundance following removal of *S. partitus*	**NO**	Asymmetric competition among congeneric species can influence population size and habitat use.	1996
no	n/a	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Density dependent mortality in first 24 hrs., density independent mortality in following 30 days	**YES**	Recruitment limitation and post-settlement density dependent not mutually exclusive, populations densities shaped at times by both recruitment, and density dependent processes.	1999
no	n/a	n/a	n/a	n/a	NO	n/a	n/a	n/a	Larval settlement is independent of adult densities	**NO**	Larvae do not select settlement sites based on number of adults present	1999
no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Population growth rate reduced in presence of interspecific competitor	**YES**	Interspecific competition strong during juvenile stage. Multiple processes structure coral reef fish communities.	1999
no	n/a	n/a	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	No effect of interspecific competitor presence on population growth	**NO**	Interspecific competition strong during juvenile stage. Multiple processes structure coral reef fish communities.	1999
no	n/a	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Intra- and intercohort density dependent mortality of settlers	**YES**	Density dependent mortality occurs primarily directly after settlement	1999
YES	aggression	n/a	n/a	n/a	n/a	NO	n/a	NO	Neither species was aggressively dominant over other, or able to displace the other from preferred habitat.	**NO**	No competitive asymmetry or reversal of dominance in preferred habitat. Social interactions and habitat preference govern distribution.	1999
no	n/a	NO	n/a	n/a	n/a	n/a	n/a	n/a	Density independent survival	**NO**	Goby not refuge limited in experiment	2000
no	n/a	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Decreased survival with increased density in predator present treatments only	**YES**	Density dependent survival entirely caused by predation	2000
no	n/a	n/a	n/a	n/a	NEGATIVE	n/a	n/a	n/a	Presence of resident *A. chrysopterus* reduced density of *D. trimaculatus* settlers by 67%	**YES**	When habitat is limited, density of residents can supress further settlement of conspecifics and heterospecifics.	2000
no	n/a	n/a	n/a	n/a	NEGATIVE	n/a	n/a	n/a	Presence of resident conspecifics reduced density of settlers by 94%	**YES**	When habitat is limited, density of residents can supress further settlement of conspecifics and heterospecifics.	2000
no	n/a	n/a	n/a	n/a	NEGATIVE	n/a	n/a	n/a	Presence of resident conspecifics reduced density of settlers by ~74%	**YES**	When habitat is limited, density of residents can supress further settlement of conspecifics and heterospecifics.	2000
YES	feeding rate, aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Large fish push smaller fish into sub-optimal feeding positions; Large fish reduce feeding rate of smaller fish, Large fish more aggressive against small fish	**YES**	Feeding rates may translate into density dependent effects on basslet populations	2000
no	n/a	NO	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Fitness consequence of competition. Both species have higher growth rate on *A. nasuta* corals compared to *A. loripes* corals. No decrease in survival of subordinate competitor in less preferred coral, but survival of dominant competitor is 5x lower in less preferred coral.	**YES**	There is a trade-off between competitive ability and cost of using alternative habitat.	2001
no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Abundance increased when interspecific competitor removed	**YES**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Species prefer same coral and are competitively equal, body size and prior residency determines which species inhabits the preferred coral. Supports coexistence via Lottery model.	**NO**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Abundance increased when interspecific competitor removed	**YES**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001

2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon brochus*	*Gobiodon histrio*	Dominance experiment	inter	among adults	aquarium	**habitat**	**none**	no	no	no	no	YES	no
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon quinquestrigatus*	*Gobiodon histrio*	Competitor density manipulation	inter	among adults	natural reef	**space**	**none**	no	no	no	no	no	YES
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon quinquestrigatus*	*Gobiodon histrio*	Dominance experiment	inter	among adults	aquarium	**habitat**	**none**	no	no	no	no	YES	no
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon rivulatus*	*Gobiodon histrio*	Competitor density manipulation	inter	among adults	natural reef	**space**	**none**	no	no	no	no	no	YES
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon rivulatus*	*Gobiodon histrio*	Dominance experiment	inter	among adults	aquarium	**habitat**	**none**	no	no	no	no	YES	no
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon unicolor*	*Gobiodon histrio*	Competitor density manipulation	inter	among adults	natural reef	**space**	**none**	no	no	no	no	no	YES
2001	Munday PL, Jones GP, Caley MJ. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology. 82(8):2177–89	Gobiidae	*Gobiodon unicolor*	*Gobiodon histrio*	Dominance experiment	inter	among adults	aquarium	**habitat**	**none**	no	no	no	no	YES	no
2002	Carr MH, Anderson TW, Hixon MA. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. Proc. Natl. Acad. Sci. U. S. A. 99(17):11241–45	Pomacentridae	*Stegastes partitus*	*Stegastes leucostictus*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**shelter**	**none**	YES	no	no	no	no	no
2002	Carr MH, Anderson TW, Hixon MA. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. Proc. Natl. Acad. Sci. U. S. A. 99(17):11241–45	Pomacentridae	*Stegastes partitus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**shelter**	**none**	YES	no	no	no	no	no
2002	Holbrook SJ, Schmitt RJ. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology. 83(10):2855–68	Pomacentridae	*Dascyllus flavicaudus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**shelter**	**none**	YES	no	no	no	YES	no
2002	Holbrook SJ, Schmitt RJ. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology. 83(10):2855–68	Pomacentridae	*Dascyllus trimaculatus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**shelter**	**none**	YES	no	no	no	YES	no
2002	Wilson J, Osenberg CW. 2002. Experimental and observational patterns of density-dependent settlement and survival in the marine fish *Gobiosoma.* Oecologia. 130(2):205–15	Gobiidae	*Gobiosoma spp.*	n/a	Competitor density manipulation	intra	juv vs. adult	natural reef	**none**	**none**	no	no	no	YES	no	no
