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Effects of climate change-induced thermal stress and habitat degradation to the biodiversity and species composition of coral-associated invertebrates

Thesis by
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Statement on the Contributions of Others

This thesis includes collaborative work with my supervisors Prof. Geoffrey Jones, Prof. Philip Munday, Prof. Morgan Pratchett, Dr. Elvira Poloczanska and Dr. Pat Hutchings as well as Dr. Niel Bruce, Dr. Stefan Walker and Dr. Craig Syms. While undertaking these collaborations, I was responsible for research concept and design, data collection, analysis and interpretation of results. My co-authors provided intellectual guidance, editorial assistance, financial support and technical assistance.

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General abstract

Coral reefs have the highest animal diversity of any ecosystem on the planet, due to the vast number of invertebrate taxa that reside within its matrix. The majority of these taxa are small, cryptic and live in symbiotic relationships with other reef organisms, such as compact branching corals, and are ecologically important to their hosts. A portion of these are obligate users of a small range of coral species, while others are facultative, or generalist, users of a broad range of corals. Specialisation is known to be strongly linked to high rates of extinction during periods of environmental instability. Coral reefs are subject to many disturbances that can destabilise the coral reef community, with lasting effects on biodiversity and ecological functions. Thermal stress induces coral bleaching, which can lead to entire colony mortality and ultimately affect all species that recruit, feed, mate and shelter within the corals' branches. As bleaching events are increasing in frequency and intensity, it is critical to understand how thermal stress and consequent habitat degradation of coral reefs will affect the vast diversity of invertebrates that associate with and rely upon corals for their persistence. Combining field observations and experiments, this study aimed to document the diversity of invertebrates associated with common coral species of the Great Barrier Reef, examine their level of specialisation to particular host corals and to evaluate their responses to thermal stress and host coral degradation via coral bleaching and mortality.

Although the high biodiversity of coral reefs is attributed to the invertebrate groups found there, few studies have documented species diversity and community structure among coral-associated invertebrates and how they might vary among coral species. Chapter 2 examined species richness (diversity) and composition of animals associated with common species of branching corals. One hundred seventy eight nominal species from 12 different phyla were extracted from 4 host coral species. Twenty seven species (15% of all taxa collected) were found on only one of the four different coral species, which may potentially indicate specialisation among host corals. The distinct assemblages on different coral species, and the presence of potential specialists, suggests invertebrate communities will be sensitive to the differential loss of branching coral species resulting from coral reef degradation

As climate change is driving habitat degradation among coral reefs via coral bleaching and mortality, numerous invertebrate taxa which are closely associated with corals are being threatened with loss of critical resources. Species specialised to a narrow range of host corals will experience greater extinction risks than generalist species, which may exploit a range of habitats. As coral declines, overall diversity may be impacted in one of two ways: either it will decline through the loss of specialised species or be promoted by the increase in habitat heterogeneity via partial coral mortality. Chapter 3 aimed to test these predictions test these predictions by sampling invertebrate assemblages from healthy, bleached and dead corals. Invertebrate diversity on healthy corals was nearly double that found on bleached colonies, but only half that found on predominantly dead colonies. This was explained by the marked decline of obligate species and the proliferation of facultative species. Different coral species were distinguished by their unique assemblages of obligate coral-dwellers, but dead corals supported communities of more random, numerous facultative species. Partial colony mortality (40-60 %) yielded the highest diversity and abundance of both obligate and facultative coral dwellers. However, as colony mortality increased, the community composition shifted from one dominated by a few obligate species to one marked by an abundance of facultative species. This study supports the hypothesis that moderate disturbances and spatial heterogeneity promote reef biodiversity, but phase shifts lead to large-scale coral loss are a major extinction risk for specialised coral-dwelling invertebrates.

Ecological specialization refers to how restricted certain animals are to a niche, as a result of evolutionary trade-offs. Corals represent a critical resource to many reef organisms, some of which have evolved to specialise on particular host corals. Episodes of coral bleaching are increasing both in frequency and intensity, yet the effects of bleaching on coral-reliant species remains poorly understood. Chapter 4 investigated the effects of host-colony bleaching on an obligate coral-dwelling crab during a natural bleaching event affecting 83 % of compact branching corals. Crabs monitored *in situ* over a 6 week period exhibited a significant decline in density on bleached corals and suffered a 40 % decline in fecundity. Host-colony bleaching also prompted crabs to emigrate and engage in aggressive interactions with crabs occupying healthy hosts, further threatening overall fitness. Decreased densities and clutch sizes, along with

increased competitive interactions of symbionts ecologically important to their host corals could potentially result in a population decline of these symbionts with cascading effects on coral health.

Although mutualisms are ubiquitous in nature, our understanding of the potential impacts of climate change on these important ecological interactions is deficient. Chapter 5 examined a thermal-stress related shift from cooperation to antagonism between members of a mutualistic coral-dwelling community. Increased mortality of coral-defending crustacean symbionts was observed in response to experimentally elevated temperatures and host coral bleaching. Strong differential effects occurred among crustaceans as a function of species and sex, due to forceful eviction from the host coral by dominant individuals. Fecundity also suffered a dramatic decline (85 %), which could have deleterious consequences for population sustainability. Elevated temperature altered the fundamental nature of this interaction from cooperation to competition, leading to asymmetrical effects on species and/or sexes, illustrating the importance of evaluating not only individual responses to climate change, but also potentially fragile interactions within and among susceptible species.

In conclusion, this thesis demonstrates that many species of coral reef invertebrates rely on coral as a habitat, with some heavily dependent on a host coral for their fitness and persistence. It also identifies key species that are affected once the coral habitat becomes bleached and/or dies. It highlights effects climate change can have on species interactions, such as changing the nature of mutualisms. The findings of this thesis suggest that many specialist species are exposed to potential extinction should their host coral species decline, with generalist species benefitting from their demise. Overall reef biodiversity is maintained at its highest when disturbance regimes are intermediate both in frequency and severity. It also emphasises the importance not only of live coral, but also of the coral structure in supporting a vast diversity of invertebrates. Degradation of the physical reef structure has the greatest potential to threaten overall reef biodiversity, with implications for critical ecological functions and ecosystem productivity.

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Chapter 1: General Introduction

Climate change is the single greatest threat to the planet's biodiversity, either directly impacting on temperature sensitive species or disrupting vital processes that sustain habitats and ecosystems (Walther et al. 2002, Hughes et al. 2003, Parmesan and Yohe 2003, Parmesan 2006, Hooper et al. 2012, Prather et al. 2013). Global mean temperature has been increasing over the last half-decade and has recently surpassed 1 °C above the estimated pre-industrialisation level and (IPCC 2013). At the species level, this has already led to geographical range shifts, declines in abundance, changes in the timing of key events such as reproduction and migration, and changes in behaviour (Walther et al. 2002, Parmesan and Yohe 2003, Walther et al. 2005, Hickling et al. 2006, Parmesan 2006). At the ecosystem level, climate change is accelerating biodiversity loss by disrupting nutrient cycling and reducing productivity through the loss of key species (Cardinale et al. 2012). As the predicted surface warming by the end of the 21st century varies from a best-case scenario of 1.8 °C to a worst-case scenario of 4 °C (IPCC 2013), climate change will likely be a major cause of species extinctions in the near future, particularly for vulnerable species living in vulnerable ecosystems (McKinney 1997, Thomas et al. 2004).

Coral reefs are particularly vulnerable to the effects of climate change, as scleractinian corals, the key habitat-forming taxa, exhibit an extremely narrow thermal range (Hoegh-Guldberg 1999, Hughes et al. 2003). Exceeding this range results in coral bleaching, and depending on the severity and/or duration of exposure to increased temperatures, coral mortality. A mass-bleaching event triggered by the severe El Niño of 1997-98 killed 16 % of the world's coral reefs (Wilkinson 2000). As the frequency of severe El Niño events is increasing due to greenhouse gases (Cai et al. 2014), corals will experience more frequent and severe bleaching events, threatening the persistence of countless other organisms reliant upon the coral habitat. Declines in reef fish have been well documented following coral depletion, particularly for coral-reliant species (e.g. Reese 1977, Harmelin-Vivien & Bouchon-Navaro 1983, Sano 1989, Hughes 1994, Shears & Babcock 2002, Bellwood et al. 2003, Duffy 2003, Hughes et al. 2003, Jones et al. 2004, Munday 2004, Garpe et al. 2006, Graham et al. 2006, Pratchett et al. 2006, 2008, Wilson et al. 2006), resulting in overall loss of fish biodiversity and impaired ecosystem function. However, our knowledge of climate change impacts has largely overlooked the potential vulnerability of the other reef-associated animals, the invertebrates, which perform a multitude of ecologically important roles within the reef system (Prezlslawski et al. 2008, Prather et al. 2013). As invertebrates are collectively comprised of many different phyla, predicting their responses to the numerous challenges of a rapidly changing climate is inherently difficult, however, certain traits can enhance either vulnerability or adaptive capacity of particular groups to various climate change stressors (Kellert 1993, Prezlslawski et al. 2008, Stella et al. 2011). Environmental factors, such as temperature, pH, and calcium carbonate saturation, are major factors in the distribution, fitness and behaviour of marine invertebrates (Pörtner et al. 2005, Pörtner 2008, Widdicombe & Spicer 2008, Doney et al. 2009). Ocean acidification is a major threat to calcifying marine invertebrates (as reviewed by Byrne 2011). A decreases in carbonate ions as a result of acidification would directly affect the ability to form and maintain skeletal integrity, and thus alone could result in the loss of thousands of species of molluscs and echinoderms (Byrne 2011). Other invertebrate groups may be more susceptible to increases in sea temperatures. The multiple stressors exerted by climate change may be diverse enough to impact a majority of invertebrate groups. The loss of even some invertebrate groups due to their inability to cope with climate change could have resounding effects on the ecosystem. Therefore, it is vital to understand how invertebrate populations will respond to climate change in order to gain a true understanding of the threat it poses to coral reef diversity.

Coral reefs are the epitome of marine biodiversity, boasting the highest biodiversity of any marine ecosystem (Sebens 1994, Gray 1997, Hoegh-Guldberg 1999), with species estimates ranging from 200,000 to 9 million species (Reaka-Kudla 1997, Ruppert et al. 2004, Fisher et al 2011, Caley et al 2014). Often compared to tropical rainforests in term of diversity, coral reefs are actually more phylogenetically diverse, harbouring 32 of the 34 known animal phyla compared to a mere 12 found in rainforests. Corals and reef fish have long been the focus of all aspects of coral reef research, however their contribution to overall reef diversity is distinctly low; ~800 and 4,000 species respectively (Choat & Bellwood 1991, Lieske & Myers 1994, Paulay 1997, Veron 2000, Hughes et al. 2002, Bellwood et al. *2*003). Tropical reef invertebrate diversity is largely unknown, however there are currently at least 168,000 described invertebrate species (as reviewed in Stella et al. 2011) which account for over 90 % of total coral reef species (Reaka-Kudla 1997, Przeslawski et al. 2008, Stella et al. 2011).

Although up to 2,000 new marine invertebrate species are described every year (Bouchet 2006, Appeltans et al. 2012), research effort remains poor, creating large deficits in our understanding of coral reef diversity and ecological processes.