2002	Wilson J, Osenberg CW. 2002. Experimental and observational patterns of density-dependent settlement and survival in the marine fish *Gobiosoma.* Oecologia. 130(2):205–15	Gobiidae	*Gobiosoma spp.*	n/a	Competitor density manipulation	intra	juv vs. adult	natural patch reef	**none**	**none**	YES	no	no	YES	no	no
2003	Almany GR. 2003. Priority effects in coral reef fish communities. Ecology. 84(7):1920–35	*Acanthuridae*	*Acanthurus coeruleus*	*Stegastes spp.*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	no	no	no	YES	no	no
2003	Almany GR. 2003. Priority effects in coral reef fish communities. Ecology. 84(7):1920–35	Pomacentridae	*Stegastes leucostictus*	*Stegastes spp.*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	no	no	no	YES	no	no
2003	Almany GR. 2003. Priority effects in coral reef fish communities. Ecology. 84(7):1920–35	Pomacentridae	*Stegastes partitus*	*Stegastes spp.*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	no	no	no	YES	no	no
2003	Almany GR. 2003. Priority effects in coral reef fish communities. Ecology. 84(7):1920–35	*Labridae*	*Thalassoma bifasciatum*	*Stegastes spp.*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	no	no	no	YES	no	no
2003	Schmitt RJ, Holbrook SJ. 2003. Mutualism can mediate competition and promote coexistence. Ecology Letters. 6(10):898–902	Pomacentridae	*Dascyllus trimaculatus*	*Amphiprion chrysopterus*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	no	no	no	no	no	YES

no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Excluded from preferred coral species in presence of dominant interspecific competitor, subordinate species only gains competitive advantage through larger body size or prior residency.	**YES**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	n/a	n/a	n/a	n/a	n/a	NO	n/a	No change in abundance after removal of interspecific competitor	**NO**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Excluded from preferred coral species in presence of dominant interspecific competitor	**YES**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	n/a	n/a	n/a	n/a	n/a	NO	n/a	No change in abundance after removal of interspecific competitor	**NO**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	n/a	n/a	n/a	n/a	NO	n/a	n/a	Presence of interspecific competitor does not influence habitat use, prefer different coral species	**NO**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	n/a	n/a	n/a	n/a	n/a	NO	n/a	No change in abundance after removal of interspecific competitor	**NO**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	n/a	n/a	n/a	n/a	NO	n/a	n/a	Presence of interspecific competitor does not influence resource use, species can coexist on the same colony	**NO**	Interspecific competition important for governing distribution and abundance of some species in a guild but not others.	2001
no	n/a	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Density dependent mortality of juveniles only occurred when larger adult interference competitors and predators were both present. Adult interference competitors were combination of conspecifics and heterospecifics.	**YES**	Interactions with adult prior residents induces competition for predator refuges.	2002
no	n/a	NO	n/a	n/a	n/a	n/a	n/a	n/a	No refuge competition among juveniles (regardless of predator presence/absence)	**NO**	Interactions with adult prior residents induces competition for predator refuges.	2002
YES	aggression	NEGATIVE	n/a	n/a	n/a	YES	n/a	YES	Decreased survival with increased density in predator present treatments only. Resource use changes with increased density - more fish in risky shelter positions. Aggression increases with density	**YES**	DD mortality due to interference competition for refuge space from predators	2002
no	n/a	NEGATIVE	n/a	n/a	n/a	YES	n/a	YES	Survival decreases with increasing density. Resource use also changes with increased density - more fish in risky shelter positions.	**YES**	Density dependent mortality due to interference competition for refuge space from predators	2002
no	n/a	n/a	n/a	n/a	NO	n/a	n/a	n/a	Presence/absence of resident adult gobies did not influence levels of settlement to coral heads, instead settlement driven by attribute of particular coral heads	**NO**	Strong evidence of density dependent settlement and survival of juvenile gobies in the experiment contrasts with observational data, suggests 'cryptic density dependent'	2002
no	n/a	NEGATIVE	n/a	n/a	NEGATIVE	n/a	n/a	n/a	Density dependent settlement and juvenile survival for *Gobiosoma* spp. High densities of resident conspecifics (juveniles and adults) induced lower settlement and survival.	**YES**	Strong evidence of density dependent settlement and survival of juvenile gobies in the experiment contrasts with observational data, suggests 'cryptic density dependent'	2002
no	n/a	n/a	n/a	n/a	POSITIVE	n/a	n/a	n/a	Presence of resident adult interspecific competitors enhanced recruitment when predators absent, but when predators present these adult competitors reduced recruitment slightly.	**NO**	Prior resident competitors can influence recruitment, whether positive or negative effect is species-specific. Presence of predators can influence effect of competitors.	2003
no	n/a	n/a	n/a	n/a	NEGATIVE	n/a	n/a	n/a	Presence of resident adult competitors reduced recruitment when predators absent, but when predators present these adult competitors had little influence on recruitment.	**YES**	Prior resident competitors can influence recruitment, whether positive or negative effect is species-specific. Presence of predators can influence effect of competitors.	2003
no	n/a	n/a	n/a	n/a	NO	n/a	n/a	n/a	No significant effect of adult resident competitor presence/absence on recruitment	**NO**	Prior resident competitors can influence recruitment, whether positive or negative effect is species-specific. Presence of predators can influence effect of competitors.	2003
no	n/a	n/a	n/a	n/a	NO	n/a	n/a	n/a	No significant effect of adult resident competitor presence/absence on recruitment	**NO**	Prior resident competitors can influence recruitment, whether positive or negative effect is species-specific. Presence of predators can influence effect of competitors.	2003
no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Density of decreased with increasing density of interspecific space competitor	**YES**	Mutualism between anemonefish and host allows *Dascyllus* space competitors to co-exist because anemonefish presence increases the quantity of their shared resource.	2003

2003	Webster MS. 2003. Temporal density dependence and population regulation in a marine fish. Ecology. 84(3):623–28	Grammatidae	*Gramma loreto*	n/a	Competitor density manipulation	intra	among juv	natural reef	**none**	**none**	YES	YES	no	YES	no	no
2004	Almany GR. 2004. Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology. 85(10):2872–80	assemblage - Pomacentridae	*assemblage*	*assemblage*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	YES	no	no	YES	no	no