Coral reef invertebrates perform many critical ecological functions (Hutchings et al. 2007, Przeslawski et al. 2008, Glynn and Enochs 2011, Stella et al. 2011). Collectively, they are represented in all trophic levels in tropical ecosystems and are important food sources at higher trophic levels (Hiatt and Strasburg 1960, Kramer et al. 2013, Wen et al. 2016). While some groups provide food to other habitat-associated organisms, others are abundant in the water column and thus available to more pelagic organisms (Kramer et al 2013). Filter feeding invertebrate groups, such as worms and bivalves, can improve ambient water quality and transport nutrients into the reef system (Richter et al. 2001, Ribes et al. 2005). Invertebrates that dwell within soft-sediments, such as holothurian sea cucumbers, play crucial roles in bioturbation, oxygenation, nutrient cycling and may even stabilise reef water chemistry Snelgrove 1998, Uthicke 1999, 2001, Schneider et al. 2011). Invertebrates also play a major role in reef building and maintenance. Shell-building invertebrates, such as molluscs, provide calcium carbonate deposits to the reef via skeletal remains and bioeroders, such as worms and sponges, create holes and tunnels used by countless other organisms as refuge (Hutchings et al. 2007, Barbosa et al.2008). Larger invertebrates, such as corals, sponges, anemones, giant clams and crown-of-thorns starfish also provide shelter and microhabitats for a suite of smaller organisms (e.g. Puce et al. 2005, Stella et al. 2011, Hoeksema et al. 2012). Importantly, some of these smaller organisms perform ecological services to the host which maintain host health (as reviewed by Stella et al. 2011). The sheer abundance and ecological importance of invertebrates implies their loss would likely have immense indirect impacts on coral reef ecosystems under global change (Castro 1988, Traill et al. 2010, Stella et al. 2011, Prather et al. 2013).

Recent literature assessing the vulnerability of invertebrates to climate change has demonstrated a variety of responses, indicating that some groups have adaptive capacity whilst others are at great risk of going extinct. For example, some species with dispersive larvae are able to shift or expand their ranges in response to warmer temperatures (e.g. Thompson et al. 2002, Precht and Aronson 2004). However, invertebrates that are closely associated with a habitat adversely affected by climate change, such as the coral substrate, are more vulnerable than those associated with relatively unaffected habitats, such as sandy bottoms (McKinney 1997, Thompson et al 2002, Hutchings et al. 2007, Palumbi et al 2008, Prezlslawski et al. 2008). Most invertebrate species are closely associated with certain habitats and on coral reefs, many are highly specialised to live on corals (Castro 1988, Chapter 2, Stella et al. 2011, Hoeksema et al. 2012). Hence, their fate is closely linked to the future of the key habitat forming organisms – the corals.

A multitude of associations occur between scleractinian corals and other reef invertebrates. At least 44 taxa of coral are known to serve as hosts to over 800 invertebrate species (as reviewed by Stella et al. 2011, Appendix A). Recent studies on coral-associated fauna reveal large variability in the number of invertebrate species different host corals support. Hoeksema et al. (2012) documented 95 invertebrate species associated with 50 species of mushroom coral. Stella et al. (2011, Appendix) documented ~250 invertebrate species that associate with *Pocillopora* spp. Among all invertebrates known to associate with coral, the majority exhibit a strong preference for compact branching coral, possibly because, like trees of the rainforest, they provide a dense network of branches in which to live in relative safety (Castro 1988, Knowlton et al. 2010, Chapter 2, Glynn and Enochs 2011, Plaisance et al. 2011, Stella et al. 2011). These corals provide a large surface area, refuge from predation, food in the form of coral tissue, mucus and its associated detritus, and a hard skeleton used as a substratum by specialised burrowers and gall-forming animals (Castro 1988, Stella et al. 2011). In return, specialised invertebrate species provide critical ecological services to their immobile host corals, such as cleaning, protection from would-be predators and disease mitigation (Glynn 1976, Stewart et al. 2006, Pollock et al. 2012). In utilising coral in such ways, many reef invertebrates have become critically reliant on their coral home. The relationship coral-associated invertebrates have to corals can be either obligate (necessary for their survival) or facultative (beneficial for their survival) (Castro 1976). As many as 10 % of invertebrate species may be obligate coral dwellers (Coles 1980), yet it is unknown if this pattern is typical among coral-associated invertebrates. Branching corals are not considered to be hardy; they are the most susceptible taxa to nearly every possible disturbance on coral reefs. They break easily with storm driven wave action, are the preferred prey for coral predators such as crown-of-thorns, and they usually exhibit the highest bleaching and post-bleaching mortality rates (Brown and Suharsano 1990, Gleason 1993, Marshall and Baird 2000, Loya et al. 2001, Floros et al.

2004, McClanahan et al. 2004, Pratchett et al. 2010, Madin et al. 2014), lending them and all organisms that rely on them a high risk of extinction or extirpation due to bleaching via ocean warming (McKinney 1997). The loss of host corals will have fundamentally different consequences for obligate and facultative invertebrate symbionts, and hence for the structure of invertebrate assemblages. For susceptible habitats, it is critical to gain a better understanding of the factors that influence patterns of invertebrate biodiversity and what the ecological consequences are for the loss of biodiversity.

Disturbance regimes are natural processes that have shaped coral reef communities over ecological and evolutionary time scales. Coral reef organisms are, to a degree, adapted to such disturbances, and cycles of decline and recovery are common. However, anthropogenic impacts such as climate change are leading to more frequent declines and an inability of reefs to recover (Hughes 1994, Bellwood et al. 2006, Madin et al. 2014, Graham et al. 2015). It is estimated that anthropogenic impacts have already resulted in the degradation or loss of about 60% of coral reefs worldwide (Jackson 2008). However, we have very little understanding of how a decline in coral habitat affects the animals that interact with living coral and the overall effect of coral loss on reef biodiversity. The degree and nature of the association a species has with a host coral will largely determine its response to coral decline. For instance, species that use coral only as a refuge may be able to use a wide range of micro-habitats, including but not limited to live coral, dead coral and the rubble matrix, thus climate impacts that kill coral may not have adverse effects (Enochs 2012, Kramer et al 2014, Takada et al. 2014, Chapter 2). These facultative species may be unaffected or even benefit from disturbances, able to thrive in a range of environmental conditions utilizing a variety of resources. However, species that rely on live coral tissue for food or settlement (obligate species) are unlikely to be able to cope with a severe decline of coral as a result of disturbance ('the specialization-disturbance hypothesis, Vazquez & Simberloff 2002) and face a greater risk of extinction (Lawton 1993, Mckinney 1997, Munday 2004, Pratchett et al. 2008). An understanding of how coral-associated invertebrate communities respond to differing levels of disturbance and what stages of degradation are important thresholds for specialised species, is particularly important in assessing the potential impacts on reef biodiversity. In order to protect reef biodiversity, it is important to identify those species at most risk and assess their vulnerability to reef degradation.

Current research on the impacts of coral bleaching and mortality on the biodiversity of reef organisms highlights the disparity in our knowledge of different taxonomic groups. Research focused on reef fish communities have documented a heavy reliance on coral habitats and consequent dramatic responses to coral degradation (e.g. Reese 1977, Harmelin-Vivien & Bouchon-Navaro 1983, Sano 1989, Hughes 1994, Shears & Babcock 2002, Bellwood et al. 2003, Duffy 2003, Hughes et al. 2003, Jones et al. 2004, Munday 2004, Garpe et al. 2006, Graham et al. 2006, Pratchett et al. 2006, 2012, Wilson et al. 2006). However, little is known of the response to disturbance of invertebrate communities that have a stronger reliance upon coral habitats, living directly on the coral surface in a life-long association. Coral degradation may have detrimental effects on fitness levels of coral-reliant animals, affecting growth rates, reproduction, competitive interactions and the ability to evade predators, all of which influence population persistence (Kokita and Nakazono 2001, Munday 2001, Pratchett et al. 2004, Coker et al. 2009, Coker et al. 2012). As a large proportion of coral-associated invertebrates demonstrate a high reliance on coral species that are most susceptible to coral bleaching and mortality (Pratchett et al. 2009, Stella et al. 2011), these animals will likely be predisposed to increased rates of extinction via a decline in fitness and subsequent population declines if reef degradation continues unabated. Therefore, it is important to assess impacts of host coral bleaching on the fitness of obligate coral dweller, in order to determine their likely persistence through frequent and severe bleaching events.

The myriad of symbioses that occur on coral reefs facilitate the acquisition of otherwise unobtainable resources. Many of these are mutualistic in nature, benefitting both species involved. Perhaps the most conspicuous and well known coral reef symbiosis is between corals and their endo-symbiotic zooxanthellae. Corals provide the photosynthetic zooxanthellae with nutrients, carbon dioxide and shelter in return for up to 90 % of their nutritional needs (Odum and Odum 1955, Trench 1979). Corals also host a variety of mutualistic exosymbionts that rely on corals for shelter, food and reproduction (Knudsen 1967, Patton 1974, Chapter 2, Stella et al. 2011). A number of obligate coral-associated invertebrate species are known to engage in mutualistic symbioses, cooperating with each other and providing ecological services to their host corals, such as the coral guard crab and the snapping shrimp known to ban together to defend their host coral from the predatory crown-of-thorns (Glynn 1976, Lassig 1977, Vannini 1985, McKeon et al. 2012). Even species that apparently occupy the same niche have consistently been found to seek out and engage in mutualistic relationships. While mutualisms often enhance survivorship and productivity, a strong inter-dependence can seal mutualists to a shared fate during rapid environmental change (Briand and Yodzis 1982, May 1976). The very nature of a mutualism can be altered by environmental changes, such as thermal stress, having the potential to impact mutualistic species differentially, with subordinate species and/or individuals being highly disadvantaged (Sachs and Simms 2006, West et al. 2007, Kiers et al. 2012). Consequently, the effects of climate change will not only impact species directly, but also indirectly via any changes in the nature of interactions with other species in the reef community (Connell 1961, Ives and Gilchrist 1993, Wootton 1994). The majority of climate change studies to date have focussed only on individuals of a single species (Parmesan and Yohe 2003, Harley et al. 2006) with very few having considered potential effects on interactions between individuals and species (Walther 2010). Incorporating species interactions with species-specific responses will help determine the ultimate response of coral reef diversity to the effects of climate change.

In the Indo-Pacific and on the Great Barrier Reef (GBR), the most conspicuous symbiotic associations between corals and invertebrates involve tightly branching pocilloporid and acroporids corals and their obligate decapod crabs belonging to the families Trapeziidae and Alpheidae (pocilloporid hosts) and the family Tetraliidae (acroporid hosts). These obligates have occurrence rates in excess of 90 % on their host corals and are not found in any other habitat. Obligate species from these families are perhaps some of the most coral-reliant reef animals, specialised to particular host corals upon which they depend for habitat, food in the form of coral mucus, polyps and eggs, and as a breeding site (Knudsen 1967, Patton 1974, Castro 1988, Stimson 1990). These symbioses appear to have been established by the Eocene (Schweitzer 2005) and there is evidence to support co-evolution (Glynn 1983b). Trapeziids, in particular, are ecologically important to their host corals. *Trapezia* spp. have been shown to enhance coral skeletal growth (Glynn 1983c), clean host corals of sediments (Stewart et al. 2006) and mucus nets of vermetid gastropods (Stier et al. 2010) that would otherwise be detrimental to coral growth and survival (Shima et al. 2010), and actively defend their hosts from coral predators such as *Acanthaster planci* and *Drupella* snails (Weber and Woodhead 1970, Glynn 1980, Pratchett 2001, McKeon and Moore 2014). As this mutualism appears critical to the survival of both decapods and corals, any decline in one would surely affect the other. On the GBR, coral cover has declined by 50 % over the past 27 years, primarily due to severe tropical cyclones, coral predation by the crown-of-thorns starfish and climate change-induced coral bleaching (De'ath et al. 2012). The loss of coral has undoubtedly affected many other reef organisms. Although there is an increasing body of research documenting climate change-related declines in the abundance and community composition of both corals and coral reef fishes on the GBR, the fate of coral reef invertebrates remains largely unknown.

The overall aims of this thesis were to document the diversity and abundance of coral-associated invertebrate communities, observe the response in diversity, abundance and species composition to various levels of natural degradation of common host corals, and to assess the effects of climate induced thermal stress and subsequent host bleaching on specialised invertebrate species, with a particular focus on trapeziid crabs and alpheid shrimp. The thesis is comprised of four independent chapters, combining both natural field observations and experimental methods. The specific goals of each chapter were as follows:

Chapter 2 explored and compared the biodiversity of invertebrate communities living among the branches of commonly abundant compact branching corals, *Acropora millepora, Acropora nasuta, Pocillopora damicornis* and *Seriatopora hystrix*. Differences in the diversity, abundance and species composition of coral-associated invertebrates among the four host corals was examined in order to determine if specific habitat characteristics (such as structural complexity) exert a strong influence. Occurrence rates of invertebrate species across all four host corals was also compared in order to determine if some species exhibited preferences for particular host corals as this may indicate an obligate relationship with their host coral. Understanding how specialised species are to a particular habitat is important, as this can greatly enhance the risk of extirpation or extinction following disturbances that reduce the quality and/or quantity of preferred habitats (Lawton 1993, McKinney 1997).

The next chapter (Chapter 3) examined the response in diversity, abundance and species composition of coral-associated invertebrates to various levels of natural degradation of common host corals. After a thermal stress event that caused moderate bleaching of seven species of common compact branching corals (*Acropora nasuta, Acropora spathulata, Acropora valida, Pocillopora damicornis, Pocillopora verrucosa, Seriatopora hystrix* and *Stylophora pistillata*), the coral-associated invertebrates communities were compared between healthy, bleached and dead host corals with emphasis on the changes in proportions of obligate and facultative species. This focused on the taxonomic range of coral-associated invertebrates and the differences in community composition that occur as a result of host coral degradation, with particular emphasis on the effect of habitat quality on promoting local biodiversity.

Chapter 4 investigated the effects of host-colony bleaching on an obligate coral-dwelling species, using the well-known decapod *Trapezia cymodoce* as a model species. Bleaching due to thermal stress can be spatially patchy, both among and within coral species, and it is unknown how host-colony bleaching affects the fitness and behaviour of species that rely on healthy corals for their survival. Differences in the density, fecundity and behaviour of crabs inhabiting bleached or healthy corals were compared in order to determine if host coral bleaching elicits a physiological and/or behaviour response. Successful migration of crabs from bleached hosts to healthy hosts was experimentally evaluated to determine the potential role of intra-specific competition during disturbances that reduce the availability of healthy habitats.

The final chapter (Chapter 5) explicitly tested the effects of thermal stress (and subsequent coral bleaching) on a well-documented mutualistic crustacean-coral community comprised of the host coral *Pocillopora damicornis* (Linnaeus, 1758**)**, the coral crab *Trapezia cymodoce* (Herbst, 1801) and the snapping shrimp *Alpheus lottini* (Guérin Méneville, 1828), a species complex of alpheid shrimp (Williams and Knowlton 2001). Coral reefs support the highest number of mutualistic associations in the marine environment (Castro 1988, Stachowicz 2001), however it is unclear how susceptible these associations are to disturbances and if certain species will be disproportionately affected. Increasing temperatures and/or habitat degradation may potentially alter the nature of mutualisms, having detrimental effects on one or more species. Changes in the fecundity in each decapod species and the behavioural interactions between them were investigated before, during and after an experimental thermal stress event. Overall survivorship of crabs, shrimp and corals were also compared.

The implications of these findings and emerging research priorities are assembled in the General Conclusions. A published review of coral-associated invertebrates (Stella et al. 2011) that describes their diversity, ecological importance and vulnerability to disturbance is provided for further background in Appendix A. Observations of new invertebrate corallivores made during my candidature, including a new record for recently described species, are located in Appendices B and C.

Chapter 2: Variation in the structure of epifaunal invertebrate assemblages among host corals

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2.1 Abstract

The high biodiversity of coral reefs is attributable to the many invertebrate groups which live in symbiotic relationships with other reef organisms, particularly those which associate with the living coral habitat. However, few studies have examined the diversity and community structure of coral-dwelling invertebrates and how they vary among coral species. This study quantified the species richness and composition of animals associated with four common species of branching corals (*Acropora nasuta*, *A. millepora*, *Pocillopora damicornis*, and *Seriatopora hystrix*) at Lizard Island in the northern Great Barrier Reef. One hundred seventy eight nominal species from 12 different phyla were extracted across 50 replicate colonies of each host coral. A single coral colony, approximately 20 cm in diameter, harboured as many as 73 individuals and 24 species. There were substantial differences in invertebrate species composition among host corals of different families as well as genera. Twenty seven species (15% of all taxa collected) were found on only one of the four different coral species, which may potentially indicate some level of specialisation among host corals. The distinct assemblages on different coral species, and the presence of potential specialists, suggests invertebrate communities will be sensitive to the differential loss of branching coral species resulting from coral reef degradation.

2.2 Introduction

Coral reefs are among the most diverse and threatened ecosystems on the planet (Hoegh-Guldberg 1999, Veron 2000, Fisher et al. 2011, Caley et al. 2014). While most of the research into the processes which maintain or threaten this biodiversity have focussed on corals and reef fishes that rely on corals, the greatest numbers of species that directly associate with live coral are small invertebrates. There are currently ~165,000 described species of reef invertebrates other than corals (Ruppert et al. 2004, Gordon and Bock 2007) compared to 4,000 species of fishes (Choat and Bellwood 1991, Lieske and Myers 1994, Bellwood et al. 2003) and 700 species of corals (Veron 2000, Hughes et al. 2002). It has been estimated that there may be as many as 9 million species of invertebrates on coral reefs (Reaka-Kudla 1997, Caley et al 2014) belonging to at least 31 phyla (Ray and Grassle 1991). However, the factors affecting the structure of invertebrate assemblages and their likely sensitivity to global impacts on coral reefs are poorly understood.

The high biodiversity of coral reef organisms is partly attributed to the extraordinary diversity of habitats and topographic complexity provided by scleractinian corals (Luckhurst and Luckhurst 1978, Sale 1991, McClanahan 1994, Jennings et al. 1996, Öhman and Rajasuriya 1998, Lawson et al. 1999, Lindahl et al. 2001, Gratwicke and Speight 2005, Garpe et al. 2006, Wilson et al. 2007). Coral reef fishes appear to be highly dependent on live corals and dramatic changes to fish communities occur when coral communities are disturbed (e.g., Jones et al. 2004, Munday 2004, Garpe et al. 2006, Graham et al. 2006, Wilson et al. 2007). Invertebrates other than corals may be even more closely associated and therefore even more susceptible to habitat change (Stella et al 2011). From the limited data that are available, it is apparent that 10-25% of coral reef invertebrates form close associations with corals, particularly branching corals (Knudsen 1967, Tyler 1971, Bruce 1972, 1977, Serène 1972, Patton 1974, Abele and Patton 1976, Castro 1976, Coles 1980, Chang et al. 1987, Tsuchiya et al. 1992) but it is unknown to what extent these species are critically dependent upon corals or specialized on certain coral species.

Coral reef organisms may be dependent on coral for various reasons, including food, shelter, and/ or recruitment. Relatively few coral reef organisms actually feed on live coral tissues, though Rotjan and Lewis (2008) identified at least 51 species of invertebrates that feed on coral. However, many invertebrates can be found living within the interstices of live coral colonies, presumably because they provide an excellent refuge against predators (Austin et al. 1980). In general, most of these invertebrates have been found living on branching coral species, principally from the genera *Pocillopora* and *Acropora*. Branching corals, such as *Pocillopora damicornis*, display a complex growth form in comparison to massive corals, such as some *Porites* spp., and may therefore provide greater protection from potential predators (Coles 1980, Edwards and Emberton 1980, Castro 1988). Organisms that live within live corals may be divided into obligate coral-dwellers and facultative (or opportunistic) coral dwellers. One study documented 12 species of obligate coral dwellers and 115 species of facultative coral dwellers living among the branches of one species of *Pocillopora* (Coles 1980), yet it is unknown if this pattern is typical for all branching coral species or exactly how many species of coral-dwellers fall into each category.

The extent to which coral reef organisms are dependent on live corals is important for predicting potential biodiversity loss associated with sustained and ongoing coral reef degradation (McKinney 1997, Munday 2004, Jones et al. 2004, Pratchett et al. 2008, Bonin 2012). There are a number of factors that contribute to the degradation of coral reef habitats, such as pollution, destructive fishing practices including the use of explosives and cyanide, sedimentation due to coastal development and global climate change (Wilkinson 2004). However, it is climate change that may be the single greatest threat to coral reef habitats, as it is expected to cause global coral reef degradation on an unprecedented scale in the coming years (Hughes et al. 2003, West and Salm 2003, Wilkinson 2004, Munday et al. 2007, Hughes et al 2014). Coral reef degradation is largely manifested as declines in the abundance of live coral colonies (Sebens 1994, Hoegh-Guldberg 1999, Jones et al. 2004, Bellwood et al. 2006), which will in turn have devastating effects on the range of coral reef organisms that are directly dependent on live corals (reviewed by Pratchett et al. 2008). Among those species that are most severely affected by coral depletion are those that depend on live coral for food, habitat and recruitment, such as corallivorous butterflyfishes (Pratchett et al. 2006) and coral-dwelling gobies (Munday et al. 1997, Munday 2004, Brooker et al. 2010). Moreover, certain coral taxa are more susceptible to bleaching than others with fast-growing branching species, such as *Acropora* and *Pocillopora,* suffering higher bleaching mortality than slow-growing massive species, such as *Porites* and *Astreopora*

(Brown and Suharsano 1990, Gleason 1993, Marshall and Baird 2000, Loya et al. 2001, Floros et al. 2004, McClanahan et al. 2004). Specialist species that rely on only one or two species of coral for food or habitat will be particularly susceptible to population declines and extinction risks should their host coral decline in abundance (Pratchett et al. 2008).

The purpose of this study was to compare epifaunal communities among four common branching corals, *Pocillopora damicornis, Seriatopora hystrix, Acropora nasuta* and *Acropora millepora* to determine the extent to which different corals harbour distinct epifaunal communities. The habitat characteristics of coral colonies were also examined to determine if habitat structure exerted a strong influence on the abundance and species richness of epifaunal communities. It was hypothesized that although species overlap may occur between epifaunal communities associated with different coral species, there would be distinct differences in the species assemblages of the four host corals. These differences in species composition could be indicative of the proportion of taxa specialised to one or two of the four branching corals. Understanding how specialised or rare some species are to a certain habitat is important, as these factors can greatly enhance the risk of extirpation or extinction following declines in the availability of potential habitats (Lawton 1993, McKinney 1997, Bonin 2012, Hughes et al 2014).