2004	Almany GR. 2004. Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology. 85(10):2872–80	assemblage - Chaetodontidae	*assemblage*	*assemblage*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	YES	no	no	YES	no	no
2004	Almany GR. 2004. Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology. 85(10):2872–80	assemblage - Acanthuridae	*assemblage*	*assemblage*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	YES	no	no	YES	no	no
2004	Almany GR. 2004. Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology. 85(10):2872–80	assemblage - Siganidae	*assemblage*	*assemblage*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	YES	no	no	YES	no	no
2004	Almany GR. 2004. Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology. 85(10):2872–80	Pomacentridae	Neopomacentrus cyanomos	*assemblage*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**space**	**none**	YES	no	no	YES	no	no
2004	Booth DJ. 2004. Synergistic effects of conspecifics and food on growth and energy allocation of a damselfish. Ecology. 85(10):2881–87	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density + resource manipulation	intra	juv vs. adult	experimental patch reef	**food**	**none**	no	YES	no	no	no	no
2004	Forrester G, Steele M. 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. Ecology. 85(5):1332–42	Labridae	*Coryphopterus glaucofraenum*	n/a	Competitor density + resource manipulation	intra	among adults	experimental patch reef	**shelter**	**shelter**	YES	no	no	no	no	no
2004	Hobbs J, Munday PL. 2004. Intraspecific competition controls spatial distribution and social organisation of the coral-dwelling goby *Gobiodon histrio*. Mar. Ecol. Prog. Ser. 278:253–59	Gobiidae	*Gobiodon histrio*	n/a	Dominance experiment	intra	juv vs. adult	aquarium	**habitat size**	**habitat size**	no	no	no	no	YES	no
2004	Holbrook SJ, Schmitt RJ. 2004. Population dynamics of a damselfish: Effects of a competitor that also is an indirect mutualist. Ecology. 85(4):979–85	Pomacentridae	*Dascyllus trimaculatus*	*Amphiprion chrysopterus*	Competitor density manipulation	inter	juv vs. adult	experimental patch reef	**shelter**	**none**	no	no	no	no	no	YES
2004	Munday PL. 2004. Competitive coexistence of coral-dwelling fishes: The lottery hypothesis revisited. Ecology. 85(3):623–28	Gobiidae	*Gobiodon histrio*	*Gobiodon erythrospilus*	Dominance experiment	inter	among juv	aquarium	**space**	**none**	no	no	no	no	YES	no
2004	Munday PL. 2004. Competitive coexistence of coral-dwelling fishes: The lottery hypothesis revisited. Ecology. 85(3):623–28	Gobiidae	*Gobiodon erythrospilus*	*Gobiodon histrio*	Competitor density manipulation	inter	juv vs. adult	natural reef	**space**	**none**	no	no	no	no	no	YES
2004	Munday PL. 2004. Competitive coexistence of coral-dwelling fishes: The lottery hypothesis revisited. Ecology. 85(3):623–28	Gobiidae	*Gobiodon histrio*	*Gobiodon erythrospilus*	Competitor density manipulation	inter	juv vs. adult	natural reef	**space**	**none**	no	no	no	no	no	YES
2004	Webster MS. 2004. Density dependence via intercohort competition in a coral-reef fish. Ecology. 85(4):986–94	Grammatidae	*Gramma loreto*	n/a	Competitor density manipulation	intra	juv vs. adult	natural reef	**food**	**none**	YES	YES	no	YES	YES	no
2004	Whiteman EA, Cote IM. 2004. Dominance hierarchies in group-living cleaning gobies: causes and foraging consequences. Animal Behaviour. 67:239–47	Gobiidae	*Elacatinus prochilos*	n/a	Competitor density manipulation	intra	among adults	natural reef	**food**	**none**	no	no	no	no	YES	no
2005	Hixon MA, Jones GP. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. Ecology. 86(11):2847–59	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	Intra	among juv	experimental patch reef	**none**	**none**	YES	YES	no	no	no	no
2005	Thompson AR. 2005. Dynamics of demographically open mutualists: immigration, intraspecific competition, and predation impact goby populations. Oecologia. 143(1):61–69	Gobiidae	*Ctenogobiops feroculus*	n/a	Competitor density manipulation	intra	among adults	natural reef	**shelter**	**none**	no	no	no	no	YES	YES
2005	Wilson JA. 2005. Age class interactions in a marine goby, *Elacatinus prochilos* (Bohlke and Robins, 1968). Journal of Experimental Marine Biology and Ecology. 327(2):144–56	Gobiidae	*Elacatinus prochilos*	n/a	Competitor density manipulation	intra	among juv	natural patch reef	**Habitat quality**	**habitat quality**	YES	no	no	no	no	no

YES	aggression	NEGATIVE	NO	n/a	NO	n/a	n/a	NO	Survival and emigration negative density dependent. Recruitment, growth and aggression density independent	**YES**	Population not regulated by competitive effects but by density dependent predation	2003
no	n/a	NO	n/a	n/a	NEGATIVE	n/a	n/a	n/a	Presence of resident adult interspecific competitors reduced recruitment when predators absent, but when predators present these adult competitors had little influence on recruitment.	**YES**	Prior resident competitors can influence recruitment, but whether effect is positive or negative is species-specific. Presence of predators can influence effect of competitors.	2004
no	n/a	NO	n/a	n/a	NO	n/a	n/a	n/a	No significant effect of adult resident competitor presence/absence on recruitment	**NO**	Prior resident competitors can influence recruitment, but whether effect is positive or negative is species-specific. Presence of predators can influence effect of competitors.	2004
no	n/a	NO	n/a	n/a	NO	n/a	n/a	n/a	No significant effect of adult resident competitor presence/absence on recruitment	**NO**	Prior resident competitors can influence recruitment, but whether effect is positive or negative is species-specific. Presence of predators can influence effect of competitors.	2004
no	n/a	NO	n/a	n/a	NO	n/a	n/a	n/a	No significant effect of adult resident competitor presence/absence on recruitment	**NO**	Prior resident competitors can influence recruitment, but whether effect is positive or negative is species-specific. Presence of predators can influence effect of competitors.	2004
no	n/a	NO	n/a	n/a	NO	n/a	n/a	n/a	No significant effect of adult resident competitor presence/absence on recruitment	**NO**	Prior resident competitors can influence recruitment, but whether effect is positive or negative is species-specific. Presence of predators can influence effect of competitors.	2004
YES	distance to shelter, aggression	n/a	POSITIVE	n/a	n/a	n/a	n/a	YES	Interaction between food supplementation and competitor presence. Positive effect of conspecific on growth on food supplemented reefs, no effect of conspecifics on control reefs. Unfed fish with conspecific adults present forage further away from shelter; aggression increases with supplemental food	**YES**	Recruits are food limited, but feeding augmented by presence of adults	2004