2.3 Methods

Sampling location, design and methodology

This study was conducted at Lizard Island (14°40’ S, 145°28’ E), in the northern Great Barrier Reef, Australia. Fifty individual coral colonies (ca. 20cm diameter) of each of four species of branching coral, *P. damicornis*, *S. hystrix* (F. Pocilloporidae), *A. nasuta* and *A. millepora* (F. Acroporidae) were identified following Veron (2000) and collected from shallow reef habitats (1.5-2.5m depth) within the Lizard Island lagoon. Sampling was conducted in both April and October 2008, with 25 colonies of each host coral collected and processed at each time. Individual coral colonies were collected by covering the entire colony with a plastic bag (to prevent any mobile animals from escaping) and then carefully chiseling the entire intact coral colony loose of the substrate. Coral colonies were then immediately taken to a nearby boat and placed in individual buckets of fresh seawater. All corals were transported to the laboratory within one hour of collection for processing.

Conspicuous invertebrates were initially removed using blunt probes and forceps. Corals were then submerged in 100% freshwater for up to one minute as this was found to be an effective method for expelling any undetected animals still left in the coral. Fish quickly vacated the host when gently nudged with a blunt probe and were also collected in order to account for all species found within the colony. The water was then poured through a 1 mm X 1 mm mesh net and the animals were retrieved. Use of this method excluded both boring animals and those generally less than 1 mm long, therefore the true diversity of organisms could be substantially greater. The corals were then carefully inspected for up to 30 minutes to maximize detection of small cryptic macrofauna. All animals were then placed in a freezer for several minutes before being moved to a specimen jar of formalin. All specimens were then transported back to the laboratory at James Cook University for later identification, whilst coral corals were returned to the lagoon and cemented back onto the substrate with marine epoxy.

Each individual animal was identified with the greatest possible taxonomic resolution based on all current literature and taxonomic descriptions available (e.g. the World Register of Marine Species) and with the assistance of taxonomic consultations (names in the acknowledgements). Where species level identification was not possible, species were identified to genus or family. To estimate species richness, unidentifiable organisms were differentiated into a number of distinct species groups based on color patterns and/or morphology. Group assignment was extremely conservative (only based on clear and unambiguous differences), which is likely to result in underestimates of species richness. Notably, no distinction was made among individuals identified within the family Palaemonidae or the orders Tanaidacea and Mysidacea.

Host Coral Characteristics

To account for differences in the size and quality of each host coral, detailed measurements were taken for each coral colony. Firstly, maximum diameter, perpendicular diameter and coral height were recorded. To determine how much space exists between coral branches, five measurements of inter-branch space were taken with vernier calipers. Three measures of penetration depth were taken by inserting a metal probe in three random places down into the coral between the branches. Average penetration depth was expressed as a ratio of colony height in order to examine the relative differences among coral species. Volume was measured by the displacement of a known volume of water (6000 cm^3) and then used to approximate the amount of living space within the branches. This was done by first multiplying the 3 dimensions (L×W×H) and subtracting the displacement volume of coral skeleton. This measurement was then called living space. If the coral colony exhibited partial mortality, the proportion of live tissue was visually estimated as a percent of the entire colony to the nearest 5%.

Data analysis

The overall abundance (number of individuals per colony) and species richness (number of species per colony) were compared among the four coral species (*P. damicornis*, *S. hystrix, A. nasuta* and *A. millepora)* using a Kruskal-Wallis nonparametric test. Mann-Whitney tests were then used to conduct pair-wise comparisons among each of four coral species (6 comparisons). A Bonferroni correction was required to adjust the p value for the two components of each test, resulting in a p value of 0.008 to indicate significance. Species distributions were plotted for each of the four host corals using a binning method described by Hubbell (2001). In this method, the number of individuals is plotted against the number of species. In order to detect if a log-normal distribution exists, the interval is on a $\log^2$ scale. For example, rather than plot each as an individual point, the data are assigned to a bin. Bin 1 = number of species with 1 individual per species, bin 2 = number of species with 2–3 individuals per species, bin 3 = 4–7, bin 4 = 8–15, etc. (Gray 1987, Hubbell 2001). This method can clearly illustrate how species are distributed and give insight as to how the epifaunal communities are structured (Hubbell 2001).

In order to determine species overlap, a Venn diagram was used to plot the occurrence of species on each of the four host corals. Taxa found to occur on only one of the four host corals could either be rare taxa that have a low rate of occurrence regardless of host, species which do not favour live coral as a preferred habitat and therefore are rarely found there, or habitat-specialists that only occur on certain coral species. Potential habitat-specialists may be distinguished from rare taxa based on their recurrence across replicate coral colonies of each coral species, therefore the occurrence rates were also evaluated when singletons were removed.

Variation in the invertebrate communities found within and among coral species were analysed using a multivariate analysis of variance (MANOVA). Forty four variables were included in the analysis, representing the number of commensal taxa with the highest abundance and occurrence (abundance of 10 or more individuals and present on at least 10 occasions). Pillai's Trace statistic was used to determine the significance of the MANOVA results, following Olsen (1976), as it is the most robust test statistic to deviations from multivariate normality, particularly when sample size is large and equal. Canonical discriminant analysis (CDA) was then used to display differences in the structure of epifaunal assemblages among the four coral taxa. To further aid in interpretation of these patterns, epifaunal taxa were represented by structural vectors indicating directional differences in the relative abundance of each taxa. The length of vectors indicates the strength of each commensal taxa in discriminating among groups (corals species).

In an attempt to account for variation in species abundance and richness among the four host corals, the importance of coral species, available living space (calculated as size (cm^3) minus the displacement volume (cm^3)), mean inter-branch space, mean penetration depth (expressed as a ratio of height in mm, arc sine transformed), and percent coral cover (fourth root transformed) was then examined using a backwards stepwise regression analysis based on the five variables. In this analysis, the dependent variables (abundance and species richness after undergoing a square root transformation) were regressed on all independent variables. If any variables were statistically insignificant, the one making the smallest contribution as dropped (i.e., the variable with the smallest sr^2, which will also be the variable with the smallest T value). Then the remaining variables are regressed on the dependent variable again the one making the smallest contribution is dropped. The procedure continues until all remaining variables are statistically significant.

In order to examine variation in faunal communities within host corals of the same species, a separate backwards stepwise regression analysis was conducted in the same manner described above for each coral species based on living space, mean inter-branch space, mean penetration depth ratio and percent coral cover.

2.4 Results

Taxonomic composition

A total of 2,481 individuals belonging to 12 phyla were collected from the 200 coral colonies. From these, 178 nominal species from 76 families were identified across all four host corals (Table 2.1). Overall species richness was highest for *S. hystrix* where 105 species from 55 families were recorded across all 50 colonies, compared to 102 species from 54 families for *P. damicornis. A. nasuta* contained 82 taxa belonging to 45 families and *A. millepora* contained only 64 taxa from 35 families.

A noticeable trend among all four coral species was apparent with regards to taxonomic composition at higher phylogenetic levels. Decapod crustaceans were the dominant taxa found in all four coral species. When compared to the 5 other most abundant taxa, it was clear that decapod crustaceans comprised an overwhelming proportion of total epifauna for all four coral species (Figure 2.1). The proportion of total epifauna comprised by decapod crustaceans ranged from 51% (*S. hystrix* and *A. nasuta*) to 63% for *P. damicornis* and 66% for *A. millepora*.

Table 2.1 Species abundance (A) and occurrence (O) found within each of four host corals, *Pocillopora damicornis*, *Seriatopora hystrix*, *Acropora nasuta* and *Acropora millepora*

			Pocillopora damicornis		***Seriatopora hystrix***		***Acropora nasuta***		***Acropora millepora***	
Family	Genus	Species	A	O	A	O	A	O	A	O
Trapeziidae	*Trapezia*	*cymodoce*	52	27	54	31	3	1	0	0
	Trapezia	*guttata*	3	2	22	13	0	0	0	0
	Trapezia	*serenei*	6	4	4	2	0	0	0	0
	Trapezia	*septata*	24	13	0	0	0	0	0	0
	Trapezia	*digitalis*	1	1	0	0	0	0	0	0
	Trapezia	*ferruginea*	0	0	1	1	0	0	0	0

	Trapezia	juveniles	40	18	6	5	0	0	0	0
Tetraliidae	*Tetralia*	*glaberrima*	0	0	0	0	48	24	41	23
	Tetralia	*nigrolineata*	0	0	0	0	22	11	4	3
	Tetralia	*rubridactyla*	0	0	0	0	7	4	0	0
	Tetralia	Sp. A	0	0	0	0	4	2	19	11
	Tetralia	Sp. B	0	0	0	0	6	3	18	10
	Tetralia	Sp. C	0	0	0	0	2	1	2	1
	Tetralia	Sp. D	0	0	0	0	7	4	0	0
	Tetralia	juveniles	0	0	0	0	2	2	2	2
Alpheidae	*Alpheus*	*lottini*	57	33	20	13	0	0	0	0
	Alpheus	*leviusculus*	1	1	3	2	1	1	1	1
	Alpheus	*malleodigitus*	0	0	2	1	0	0	0	0
	Alpheus	*parvirostris*	0	0	4	4	1	1	1	1
	Alpheus	Sp. A	7	3	39	16	2	2	0	0
	Alpheus	Sp. B	8	5	0	0	2	1	0	0
	Alpheus	Sp. C	7	3	19	10	1	1	1	1
	Alpheus	Sp. D	0	0	2	1	0	0	0	0
	Alpheus	Sp. E	11	4	9	7	1	1	0	0
	Synalpheus	*charon*	5	4	12	6	0	0	0	0
	Synalpheus	Sp. A	0	0	2	2	0	0	0	0
	Alpheus	juveniles	7	2	2	1	0	0	0	0
Xanthidae	*Chlorodiella*	*nigra*	2	1	8	7	0	0	1	1
	Chlorodiella	*laevissima*	8	7	16	11	2	2	1	1
	Chlorodiella	Sp. A	19	12	25	13	6	2	6	4
	unknown	Sp. A	5	5	5	3	4	1	2	2
	Macromedaeus	*nudipes*	0	0	2	2	0	0	0	0
	Cyclodius	Sp. A	3	2	9	7	0	0	0	0
	Cyclodius	Sp. B	0	0	3	3	1	1	0	0
	Pilumnus	*spp.*	1	1	2	2	0	0	0	0
	Cymo	*andreossyi*	15	12	19	15	0	0	4	4
	Cymo	*melanodactylus*	0	0	1	1	2	2	4	4
	Cymo	Sp. A	2	2	4	3	3	1	1	1
	unknown	juveniles	20	13	18	11	5	3	5	4
Majidae	unknown	Sp. A	21	13	10	8	7	5	1	1
	unknown	Sp. B	13	8	3	3	1	1	0	0
Palaeomonidae	*Periclimenes*	*spp.*	149	35	68	30	17	9	37	18
	Coralliocaris	*superba*	0	0	0	0	2	2	0	0
	Coralliocaris	*graminea*	0	0	0	0	0	0	15	6
	Harpiliopsis	*spp.*	0	0	0	0	3	2	16	12
Hippolytidae	*Thor*	*amboinensis*	1	1	0	0	0	0	0	0

	Saron	*spp.*	0	0	2	1	3	3	1	1
	unknown	spp.	1	1	0	0	0	0	0	0
Rhynchocinetidae	unknown	spp.	4	2	0	0	1	1	2	1
Porcellanidae	unknown	Sp. A	10	4	5	3	1	1	0	0
	unknown	Sp. B	13	8	3	3	0	0	0	0
	unknown	Sp. C	0	0	1	1	0	0	0	0
Galathiidae	*Galathea*	*spp.*	20	11	18	9	2	2	3	2
Diogenidae	*Calcinus*	latens	7	3	2	2	0	0	1	1
	Calcinus	Sp. A	3	2	2	1	0	0	0	0
	unknown	spp.	49	15	12	6	0	0	0	0
Paguridae	unknown	spp.	9	5	11	7	0	0	2	2
Cryptochiridae	*Hapalocarcinus*	*marsupialis*	1	1	14	8	0	0	0	0
Gonodactylidae	unknown	spp.	4	4	6	6	0	0	1	1
Gammaridea (So)	unknown	Sp. A	73	21	37	12	39	8	4	3
	unknown	Sp. B	16	7	16	8	1	1	7	3
	unknown	Sp. C	6	4	9	6	1	1	2	2
	unknown	Sp. D	3	3	0	0	0	0	0	0
	unknown	Sp. E	0	0	7	2	0	0	0	0
Anthuridae	unknown	spp.	7	4	0	0	0	0	0	0
Tanaidacea	unknown	spp.	3	3	17	8	5	4	0	0
unknown	unknown	spp.	4	1	0	0	0	0	0	0
unknown	unknown	sp.	1	1	0	0	0	0	0	0
unknown	unknown	sp.	1	1	0	0	0	0	0	0
unknown	unknown	sp.	0	0	0	0	1	1	0	0
Ischnochitonidae	unknown	sp.	0	0	0	0	0	0	1	1
Triviidae	*Trivirostra*	*oryza*	5	5	4	4	1	1	0	0
Muricidae	*Coralliophila*	*violacea*	7	5	8	6	0	0	0	0
	Coralliophila	Sp. A	6	5	6	5	0	0	0	0
	Drupella	*cornus*	1	1	7	5	2	1	9	3
	Morula	Sp. A	0	0	0	0	1	1	1	1
	Morula	Sp. B	0	0	0	0	1	1	1	1
	unknown	Sp. C	1	1	7	3	0	0	0	0
	unknown	Sp. D	0	0	3	2	0	0	0	0
Buccinidae	unknown	Sp. A	6	4	6	5	1	1	3	2
	Pisania	*fasciculata*	1	1	1	1	0	0	0	0
Mitridae	*Mitra*	Sp. A	1	1	1	1	0	0	3	1
	Mitra	Sp. B	1	1	3	2	0	0	0	0
	Mitra	*ferruginea*	1	1	0	0	0	0	0	0

Trochidae	unknown	Sp. A	3	3	1	1	0	0	1	1
Terebridae	unknown	Sp. A	4	3	2	2	0	0	0	0
	unknown	Sp. B	0	0	0	0	2	2	1	1
	unknown	Sp. C	0	0	0	0	1	1	0	0
Turbinidae	*Turbo*	*brunneus*	0	0	1	1	0	0	0	0
	Turbo	Sp. A	4	1	0	0	1	1	1	1
	Turbo	Sp. B	0	0	0	0	2	1	0	0
	Turbo	Sp. C	0	0	0	0	1	1	0	0
	Phasianella	sp.	0	0	0	0	0	0	4	2
Strombidae	*Strombus*	*mutabilis*	0	0	1	1	0	0	0	0
	Strombus	Sp. A	2	2	1	1	0	0	0	0
	Strombus	Sp. B	0	0	0	0	1	1	0	0
	Strombus	Sp. C	0	0	0	0	1	1	0	0
Cypraeidae	*Cypraea*	*asellus*	0	0	1	1	0	0	0	0
	unknown	Sp. A	1	1	1	1	0	0	0	0
Olividae	unknown	Sp. A	2	2	0	0	0	0	0	0
Natacidae	unknown	Sp. A	1	1	0	0	1	1	0	0
Epitonidae	*Cirsotrema*	Sp. A	0	0	0	0	1	1	0	0
Columbellidae	unknown	Sp. A	0	0	0	0	1	1	0	0
Cassidae	unknown	Sp. A	0	0	1	1	0	0	0	0
Arcidae	unknown	Sp. A	0	0	0	0	0	0	1	1
Littorinidae	unknown	Sp. A	0	0	0	0	0	0	1	1
	unknown	Sp. B	0	0	1	1	0	0	0	0
Costellaridae	Unknown	Sp. A	0	0	0	0	0	0	2	1
	Unknown	Sp. B	0	0	0	0	0	0	1	1
	Unknown	Sp. C	0	0	0	0	0	0	1	1
	unknown	Sp. D	1	1	0	0	0	0	0	0
Patellidae	unknown	spp.	6	5	4	4	1	1	0	0
Neritidae	unknown	Sp. A	0	0	0	0	1	1	0	0
Mytilidae	*Lithophaga*	Sp. A	2	2	2	2	0	0	0	0
	unknown	Sp. A	3	3	2	2	0	0	0	0
Pholadidae	unknown	Sp. A	0	0	1	1	0	0	0	0
Pectinidae	*Chlamys*	Sp. A	0	0	5	4	0	0	0	0
	Mimachlamys	*lentiginosa*	1	1	0	0	0	0	0	0
	Chlamys	Sp. B	0	0	0	0	1	1	0	0
	Chlamys	*madreporarum*	0	0	0	0	0	0	1	1
	unknown	Sp. A	0	0	0	0	1	1	0	0
	unknown	Sp. B	1	1	0	0	0	0	0	0
Pteriidae	unknown	SP. A	1	1	2	1	1	1	3	3
	unknown	Sp. B	0	0	2	1	0	0	0	0

	unknown	Sp. C	0	0	1	1	0	0	0	0
	unknown	Sp. D	0	0	0	0	0	0	2	1
Cryptoplacidae	*Cryptoplax*	sp.	1	1	1	1	0	0	2	2
	unknown	spp	0	0	0	0	2	1	0	0
Amphinomidae	*Eurythoe*	*complanata*	3	3	8	5	0	0	1	1
	Chloeia	*flava*	1	1	5	4	4	3	0	0
	unknown	spp.	24	14	18	11	6	4	6	6
Eunicidae	unknown	sp.	1	1	0	0	3	2	2	2
Nereididae	unknown	sp.	1	1	5	4	1	1	2	2
Polynoidae	unknown	spp.	1	1	0	0	0	0	0	0
	Harmothoe	sp.	0	0	0	0	1	1	0	0
Syllidae	unknown	sp.	0	0	1	1	0	0	0	0
Sabellidae	unknown	sp.	1	1	1	3	1	1	1	1
Serpulidae	unknown	sp.	1	1	2	1	0	0	0	0
	Spirobranchus	*giganteus*	0	0	1	1	0	0	0	0
	unknown	sp.	12	5	3	3	4	2	1	1
	unknown	spp.	0	0	1	1	0	0	0	0
	unknown	spp.	1	1	0	0	0	0	0	0
	unknown	spp.	2	2	0	0	0	0	0	0
	unknown	spp.	2	1	0	0	0	0	0	0
unknown	unknown	Sp. A	0	0	0	0	1	1	0	0
	unknown	Sp. B	0	0	0	0	1	1	0	0
Ophiactidae	*Ophiactis*	*savignyi*	29	11	38	14	6	5	2	2
	Ophiactis	Sp. A	0	0	0	0	1	1	1	1
Ophiocomidae	*Ophiocoma*	Sp. A	13	9	25	13	0	0	1	1
	Ophiocoma	Sp. B	17	12	17	8	0	0	1	1
	Ophiocoma	Sp. C	1	1	8	6	0	0	0	0
	Ophiocoma	Sp. D	0	0	1	1	1	1	0	0
	Ophiocoma	*erinaceus*	2	2	1	1	2	2	0	0
	Ophiocoma	Sp. E	1	1	0	0	0	0	0	0
Ophiotrichidae	*Ophiothrix*	Sp. A	16	12	3	3	2	2	5	2
	Ophiothrix	Sp. B	8	7	2	1	2	2	0	0
	Ophiomastix	spp.	4	2	1	2	0	0	0	0
	Macrophiothrix	spp.	0	0	1	1	0	0	1	1
Amphiuridae	*Ophiostigma*	spp.	0	0	4	3	3	2	0	0
Asterinidae	*Asterina*	Sp. A	1	1	0	0	1	1	0	0
	Asterina	Sp. B	1	1	0	0	0	0	0	0
Synaptidae	unknown	Sp. A	1	1	0	0	0	0	0	0
Holothuriidae	unknown	Sp. A	0	0	1	1	0	0	0	0
Himerometridae	unknown	Sp. A	0	0	4	3	0	0	0	0

Toxopneustidae	unknown	Sp. A	0	0	1	1	0	0	0	0
Cidaridae	*Eucidaris*	*metularia*	0	0	2	2	0	0	0	0
Echinometridae	*Colobocentrotus*	*atratus*	0	0	4	2	1	1	0	0
unknown	unknown	Sp. A	0	0	0	0	3	1	0	0
Gobiidae	*Paragobiodon*	*xanthosomus*	7	5	85	36	0	0	0	0
	Paragobiodon	Sp. A	6	5	7	5	0	0	0	0
	Paragobiodon	*echinocephalus*	6	3	9	5	0	0	0	0
	Eviota	*sp.*	9	7	19	12	1	1	1	1
	Gobiodon	*histrio*	0	0	0	0	23	21	14	12
	Gobiodon	*brochus*	0	0	0	0	7	6	0	0
	Gobiodon	*quinquestrigatus*	0	0	0	0	3	2	5	3
	Gobiodon	*citrinus*	0	0	0	0	5	4	0	0
	Gobiodon	*okinawa*	0	0	0	0	0	0	3	3
Pomacentridae	*Chromis*	Sp. A	0	0	0	0	1	1	0	0

Abundance and species richness

The mean abundance of epifauna was highest for the two pocilloporid corals, (18.62 ± 2.16 for *P. damicornis* and 15.8 ± 1.35 for *S. hystrix*), which was approximately three times the means recorded in *Acropora* corals (5.7 ± 1.10 for *A. nasuta* and 5.28 ± 0.76 for *A. millepora*) (Figure 2.1). There was significant variation in abundance of epifauna across all four host corals (Kruskal-Wallis test, H=88.868, df=3, $p<0.001$), but there was no difference between *P. damicornis* and *S. hystrix* (Mann-Whitney U=1156.00, $p>0.05$) or *A. nasuta* and *A. millepora* (Mann-Whitney U=1238.00, $p>0.05$). The number of animals recorded within each coral colony varied greatly even within colonies of the same host coral, ranging from 1-73 organisms in *P. damicornis*, 4-48 in *S. hystrix*, 1-42 in *A. nasuta* and 1-31 in *A. millepora.*

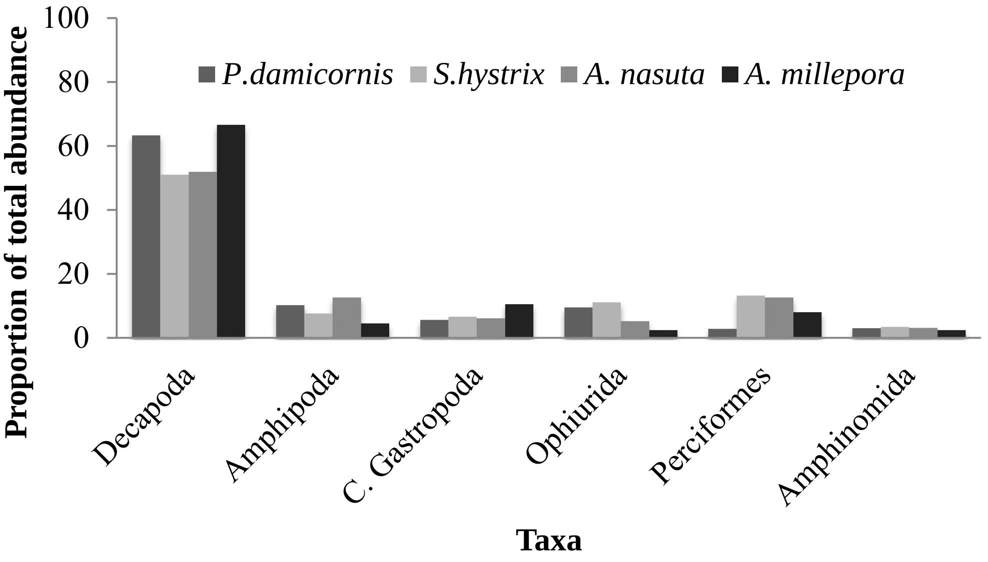


Figure 2.1 Proportional abundance of the 6 most dominant taxa to total coral-associate abundance among four host coral species, Pocillopora damicornis, *Seriatopora hystrix*, *Acropora nasuta* and *Acropora millepora*.