YES	feeding rate, aggression, distance to shelter	NEGATIVE	n/a	n/a	n/a	n/a	n/a	YES	Density dependent aggression and survival, exacerbated by refuge limitation. No difference in effect between scales	**YES**	Density dependent mortality due to interference competition for refuge space from predators	2004
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Small and large fish both prefer large corals, but small fish excluded from large corals when large fish present	**YES**	Ability to compete for large corals influences reproductive success	2004
no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Negative effect of resident anemonefish on density of juvenile , but effect of competitor on total abundance was weak because anemonefish increase the growth of shared resource, meaning more resource to go around when they are present.	**YES**	Mutualisms can mediate the effects of competition. In this case the mutualism reduced the negative effect of a superior competitor (anemonefish) on an inferior competitor *(Dascyllus)*	2004
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Prior residents of either species able to exclude newcomers of other species from shared habitat.	**YES**	Equal competitive ability, coexistence via lottery with prior residents able to exclude arriving space competitors.	2004
no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Removal of interspecific competitor caused increase in abundance	**YES**	Equal competitive ability, coexistence via lottery with prior residents able to exclude arriving space competitors.	2004
no	n/a	n/a	n/a	n/a	n/a	n/a	YES	n/a	Removal of interspecific competitor caused increase in abundance	**YES**	Equal competitive ability, coexistence via lottery with prior residents able to exclude arriving space competitors.	2004
YES	aggression	NEGATIVE	NO	n/a	NO	YES	n/a	NO	Survival decreased with increased density of adults; juvenile feeding in suboptimal position when adults present, aggression and growth unaffected by presence of adults	**YES**	Adults force juveniles to feed in less optimal positions, with higher risk of predation, thus regulating local populations	2004
YES	aggression, feeding rate	n/a	n/a	n/a	n/a	YES	n/a	YES	Removal of highest ranked individual results in shift in distribution of lower ranked individuals into the territories previously occupied by dominant gobies	**YES**	Gobies demonstrate size-structured social groups, with stable dominance hierarchies supported and maintained by physical attributes	2004
no	n/a	NEGATIVE	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Density dependent survival only after 17 months, in both presence and absence of predators. Variability in size decreased at higher densities.	**YES**	Competition is major agent of density dependence, predation is the terminal cause and is intrinsically linked to the availability of prey refuges in microhabitat.	2005
no	n/a	n/a	n/a	n/a	n/a	YES	NO	n/a	Experimental addition of gobies to replicate plots resulted in no increase in total abundance. But larger fish displaced smaller fish from shrimp burrows.	**YES**	Strong intraspecific competition for limited number of shrimp burrows. Mutualistic populations remain stable by competition over shelter holes and immigration	2005
no	n/a	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Survival of both recruits and adults decrease with increasing density of adults; Recruits decreased survival on lower quality habitat	**YES**	While competition is acting in system, population appears unstructured. Intercohort experiments crucial to extrapolate competitive effects over larger spatial and temporal scales.	2005

2006	Forrester GE, Evans B, Steele MA, Vance RR. 2006. Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. Oecologia. 148(4):632–40	Gobiidae	*Coryphopterus glaucofraenum*	*Gnatholepis thompsoni*	Competitor density manipulation	inter	among adults	experimental patch reef	**shelter**	**none**	no	YES	no	no	no	no
2006	Forrester GE, Evans B, Steele MA, Vance RR. 2006. Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. Oecologia. 148(4):632–40	Gobiidae	*Gnatholepis thompsoni*	*Coryphopterus glaucofraenum*	Competitor density manipulation	inter	among adults	experimental patch reef	**shelter**	**none**	no	YES	no	no	no	no
2006	Forrester GE, Evans B, Steele MA, Vance RR. 2006. Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. Oecologia. 148(4):632–40	Gobiidae	*Coryphopterus glaucofraenum*	n/a	Competitor density manipulation	intra	among adults	experimental patch reef	**shelter**	**none**	no	YES	no	no	no	no
2006	Forrester GE, Evans B, Steele MA, Vance RR. 2006. Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. Oecologia. 148(4):632–40	Gobiidae	*Gnatholepis thompsoni*	n/a	Competitor density manipulation	intra	among adults	experimental patch reef	**shelter**	**none**	no	YES	no	no	no	no
2006	McCormick MI. 2006. Mothers matter: crowding leads to stressed mothers and smaller offspring in marine fish. Ecology. 87(5):1104–9	Pomacentridae	*Pomacentrus amboinensis*	n/a	Competitor density manipulation	intra	among adults	experimental patch reef	**mates**	**none**	no	no	YES	no	no	no
2007	Schmitt RJ, Holbrook SJ. 2007. The scale and cause of spatial heterogeneity in strength of temporal density dependence. Ecology. 88(5):1241–49	Pomacentridae	*Dascyllus flavicaudus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**shelter**	**none**	YES	no	no	no	no	no
2008	Forrester GE, Steele MA, Samhouri JF, Evans B, Vance RR. 2008. Spatial density dependence scales up but does not produce temporal density dependence in a reef fish. Ecology. 89(11):2980–85	Gobiidae	*Gnatholepis thompsoni*	*Coryphopterus glaucofraenum*	Competitor density manipulation	inter	among adults	experimental patch reef	**none**	**none**	YES	no	no	no	no	no
2008	Forrester GE, Steele MA, Samhouri JF, Evans B, Vance RR. 2008. Spatial density dependence scales up but does not produce temporal density dependence in a reef fish. Ecology. 89(11):2980–85	Gobiidae	*Gnatholepis thompsoni*	n/a	Competitor density manipulation	intra	among adults	experimental patch reef	**none**	**none**	YES	no	no	no	no	no
2008	Johnson DW. 2008. Combined effects of condition and density on post-settlement survival and growth of a marine fish. Oecologia. 155(1):43–52	Pomacentridae	*Stegastes partitus*	n/a	Competitor density manipulation	intra	among juv	natural reef	**none**	**none**	YES	YES	no	no	no	no
2008	Johnson DW. 2008. Combined effects of condition and density on post-settlement survival and growth of a marine fish. Oecologia. 155(1):43–52	Pomacentridae	*Stegastes partitus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**none**	**none**	YES	YES	no	no	no	no
2008	Wong MYL, Munday PL, Buston PM, Jones GP. 2008. Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. Behavioral Ecology. 19(2):353–61	Gobiidae	*Paragobiodon xanthosomus*	n/a	Resource manipulation	intra	among adults	experimental patch reef	**food**	**food**	no	no	YES	no	no	no