Mean species richness per colony was approximately 2.5 times higher for pocilloporid colonies compared to *Acropora* corals (Figure 2.2). A Kruskal-Wallis tests revealed a significant difference in species richness among the coral species (H=85.717, df=3, P<0.001), yet these differences were only found to be significant among host corals of differing families (Mann-Whitney U; *P. damicornis* X *A. nasuta* , U=426.00, p<0.001, *P. damicornis* X *A. millepora* , U=394.00, p<0.001, *S. hystrix* X *A. nasuta* , U=233.5, p<0.001, *S. hystrix X A. millepora* , U=200.00, p<0.001).

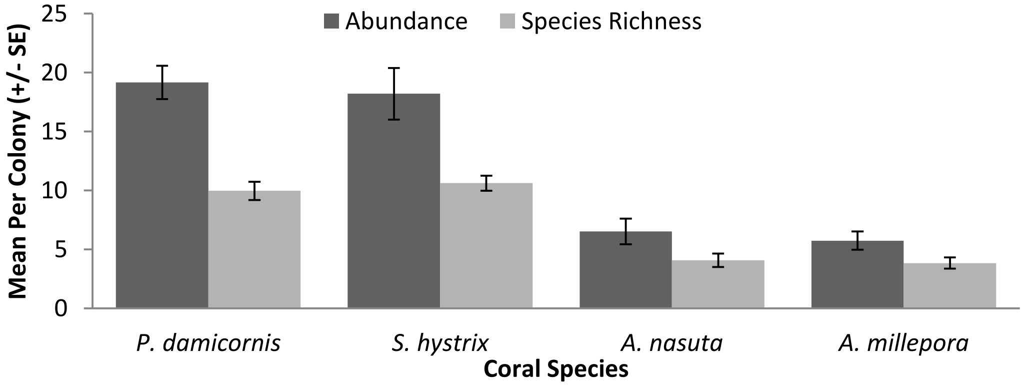


Figure 2.2 Variation in the abundance and mean species richness of commensal fauna associated with the host corals *Pocillopora damicornis*, *Seriatopora hystrix*, *Acropora nasuta* and *Acropora millepora*

Species composition

The MANOVA confirmed that the epifaunal assemablages were significantly different among coral species (Pillais trace = 1.67, df = 132, 465, F = 4.45, p<0.001). A canonical discriminant analysis (CDA) shows considerable overlap in the commensal community between *A. nasuta* and *A. millepora*, but clear distinction between the acroporid and pocilloporid corals (Figure 2.3a). The first axis accounts for 74.19% of the variation between the two coral families, Acroporidae and the Pocilloporidae. The second axis accounts for 20.77% of the variation between coral species of the same family, mainly between P. *damicornis* and *S. hystrix*. Although the differences in species composition between *A. nasuta* and *A. millepora* were slight, there was significant difference in the epifaunal assemblages of the two familial corals belonging to different genera (*P. damicornis* and *S. hystrix*). A distinguishing difference among coral families is apparent in the commensal communities; the two acroporids were characterized by the abundance of *Tetralia glaberrima* and the two pocilloporids were characterized by the abundance of *Trapezia cymodoce. A. millepora* differed from *A. nasuta* by the abundance of *Harpiliopsis* spp. (16 individuals in *A. millepora* compared to only 3 in *A. nasuta*) and the rarity of *Tetralia nigrolineata (*only 4 found in *A. millepora* compared to 22 in *A. nasuta). P.damicornis* differed from *S. hystrix* in the abundance of *Alpheus lottini* (57 in *P. damicornis* compared to only 20 in *S. hystrix)* and *Periclimenes* shrimp (149 in *P. damicornis* compared to 68 in *S. hystrix)* and the only occurrences of *Trapezia septata* (Figure 2.3b).

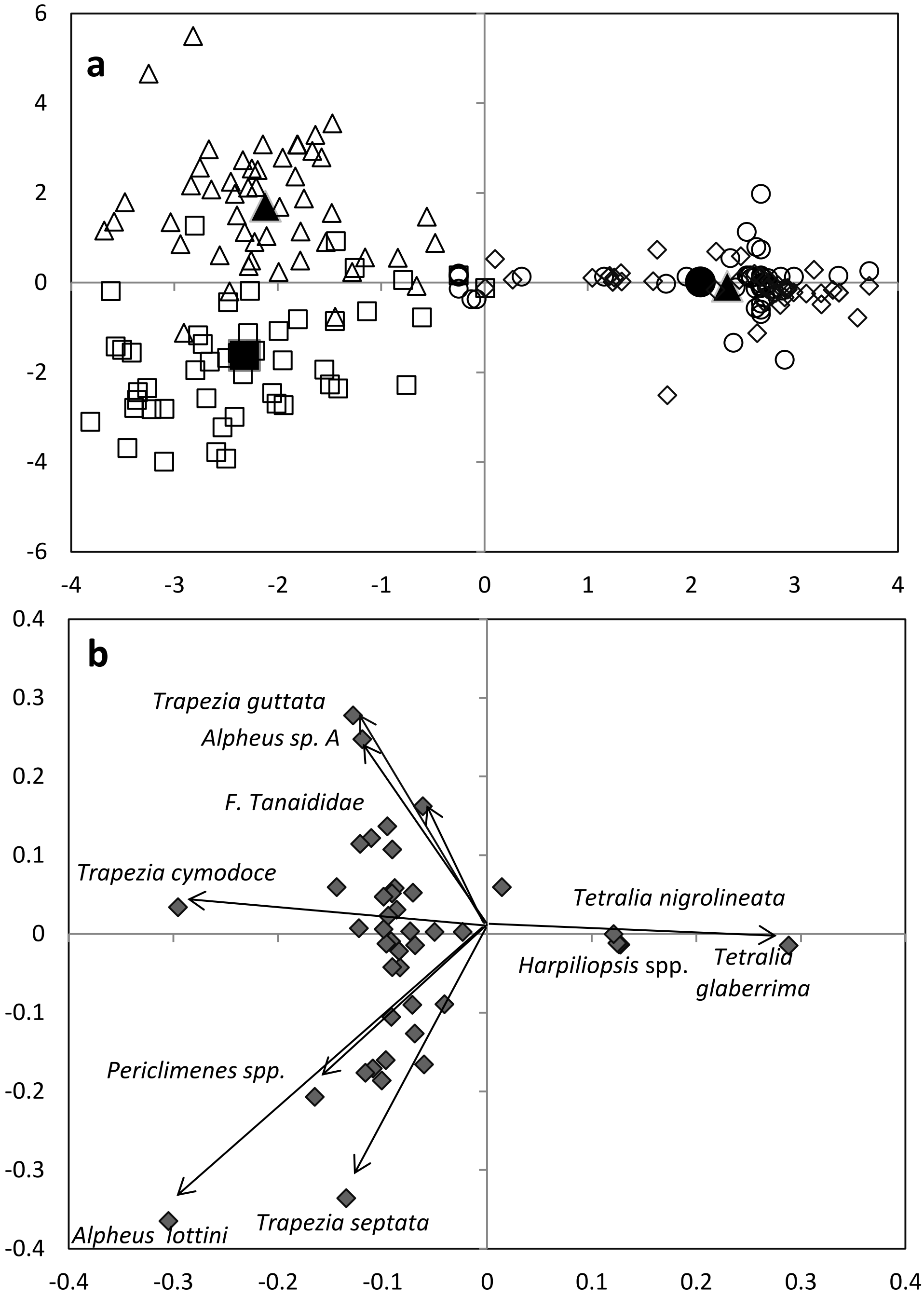


Figure 2.3 Canonical discriminant analysis of invertebrate assemblages on the four host corals: a) the position of each host coral species and the centroids of the four groups (*Pocillopora damicornis*, *Seriatopora hystrix*, *Acropora nasuta* and *Acropora millepora*) and b) the correlation between each species and the canonical values (structure coefficients). The vectors represent strength of correlations between taxa and canonical variates

Species overlap amongst host corals

Of the 178 species surveyed, only 13% (23 species) were found in all four host corals, whereas 42% (75 species) were found in only one of the four host corals (Figure 2.4). However, most of those 75 species were represented by a single organism or were found on a single coral colony. With the exclusion of singletons, the percent of taxa found on just one of the four host corals was 15% (27 species) (Figure 2.4). Approximately 21% of taxa found in *P. damicornis* and 22% of taxa found in *S. hystrix* were exclusive to their host coral. *A. nasuta* had the highest percentage of exclusive taxa (25%) whereas in *A. millepora* only 16% of taxa were exclusive to their host coral. Taxonomic overlap in epifaunal composition was greatest among corals from the same family. *P. damicornis* and *S. hystrix* shared 30 taxa and 14 taxa were shared between *A. nasuta* and *A. millepora*. In comparison, only 4 taxa occurred on both *P. damicornis* and *A. nasuta* and *S. hystrix* and *A. millepora* did not share any taxa exclusively. Colonies of the same host coral displayed a large variation in species richness. Total species within a single colony of *P. damicornis* ranged from 1-23, 3-23 in *S. hystrix*, 1-24 in *A. nasuta* and 1-21 in *A. millepora.*

The recurrence of epifaunal taxa (the number of coral colonies on which each species was recorded) was low for the majority of taxa. Species abundance distributions (SADs) were plotted for all four coral species based on a binning method described by Hubbell (2001) (Figure 2.5). This distribution was similar for all four host coral species: rare taxa were prevalent, constituting the majority of taxa surveyed. Many taxa were only found on fewer than 10 colonies of a given host. Only a very few were found on more than 30 corals and no taxa were found on all 50 corals of one host species. Some taxa were only represented by a single individual. From 50 colonies of *P. damicornis*, 83% of taxa occurred on less than 10 colonies, 85% for *S. hystrix*, 96% for *A. nasuta* and 92% for *A. millepora*. The taxa that were found in relatively high occurrence also exhibited relatively high abundance. These taxa required further investigation as they were most likely to be specialist taxa.

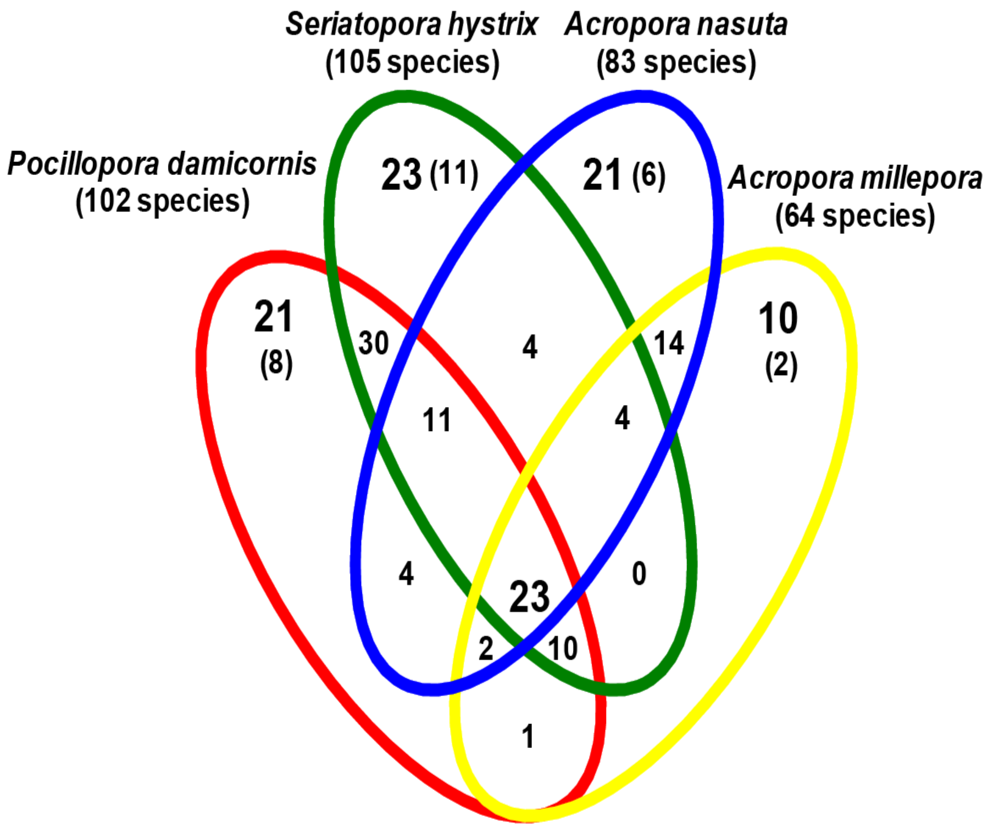
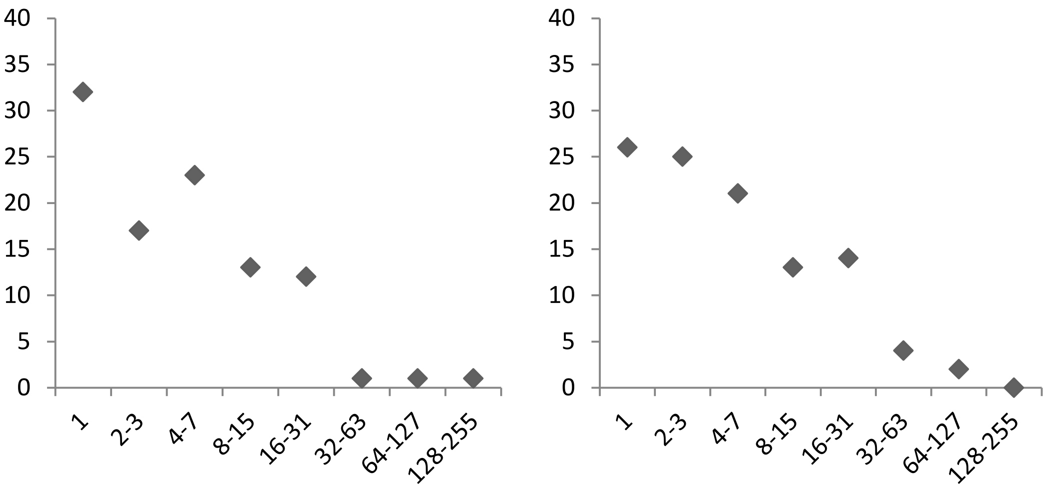
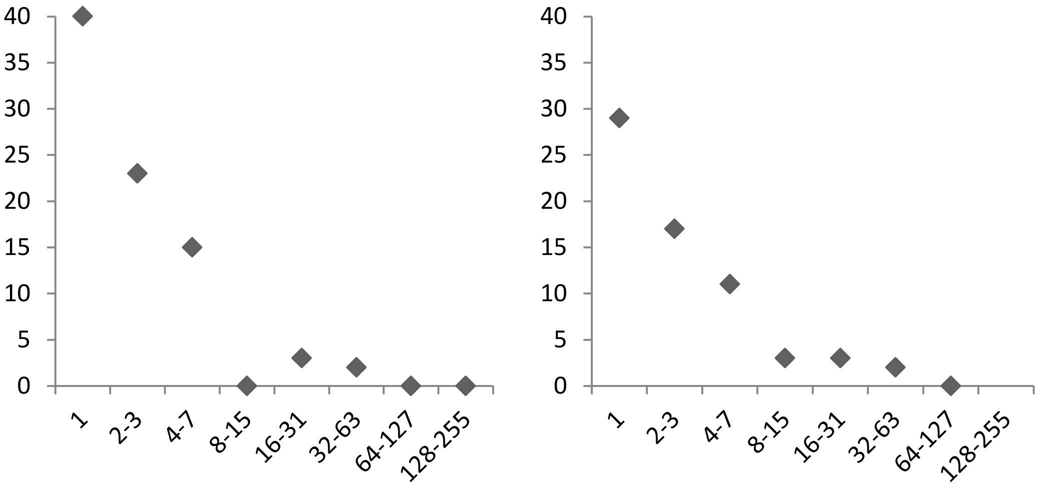


Figure 2.4 Venn diagram showing taxonomic overlap in species found within each of the four corals (*Pocillopora damicornis*, *Seriatopora hystrix*, *Acropora nasuta and Acropora millepora*). Bracketed numbers reflect the total species number excluding singletons. A total of 178 taxa were recognized with 15% unique to ¼ of coral species surveyed



Pocillopora damicornis ***Seriatopora hystrix***



Acropora nasuta ***Acropora millepora***

Figure 2.5 Species abundance distributions for taxa found within four host corals (*Pocillopora damicornis*, *Seriatopora hystrix*, *Acropora nasuta* and *Acropora millepora*). Abundance is plotted on a $\log^2$ scale, with each bin or octave containing twice the number as the previous one (based on Hubbell 2001)

Variation in coral attributes

Variation in the attributes of each coral species was examined by comparing measured habitat characteristics (Table 2.2). The mean living space was greatest in *P. damicornis* and smallest in *S. hystrix* yet did not differ significantly among any of the four coral species (ANOVA, F=0.8972, df=3, p=0.444). However, inter-branch space did differ significantly among coral species (F=7.055, df=3, p=<0.001), whereby *P. damicornis* and *S. hystrix* had significantly greater mean inter-branch space than *A. nasuta* and *S. hystrix* had significantly greater mean inter-branch space than *A. millepora* (Table 2.2).

Table 2.2 Variation in habitat characteristics among four branching host corals; *Acropora nasuta*, *Acropora millepora*, *Pocillopora damicornis* and *Seriatopora hystrix*

Habitat characteristic	*A. nasuta*	*A. millepora*	*P. damicornis*	*S. hystrix*	Variation
Living space	1809.42 cm^2 (± 140.22)	1839.58 cm^2 (± 149.92)	1884.23 cm^2 (± 148.37)	1580.68 cm^2 (± 132.59)	303.55 cm^2
Inter-branch space	5.13mm (± 0.25)	5.73mm (± 0.23)	6.22mm (± 0.23)	6.75mm (± 0.33	1.62 mm
Penetration depth ratio	71.81% (± 2.15)	69.52% (± 2.27)	60.9% (± 2.99)	70.78% (± 2.47)	10.91%
Percent Live Tissue	91.7% (± 2.41)	95.3% (± 1.97)	76.1% (± 2.86)	82.6 % (± 2.66)	12.7%

Penetration depth was found to differ significantly among coral species (F= 3.37, df= 3, p= 0.019). A Tukey's H.S.D. revealed that *P. damicornis* differed from all other coral species (Table 2.2). *P. damicornis* typically has thick branches that do not follow a vertical growth pattern, but rather coil and bend. The two acroporids species exhibited a digitate growth form, with long cylindrical branches stemming from the coral base and growing straight up and outward. *S. hystrix* displays a lattice growth form, with relatively thin branches. The space between branches is relatively wide, allowing for penetration depth to approach total colony height.

The amount of live tissue (as a percent of the whole colony) was found to differ significantly among coral species (F= 23.13, df= 3, p= <0.001). A Tukey's H.S.D.

indicated that two acroporids had significantly more live tissue as measured by percentage whole colony than both the pocilloporids (Table 2.2). The non-living part of a coral can act as substrate to other settling organisms such as turf algae, bryozoans, tunicates, sponges and even other coral species (Coles 1980). Therefore, the death of some coral tissue usually creates other microhabitats within the same colony and can result in the immigration of new inhabitants.

The large variation in species abundance and richness among and within host corals was examined by conducting backwards stepwise regression analyses. Variation among host corals was examined using five variables; coral species, living space (cm^3), mean inter-branch space (mm), live tissue (as the fourth root of the percentage of the whole colony) and mean penetration depth (as a ratio of height in mm, arc sine transformed). Species abundance was found to be most affected by coral species, the amount of living space and live tissue ($F_{3, 196} = 35.27$, $p<0.001$, adjusted $R^2= 0.34$) (Table 2.3). Coral species was the most significant factor of the three (F= 68.19, p<0.001, Beta= -0.49), then live tissue (F= 9.95, p= 0.001, Beta= -0.18) with living space having the least impact (F= 7.25, p= 0.007, Beta= 0.15). Species richness was affected most by host coral species and the amount of live tissue ($F_{2, 197} = 46.77$, $p<0.001$, adjusted $R^2= 0.32$). Coral species was again the most significant factor (F=69.66, p<0.001, Beta= -.50) with the amount of live tissue having a smaller impact (F=6.99, p=0.008, Beta= -0.16). Although the amount of living space and live tissue had a small influence on species abundance and richness, coral species was the strongest predictor of abundance and richness.

Table 2.3 Results of backwards stepwise regression analysis and parameters estimates for the relationships between coral attributes and species abundance and richness among host corals, *Acropora nasuta*, *Acropora millepora*, *Pocillopora damicornis* and *Seriatopora hystrix*.

	Abundance					Species richness				
Variables	DF	MS	F	p	Beta (ß)	DF	MS	F	p	Beta (ß)
Coral species	1	101.59	68.19	0.000	-0.49	1	46.83	69.65	0.00	-0.51
Living space	1	10.79	7.24	0.01	0.15	0				
Inter-branch space	0					0				
Penetration depth	0					0				
Live tissue	1	14.82	9.95	0.002	-0.10	1	4.70	6.99	0.01	-0.16
Error	196	1.49				197	0.67			

To assess whether variation in species abundance and richness within host corals was related to any of the four habitat characteristics (living space, mean inter-branch space, percent live tissue and mean penetration depth), a separate backwards stepwise regression analysis was conducted for each coral species for each dependent variable (abundance and species richness). Although the multiple regression analyses only accounted for a small portion of the variation in species abundance within coral species, living space was an important predictor of abundance for 3 coral species (*P. damicornis*, *S. hystrix* and *A. millepora*) and the proportion of live tissue was an important predictor of abundance in 2 coral species (*P. damicornis* and *A. nasuta*) (Table 2.4). In terms of species richness, living space was an important predictor in just one coral species (*P. damicornis*) and the proportion of live tissue was an important predictor of species richness in 3 coral species (*P. damicornis*, *A. nasuta* and *A. millepora*). Where living space was an important factor, both species abundance and richness were higher in colonies with greater living space. However, the opposite effect was noticed where live tissue was an important factor. Species richness and abundance was lower in colonies with a higher proportion of live tissue.