2008	Wong MYL, Munday PL, Buston PM, Jones GP. 2008. Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. Behavioral Ecology. 19(2):353–61	Gobiidae	*Paragobiodon xanthosomus*	n/a	Resource manipulation	intra	among adults	aquarium	**food**	**food**	no	YES	YES	no	no	no
2008	Wong MYL, Munday PL, Buston PM, Jones GP. 2008. Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. Behavioral Ecology. 19(2):353–61	Gobiidae	*Paragobiodon xanthosomus*	n/a	Resource manipulation	intra	among adults	aquarium	**mates**	**mates**	no	no	no	no	YES	no
2009	Bonin MC, Srinivasan M, Almany GR, Jones GP. 2009. Interactive effects of interspecific competition and microhabitat on early post-settlement survival in a coral reef fish. Coral Reefs. 28(1):265–74	Pomacentridae	*Chrysiptera parasema*	*Dascyllus melanurus*	Competitor density manipulation	inter	among juv	experimental patch reef	**habitat**	**microhabitat type**	YES	no	no	no	no	no
2009	Bonin MC, Srinivasan M, Almany GR, Jones GP. 2009. Interactive effects of interspecific competition and microhabitat on early post-settlement survival in a coral reef fish. Coral Reefs. 28(1):265–74	Pomacentridae	*Chrysiptera parasema*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**habitat**	**microhabitat type**	YES	no	no	no	no	no
2009	Bonin MC, Srinivasan M, Almany GR, Jones GP. 2009. Interactive effects of interspecific competition and microhabitat on early post-settlement survival in a coral reef fish. Coral Reefs. 28(1):265–74	Pomacentridae	*Dascyllus melanurus*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**habitat**	**microhabitat type**	YES	no	no	no	no	no
2009	Geange SW, Stier AC. 2009. Order of arrival affects competition in two reef fishes. Ecology. 90(10):2868–78	Labridae	*Thalassoma hardwicke*	*Thalassoma quinquevittatum*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2009	Geange SW, Stier AC. 2009. Order of arrival affects competition in two reef fishes. Ecology. 90(10):2868–78	Labridae	*Thalassoma quinquevittatum*	*Thalassoma hardwicke*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no

YES	aggression, feeding rate	n/a	NEGATIVE	n/a	n/a	n/a	n/a	YES	Density dependent effect of heterospecifics on growth and aggression, but not feeding rates	**YES**	Intraspecific effects on growth are stronger than interspecific effects.	2006
YES	aggression, feeding rate, refuge use	n/a	NEGATIVE	n/a	n/a	n/a	n/a	YES	Density dependent effect of heterospecifics on growth and refuge use, but not aggression or feeding rates	**YES**	Intraspecific effects on growth are stronger than interspecific effects.	2006
YES	aggression, feeding rate	n/a	NEGATIVE	n/a	n/a	n/a	n/a	YES	Growth rate was density dependent and conspecific effect was 2x stronger than interspecific effect. Aggression increased and foraging rate unaffected by increased density of conspecifics.	**YES**	Intraspecific effects on growth are stronger than interspecific effects.	2006
YES	aggression, feeding rate, refuge use	n/a	NEGATIVE	n/a	n/a	n/a	n/a	YES	Growth rate was density dependent and conspecific effect was 3x stronger than interspecific effect. Aggression increased, shelter use decreased, and foraging rate unaffected by increased density of conspecifics.	**YES**	Intraspecific effects on growth are stronger than interspecific effects.	2006
YES	aggression	n/a	n/a	NEGATIVE	n/a	n/a	n/a	YES	Addition of competing females increased aggression and stress levels of breeding females. Length of larvae produced by breeding females decreased with addition of competing females.	**YES**	Competition over access to mates affects fecundity of breeding females, may mitigate Allee effect	2006
no	n/a	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Negative density dependent survival, replicated temporally rather than spatially because of large differences in predator abundance between experimental sites	**YES**	Failure to replicate experiments temporally rather than spatially may lead to under-estimation of regulatory processes	2007
no	n/a	NO	n/a	n/a	n/a	n/a	n/a	n/a	No density dependent effect of *C. glaucofraenum* on survival of *G. thompsoni*	**NO**	Intraspecific (but not interspecific) competition leads to density dependent mortality in . Unclear what resource is being competed over since density dependent mortality was actually stronger in the year that resources were less limited.	2008
no	n/a	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Density dependent survival, but strength of density dependence varied dramatically between years.	**YES**	Intraspecific (but not interspecific) competition leads to density dependent mortality in . Unclear what resource is being competed over since density dependent mortality was actually stronger in the year that resources were less limited.	2008
no	n/a	NEGATIVE	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Density dependent survival, and strong effect of condition on survival. Density dependent growth only in high condition treatments	**YES**	Variation in condition when settling may influence regulatory effect of density	2008
YES	aggression, time spent sheltering	NO	NEGATIVE	n/a	n/a	n/a	n/a	YES	Levels of aggression predict growth better than density. Level of aggression more strongly density dependent in high condition treatments. No detectable effect of density on survival or time spent sheltering.	**YES**	Variation in condition when settling may influence regulatory effect of density	2008
no	n/a	n/a	n/a	NEGATIVE	n/a	n/a	n/a	n/a	Egg clutches larger from fed females	**YES**	Competition over food and paternal care suppress subordinate females	2008
no	n/a	n/a	n/a	NO	n/a	n/a	n/a	n/a	No effect of feeding on maturation of subordinate females	**NO**	Competition over food and paternal care suppress subordinate females	2008
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Breeding females aggressive towards same sex, not opposite. Maturity and size affects frequency of eviction (mature, larger evicted most often)	**YES**	Competition over food and paternal care suppress subordinate females	2008
no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Presence of *D. melanus* reduced survival of *C. parasema* in both microhabitats	**YES**	Interspecific competition between juveniles can reduce their survival. Competitive effects consistent across microhabitat types.	2009
no	no	NO	n/a	n/a	n/a	n/a	n/a	n/a	No evidence of density dependent mortality on either habitat type	**NO**	Interspecific competition between juveniles can reduce their survival. Competitive effects consistent across microhabitat types.	2009
no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Density dependent mortality on both coral types	**YES**	Interspecific competition between juveniles can reduce their survival. Competitive effects consistent across microhabitat types.	2009
YES	aggression	NEGATIVE	n/a	n/a	n/a	n/a	n/a	YES	Prior residence by juvenile interspecific competitor decreased survival and negative effect was stronger with longer prior residence times. Survival decreased with increasing aggression, and aggression rates were highest with longer prior residence times.	**YES**	Order of arrival influences competitive dominance, supports co-existence via lottery.	2009
YES	aggression	NEGATIVE	n/a	n/a	n/a	n/a	n/a	YES	Prior residence by juvenile interspecific competitor decreased survival and negative effect was stronger with longer prior residence times. Survival decreased with increasing aggression, and aggression rates were highest with longer prior residence times.	**YES**	Order of arrival influences competitive dominance, supports co-existence via lottery.	2009

2009	Geange SW, Stier AC. 2009. Order of arrival affects competition in two reef fishes. Ecology. 90(10):2868–78	Labridae	*Thalassoma hardwicke*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2009	Samhouri JF. 2009. Food supply influences offspring provisioning but not density-dependent fecundity in a marine fish. Ecology. 90(12):3478–88	Pomacentridae	*Stegastes partitus*	n/a	Resource manipulation	intra	among adults	experimental patch reef	**food, mates**	**food**	no	YES	YES	no	no	no
2009	Samhouri JF, Steele MA, Forrester GE. 2009. Inter-cohort competition drives density dependence and selective mortality in a marine fish. Ecology. 90(4):1009–20	Gobiidae	*Gnatholepis thompsoni*	n/a	Resource manipulation	intra	juv vs. adult	natural reef	**shelter**	**shelter**	YES	YES	no	no	no	no
2011	Forrester G, Harmon L, Helyer J, Holden W, Karis R. 2011. Experimental evidence for density-dependent reproductive output in a coral reef fish. Popul Ecol. 53(1):155–63	Labridae	*Coryphopterus glaucofraenum*	n/a	Competitor density manipulation	intra	among adults	experimental patch reef	**mates, nesting sites**	**none**	no	no	YES	no	no	no
2010	Geange SW. 2010. Effects of larger heterospecifics and structural refuge on the survival of a coral reef fish, *Thalassoma hardwicke*. Mar. Ecol. Prog. Ser. 407:197–207	Labridae	*Thalassoma hardwicke*	*Thalassoma quinquevittatum*	Competitor density manipulation	inter	juv vs. adult	natural patch reef	**shelter**	**microhabitat complexity**	YES	no	no	no	no	no
2010	Geange SW, Stier AC. 2010. Priority effects and habitat complexity affect the strength of competition. Oecologia. 163(1):111–18	Labridae	*Thalassoma quinquevittatum*	n/a	Resource manipulation	intra	among juv	experimental patch reef	**habitat complexity**	**habitat complexity**	YES	no	no	no	no	no
2011	Adam TC. 2011. High-quality habitat and facilitation ameliorate competitive effects of prior residents on new settlers. Oecologia. 166(1):121–30	Labridae	*Labroides dimidiatus*	n/a	Competitor density manipulation	intra	juv vs. adult	natural patch reef	**food, habitat quality**	**none**	YES	YES	no	no	no	no
2012	Coker DJ, Pratchett MS, Munday PL. 2012. Influence of coral bleaching, coral mortality and conspecific aggression on movement and distribution of coral-dwelling fish. Journal of Experimental Marine Biology and Ecology. 414:62–68	Pomacentridae	*Dascyllus aruanus*	n/a	Competitor density manipulation	intra	size/age not reported	experimental patch reef, aquarium	**Habitat quality**	**habitat quality**	no	no	no	no	YES	no
2012	Hixon MA, Anderson TW, Buch KL, Johnson DW, McLeod JB, Stallings CD. 2012. Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. Ecol. Monogr. 82(4):467–89	Pomacentridae	*Stegastes partitus*	n/a	Competitor density manipulation	intra	size/age not reported	natural reef	**space, food**	**none**	YES	YES	YES	no	no	no
2012	McCormick MI. 2012. Lethal effects of habitat degradation on fishes through changing competitive advantage. Proc. R. Soc. Lond. Ser. B-Biol. Sci. 279(1744):3899–3904	Pomacentridae	*Pomacentrus amboinensis*	*Pomacentrus moluccensis*	Competitor density manipulation	inter	among juv	experimental patch reef	**habitat**	**habitat quality**	YES	no	no	no	YES	no
2012	McCormick MI. 2012. Lethal effects of habitat degradation on fishes through changing competitive advantage. Proc. R. Soc. Lond. Ser. B-Biol. Sci. 279(1744):3899–3904	Pomacentridae	*Pomacentrus moluccensis*	*Pomacentrus amboinensis*	Competitor density manipulation	inter	among juv	experimental patch reef	**habitat**	**habitat quality**	YES	no	no	no	YES	no
2012	McCormick MI, Weaver CJ. 2012. It Pays to Be Pushy: Intracohort interference competition between two reef fishes. PLoS ONE. 7(8):e42590	Pomacentridae	*Pomacentrus amboinensis*	*Pomacentrus moluccensis*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2012	McCormick MI, Weaver CJ. 2012. It Pays to Be Pushy: Intracohort interference competition between two reef fishes. PLoS ONE. 7(8):e42590	Pomacentridae	*Pomacentrus moluccensis*	*Pomacentrus amboinensis*	Dominance experiment	inter	among juv	experimental patch reef	**space**	**none**	no	no	no	no	YES	no
2012	McCormick MI, Weaver CJ. 2012. It Pays to Be Pushy: Intracohort interference competition between two reef fishes. PLoS ONE. 7(8):e42590	Pomacentridae	*Pomacentrus moluccensis*	*Pomacentrus amboinensis*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2013	Boström-Einarsson L, Bonin MC, Munday PL, Jones GP. 2013. Strong intraspecific competition and habitat selectivity influence abundance of a coral-dwelling damselfish. Journal of Experimental Marine Biology and Ecology. 448:85–92	Pomacentridae	*Chrysiptera parasema*	n/a	Competitor density manipulation	intra	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2013	Geange SW, Stier AC, Shima JS. 2013. Competitive hierarchies among three species of juvenile coral reef fishes. Mar. Ecol. Prog. Ser. 472:239	Labridae	*Gomphosus varius*	*Thalassoma hardwicke*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2013	Geange SW, Stier AC, Shima JS. 2013. Competitive hierarchies among three species of juvenile coral reef fishes. Mar. Ecol. Prog. Ser. 472:239	Labridae	*Gomphosus varius*	*Thalassoma quinquevittatum*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2013	Geange SW, Stier AC, Shima JS. 2013. Competitive hierarchies among three species of juvenile coral reef fishes. Mar. Ecol. Prog. Ser. 472:239	Labridae	*Thalassoma hardwicke*	*Gomphosus varius*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no

YES	aggression	NEGATIVE	n/a	n/a	n/a	n/a	n/a	YES	Prior residence of conspecifics increased mortality and aggression, and strength of effect increased with longer residence times. Strength of intraspecific and interspecific effects on mortality were similar.	**YES**	Order of arrival influences competitive dominance, supports co-existence via lottery.	2009
YES	Chases, feeding rate, courting, sheltering	n/a	NEGATIVE	NEGATIVE	n/a	n/a	n/a	YES	Female growth negatively density dependent, and increases with feeding. Male growth unaffected by food and density. Fecundity negatively density dependent, but unaffected by food. Food increases larval provisioning (oil globule size). Chases increase with density while foraging and mating activities decrease.	**YES**	Density dependent growth and fecundity due to increased aggression in crowded aggregations, not food limitation. Excess food is instead allocated to enhance offspring quality.	2009
no	n/a	NEGATIVE	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Negative density dependent survival and growth of juveniles with adult density. Stronger density dependent mortality on low shelter reefs. Bigger juveniles more likely to survive at high adult density, small juveniles more likely to survive at low adult density	**YES**	Availability of shelter mediates interactions between juveniles and adults. Limited shelter and high density of adults decreases survival of juveniles.	2009
no	n/a	n/a	n/a	NEGATIVE	n/a	n/a	n/a	n/a	Only largest male nests, so negatively density dependent with other fish present. Clutch production and clutch size negatively density dependent with increasing density	**YES**	Constant number of females may spawn, but fecundity is decreased with increased competition, causing population regulation.	2011
no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Presence of larger heterospecific competitors reduced survival of juvenile *T. hardwicke*. This negative effect of competition occurred in both high and low complexity habitats. Effects of habitat complexity on survival were stronger than those of competitors.	**YES**	Competitive effects independent of habitat complexity.	2010
YES	aggression	NEGATIVE	n/a	n/a	n/a	n/a	n/a	YES	Increased habitat complexity increases survival, while prior residents decrease survival due to increased aggression	**YES**	Prior residents greatly increase rates of aggression and decrease chance for survival for new arrivals. Survival chances not mediated by increased habitat complexity, probably due to exclusion by prior residents.	2010
no	n/a	NO	NEGATIVE	n/a	n/a	n/a	n/a	n/a	Negatively density dependent growth of settlers, but facilitated by conspecific attraction of clients. May be linked to conspecifics preferentially selecting high quality habitat	**YES**	Facilitation by resident conspecifics outweigh competitive costs for settlers	2011
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	No fish moved off bleached coral, while 67% moved from dead colonies to healthy ones. Fish remaining on dead colonies were prevented from entering live corals by aggressive interactions with conspecifics. Despite this fish are strongly attracted to conspecifics.	**YES**	Movement may mediate impact of habitat degradation, but may be limited by increased competition and scale of disturbance.	2012
no	n/a	NEGATIVE	NO	NEGATIVE	n/a	n/a	n/a	n/a	Temporal density dependent mortality, survival to adulthood and fecundity at two reefs with naturally high settlement, density independent or inverse density dependent parameters at reefs with naturally low settlement,	**YES**	Environmental factors, like reef structure and predator abundance, more important in regulating populations than recruitment	2012
YES	aggression	NO - ASYMMETRIC	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	NO	No effect of interspecific competitor on survival or distribution. Levels of aggression were higher on degraded habitats.	**NO**	Habitat degradation intensifies negative effects of interspecific interactions.	2012
YES	aggression	NEGATIVE	n/a	n/a	n/a	YES	n/a	YES	Presence of interspecific competitor *P. amboinensis* reduced survival of *P. moluccensis*, but not vice versa. Levels of aggression and the negative effects of competitor on survival were stronger on degraded habitats. *P. moluccensis* took a higher position on the reef when competitor was present.	**YES**	Habitat degradation intensifies negative effects of interspecific interactions.	2012
no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Presence of larger interspecific competitor decreased survival	**YES**	Body size (not prior residence) governs dominance among interspecific cohorts.	2012
YES	aggression	n/a	n/a	n/a	n/a	YES	n/a	YES	Shifted to a higher position on the reef and was more aggressive when interspecific competitor was present	**YES**	Body size (not prior residence) governs dominance among interspecific cohorts.	2012
no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Presence of a larger juvenile interspecific competitor decreased survival	**YES**	Body size (not prior residence) governs dominance among interspecific cohorts.	2012
YES	Aggression, distance to shelter	NEGATIVE	n/a	n/a	n/a	n/a	n/a	NO	Negatively density dependent survival, however behaviours were density independent	**YES**	Density dependent survival not caused by decreased vigilance through aggression, and may cause rapid decline in crowded populations following habitat degradation	2013
no	no	NO - ASYMMETRIC	n/a	n/a	n/a	n/a	n/a	n/a	Effect of interspecific competitor was not as strong as conspecifics	**NO**	Asymmetric competitive hierarchies among these wrasses. Relative strength of intra- vs. interspecific competition depends on species identity.	2013
no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Presence of interspecific competitor reduced survival more than conspecifics	**YES**	Asymmetric competitive hierarchies among these wrasses. Relative strength of intra- vs. interspecific competition depends on species identity.	2013
no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Presence of interspecific competitor reduced survival more than conspecifics	**YES**	Asymmetric competitive hierarchies among these wrasses. Relative strength of intra- vs. interspecific competition depends on species identity.	2013

2013	Geange SW, Stier AC, Shima JS. 2013. Competitive hierarchies among three species of juvenile coral reef fishes. Mar. Ecol. Prog. Ser. 472:239	Labridae	*Thalassoma hardwicke*	*Thalassoma quinquevittatum*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2013	Geange SW, Stier AC, Shima JS. 2013. Competitive hierarchies among three species of juvenile coral reef fishes. Mar. Ecol. Prog. Ser. 472:239	Labridae	*Thalassoma quinquevittatum*	*Thalassoma hardwicke*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2013	Geange SW, Stier AC, Shima JS. 2013. Competitive hierarchies among three species of juvenile coral reef fishes. Mar. Ecol. Prog. Ser. 472:239	Labridae	*Thalassoma quinquevittatum*	*Gomphosus varius*	Competitor density manipulation	inter	among juv	experimental patch reef	**space**	**none**	YES	no	no	no	no	no
2013	McCormick MI, Watson S-A, Munday PL. 2013. Ocean acidification reverses competition for space as habitats degrade. Sci. Rep. 3:3280	Pomacentridae	*Pomacentrus amboinensis*	*Pomacentrus moluccensis*	Dominance experiment	inter	among juv	experimental patch reef	**space**	**habitat quality, CO2 levels**	YES	no	no	no	YES	no
2013	McCormick MI, Watson S-A, Munday PL. 2013. Ocean acidification reverses competition for space as habitats degrade. Sci. Rep. 3:3280	Pomacentridae	*Pomacentrus moluccensis*	*Pomacentrus amboinensis*	Dominance experiment	inter	among juv	experimental patch reef	**space**	**habitat quality, CO2 levels**	YES	no	no	no	YES	no
2014	Boström-Einarsson LE, Bonin MC, Munday PL, Jones GP. 2014. Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. Ecology. 95:3056–67	Pomacentridae	*Chrysiptera parasema*	*Dascyllus melanurus*	Competitor density + resource manipulation	inter	among juv	experimental patch reef	**space**	**habitat quality**	YES	no	no	no	no	no
2014	Boström-Einarsson LE, Bonin MC, Munday PL, Jones GP. 2014. Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. Ecology. 95:3056–67	Pomacentridae	*Dascyllus melanurus*	*Chrysiptera parasema*	Competitor density + resource manipulation	inter	among juv	experimental patch reef	**space**	**habitat quality**	YES	no	no	no	no	no
2014	Boström-Einarsson LE, Bonin MC, Munday PL, Jones GP. 2014. Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. Ecology. 95:3056–67	Pomacentridae	*Chrysiptera parasema*	n/a	Competitor density + resource manipulation	intra	among juv	experimental patch reef	**space**	**habitat quality**	YES	no	no	no	no	no
2014	Boström-Einarsson LE, Bonin MC, Munday PL, Jones GP. 2014. Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. Ecology. 95:3056–67	Pomacentridae	*Dascyllus melanurus*	n/a	Competitor density + resource manipulation	intra	among juv	experimental patch reef	**space**	**habitat quality**	YES	no	no	no	no	no
2015	Pereira PH, Munday PL, Jones GP. (2015) Ecology, *in press*	Gobiidae	*Gobiodon histrio*	*Gobiodon erythrospilus*	Dominance experiment	inter	among adults	aquarium	**habitat**	**habitat type**	no	no	no	no	YES	no
2015	Pereira PH, Munday PL, Jones GP. (2015) Ecology, *in press*	Gobiidae	*Gobiodon erythrospilus*	*Gobiodon histrio*	Dominance experiment	inter	among adults	aquarium	**habitat**	**habitat type**	no	no	no	no	YES	no
2015	Pereira PH, Munday PL, Jones GP. (2015) Ecology, *in press*	Gobiidae	*Gobiodon histrio*	*Gobiodon erythrospilus*	Dominance experiment	inter	among juv	aquarium	**habitat**	**habitat type**	no	no	no	no	YES	no
2015	Pereira PH, Munday PL, Jones GP. (2015) Ecology, *in press*	Gobiidae	*Gobiodon erythrospilus*	*Gobiodon histrio*	Dominance experiment	inter	among juv	aquarium	**habitat**	**habitat type**	no	no	no	no	YES	no

no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Presence of interspecific competitor reduced survival more than conspecifics	**YES**	Asymmetric competitive hierarchies among these wrasses. Relative strength of intra- vs. interspecific competition depends on species identity.	2013
no	no	NO - ASYMMETRIC	n/a	n/a	n/a	n/a	n/a	n/a	Effect of interspecific competitor was not as strong as conspecifics	**NO**	Asymmetric competitive hierarchies among these wrasses. Relative strength of intra- vs. interspecific competition depends on species identity.	2013
no	no	NO - ASYMMETRIC	n/a	n/a	n/a	n/a	n/a	n/a	Effect of interspecific competitor was not as strong as conspecifics	**NO**	Asymmetric competitive hierarchies among these wrasses. Relative strength of intra- vs. interspecific competition depends on species identity.	2013
YES	aggression	NEGATIVE	n/a	n/a	n/a	YES	n/a	YES	Under ambient carbon dioxide, dominant over on both bleached and unbleached coral and dominant *P. amboinensis* was more aggressive and stayed closer to shelter than subordinate. Under high carbon dioxide, dominant on bleached coral but dominant on healthy coral. In these high carbon dioxide conditions *P. moluccensis* was more	**YES**	Elevated carbon dioxide reverses competitive dominance and this reversal is accentuated in degraded habitats.	2013
YES	aggression	NEGATIVE	n/a	n/a	n/a	YES	n/a	YES	Under ambient carbon dioxide, dominant over on both bleached and unbleached coral and dominant *P. amboinensis* was more aggressive and stayed closer to shelter than subordinate. Under high carbon dioxide, dominant on bleached coral but dominant on healthy coral. In these high carbon dioxide conditions *P. moluccensis* was more	**YES**	Elevated carbon dioxide reverses competitive dominance and this reversal is accentuated in degraded habitats.	2013
no	no	NEGATIVE	n/a	n/a	n/a	n/a	n/a	n/a	Survival decreased with increasing density of interspecific competitor on healthy habitat, and this effect was stronger than conspecific effect. On degraded habitats survival was density independent.	**YES**	Habitat degradation alters the effects of intra- and interspecific competition	2014
no	no	NO - ASYMMETRIC	n/a	n/a	n/a	n/a	n/a	n/a	No effect of increasing interspecific competitor density on survival in healthy or degraded habitat.	**NO**	Habitat degradation alters the effects of intra- and interspecific competition	2014
YES	aggression	NEGATIVE	n/a	n/a	n/a	n/a	n/a	YES	Survival decreased with increasing density of conspecifics on healthy habitat, but survival was density independent on degraded habitat. Aggression increased with increasing conspecific density on degraded reefs only.	**YES**	Habitat degradation alters the effects of intra- and interspecific competition	2014
YES	aggression	NO	n/a	n/a	n/a	n/a	n/a	YES	No effect of conspecific density on survival in healthy or degraded habitat. Aggression increased with increasing conspecific density on degraded reefs only.	**YES**	Habitat degradation alters the effects of intra- and interspecific competition	2014
no	n/a	n/a	n/a	n/a	n/a	NO - ASYMMETRIC	n/a	n/a	Adult *G. histrio* is competitively dominant over *G. erythrospilus*	**NO**	Lottery vs. niche partitioning not mutually exclusive, but shift with ontogeny of species (lottery in juveniles, niche partitioning between adults)	2015
no	n/a	n/a	n/a	n/a	n/a	YES	n/a	n/a	Adult *G. histrio* is competitively dominant over *G. erythrospilus*	**YES**	Lottery vs. niche partitioning not mutually exclusive, but shift with ontogeny of species (lottery in juveniles, niche partitioning between adults)	2015
no	n/a	n/a	n/a	n/a	n/a	NO	n/a	n/a	Juveniles equal dominance between species	**NO**	Lottery vs. niche partitioning not mutually exclusive, but shift with ontogeny of species (lottery in juveniles, niche partitioning between adults)	2015
no	n/a	n/a	n/a	n/a	n/a	NO	n/a	n/a	Juveniles equal dominance between species	**NO**	Lottery vs. niche partitioning not mutually exclusive, but shift with ontogeny of species (lottery in juveniles, niche partitioning between adults)	2015