Table 2.4 Results of backwards stepwise regression analysis and parameters estimates for the relationships between coral attributes and species abundance and richness within host corals, *A. nasuta*, *A. millepora*, *P. damicornis* and *S. hystrix*.

Abundance

Coral Species	Regression	Living space	Inter-branch	Penetration depth	Live tissue
P. damicornis	$F_{2,47}$= 9.54 p<0.001 R^2=0.26	F=5.40 Beta=0.29	ns	ns	F=10.83 Beta=-0.41
S. hystrix	$F_{3,46}$=4.22 p=0.01 R^2=0.16	F=9.93 Beta=0.46	F=5.37 Beta = 0.33	F=4.36 Beta =0.28	ns
A. nasuta	$F_{1,48}$=9.58 p=0.003 R^2=0.15	ns	ns	ns	F=9.58, Beta=-0.41
A. millepora	$F_{1,48}$=6.71 p=0.01 R_2=0.10	F=6.71 Beta =0.35	ns	ns	ns

Species richness

P. damicornis	$F_{2,47}$= 10.83 p<0.001 R^2 = 0.29	F= 5.13, Beta = 0.28	ns	ns	F= 13.40 Beta=-0.48
S. hystrix	F=2.23 p=0.12	ns	ns	ns	ns
A. nasuta	$F_{1,48}$=9.28 p=0.003 R^2=0.14	ns	ns	ns	F=9.28 Beta=-0.40
A. millepora	$F_{1,48}$=4.53 p=0.04, R^2=0.07	ns	ns	ns	F=4.53 Beta=-0.29

2.5 Discussion

The substantial differences in the abundance, species richness and species composition of epifauna among corals suggests that habitat attributes play an important role in structuring epifaunal communities. Pocilloporid corals, *P. damicornis* and *S. hystrix*, exhibited a higher species abundance and richness than acroporid corals, *A. nasuta* and *A. millepora*, containing on average three times as many individuals per coral colony and two and a half times the number of species. Variation in epifaunal abundance, species richness and composition may be partly attributable to differences in the morphology of different host corals. The space between branches was found to be greater in *P. damicornis* and *S. hystrix* than both *A. nasuta* and *A. millepora*. The smaller inter-branch space of the acroporids may serve as a limiting factor to larger sized epifaunal associates. As well, the ratio of penetration depth to colony height was smallest in *P. damicornis*, indicating a more complex branch growth form. *A. nasuta* and *A. millepora* share similar digitate growth forms; branches grow at a slight angle but nonetheless straight up, unhampered. *P. damicornis*' branches have kinks in them, creating a canopy of branches. *S. hytrix* grows in a lattice formation, with many branch crossings at various angles. Vytopil and Willis (2001) also found that associates of *Acropora* spp. preferred tightly branching, complex habitats over open-branching coral habitats. The more complex habitat is thought to provide better refuge from predation (Castro 1988, Vytopil and Willis 2001, Munday et al. 1999, Munday 2004, Fabricius et al 2014).

Even among coral colonies of the same species, there were substantial differences in the abundance (ranging from 1-73 individuals) and species richness (ranging from 1-24 different taxa). Measures of habitat characteristics were not strong predictors of either abundance or species richness. As all coral colonies were approximately the same size, habitat complexity as measured by size of living space, mean inter-branch space and mean penetration depth, did not vary greatly among coral colonies within each coral species. Living space was an important predictor of abundance for 3 coral species (*P. damicornis*, *S. hystrix* and *A. millepora*) and the proportion of live tissue was an important predictor of species richness for 3 coral species (*P. damicornis*, *A. nasuta* and *A. millepora*) yet the relationship between abundance and species richness and coral attributes was weak overall.

The coral colonies displaying partial mortality, and thus less than 100% live tissue cover, exhibited an increase in both species abundance and richness. This could imply that as coral cover declines within the colony, uniformity of habitat is lost and new microhabitats within the colony allow for other species to utilize new resources.

The relationship between live coral cover and species abundance and richness would need to be clarified with more intense sampling of colonies approaching 0% live coral cover. Other studies have shown that habitat degradation and consequent loss of coral cover have resulted in severe declines in the abundance and diversity of coral-associated fishes, with greater impact on coral specialists (Jones et al. 2004, Munday 2004). Pratchett et al. (2006) documented significant declines in chaetodontids known to be obligate hard-coral feeders. One study documented no effect of coral decline on abundance and diversity, but noted a marked shift in community composition from one with a high abundance of specialised coral associates to one with a high abundance of species less habitat specific (Bellwood et al. 2006).

Species overlap was greatest among the corals within the same family and genus, with coral belonging to different families and genera exhibiting more distinct assemblages. Although many other branching coral species were excluded from this study, this may provide evidence that corals host specific assemblages of epifauna and that whilst overlap does occur, certain taxa may be specific to just one species, genus, or family, of host. Although habitat specialisation has been well documented for some fish species (e.g. *Gobiodon* spp, Munday et al. 1997, 1999) few studies have looked at the proportion of specialist species found within complete epifaunal assemblages of branching coral, instead focussing on only a few species (e.g. *Tetralia* spp, Sin 1999). Based on rates of occurrence, this study documented that 15% (27 species) of the 178 taxa collected were found to occur on only one of the four coral species studied and therefore have the potential to be specialised to some degree. As specialists species are known to exhibit a higher extinction rate due to habitat degradation (McKinney 1997, Bonin 2012, Pratchett et al. 2012) further research needs to be conducted to determine the degree of host specialisation and thus the vulnerability of these species to the potential loss of coral cover expected with a changing climate.

Epifaunal assemblages were quite distinct among the four coral species sampled. In general, *P damicornis* was characterised by *Trapezia septata*, *Alpheus lottini*, and Periclimenes shrimp whereas *S. hystrix* was characterized by *Trapezia guttata* and *Alpheus sp.* A. Although *A. nasuta* and *A. millepora* had extensive overlap, *A. nasuta* was characterized by the high abundance of *Tetralia nigrolineata* whilst *A. millepora* was characterized by the high abundance of *Harpiliopsis* spp. The large variation in species composition amongst corals of different families and genera indicates that the occurrence of specialisation may be high amongst coral-dwelling invertebrates. However, further research on other coral species is needed to confirm these results. Many species of coral associates are known to have highly specific patterns of coral use (Patton 1974, 1994, Sin 1999, Vytopil and Willis 2001, Munday 2004, Stella et al. 2011, Hoeksema et al. 2012), including trapeziids, tetralids and gobies. Why some species have specialized to one host whilst others are more host-generalized is not yet known. Theory predicts that natural selection favours host specialization if hosts are abundant and predictable (i.e., environmental conditions are stable), whereas generalist strategies evolve if conditions are more variable (Townsend et al. 2003). The reasons behind this evolutionary path are not clear (Fox and Morrow 1981), however species with a highly specialized ecological niche may be far superior competitors than generalists (Townsend et al. 2003). If many species are competing for scarce resources, specialization may also lead to speciation, resulting in a variety of species with various adaptations that act to reduce competition and allow for greater resource partitioning (Miller 2005). As specialists may hold a competitive edge when environmental conditions are stable, expected changes in climate will favour generalists which are able to thrive in a range of environmental conditions utilizing a variety of resources. In order to protect reef biodiversity, it is important to identify specialist species and assess their vulnerability to reef degradation.

The most abundant taxa for all four coral species studied were the decapod crustaceans, accounting for up to 66% of all epifaunal animals collected. This is a particularly strong trend found in all other studies of branching coral epifauna (Abele and Patton 1976, Austin et al. 1980, Black and Prince 1983, Patton 1994, Vytopil and Willis 2001). As most other published studies of commensal communities have focused on the decapod and fish assemblages, it is unknown how persistent this pattern is among other coral species. This study found that although the decapod crustaceans were the dominant taxa of all four host coral species, other taxa, such as amphipods, echinoderms, molluscs and various worm phyla, were also present in high abundance. Other studies have not found such a wide breadth of taxa to co-exist among colonies of branching corals (but see Austin et al. 1980). As decapod crustaceans were by far the most dominant taxa found in all host corals, their ecology may be vital to localized coral reef processes. Little is known on the ecology of decapod crustaceans with the exception of a few species that occur in high abundance, such as crabs of the genera *Trapezia* and *Tetralia* (Glynn 1983, Huber 1987, Tsuchiya et al. 1992, Sin 1999). These crabs enhance colony health (Glynn 1983, Stewart et al. 2006) and exhibit aggressive behavior towards coral predators, such as crown-of-thorns starfish (Glynn 1980, Pratchett 2001). As the crabs are trophically dependent on their host coral and many are host specific to either species or genus (Sin 1999), this intense territoriality may reflect their strong reliance on their host coral for their survival (Huber and Coles 1986). For these reasons, it is crucial that we gain a better understanding of the ecological processes maintaining coral health on such a small spatial scale.

Considering that at the level of phylum, this study found a diversity equivalent to that of tropical rainforests (12 phyla) within the branches of just four coral species, it is important to appreciate that branching coral colonies serve as microhabitats of highly concentrated diversity within the reef ecosystem. Given this diversity, it is important to gain a better understanding of how these communities are structured. Animals so intimately associated with their habitat may be vital to the maintenance of critical ecological systems pertaining to coral health. As the invertebrate groups account for the greatest numerical abundance and diversity on coral reefs, yet have received the least attention, our knowledge of coral reef ecosystem function is derived from what we know about a relatively small proportion of coral reef species. If preventing the loss of species and reversing declines in biodiversity is the fundamental aim of coral reef conservation (Naeem et al. 1994, Agardy 1994, Hastings and Botsford 2003, Knowlton et al. 2010, Plaisance et al. 2011), then more research effort on the other possible 9 million species of coral reef invertebrates (Reaka-Kudla 1997) is clearly needed. This analysis of the differentiation among communities on just four coral species highlights the potential for a dramatic impact of coral reef degradation on the most speciose coral reef taxa.

Chapter 3: Wanted dead or alive: Moderate disturbance to coral habitat promotes invertebrate biodiversity on tropical reefs

3.1 Abstract

Habitat degradation is one of the greatest threats to biodiversity, posing a particular threat to species specialised on key habitat-forming organisms. Coral reef habitats support a high diversity of invertebrate taxa, some of which are highly specialized on scleractinian corals, while others are closely associated with dead surfaces and algal turfs. Moderate levels of disturbance that cause partial mortality or a matrix of live and dead corals may promote diversity by increasing spatial heterogeneity. However, increasing anthropogenic effects that eliminate live corals may lead to decline in the biodiversity of obligate coral-dwellers. Here I test these predictions by surveying the presence and abundance of obligate and facultative invertebrates on corals during a bleaching episode that left corals varying from 0 to 100% dead tissue. Species richness on 100% healthy coral colonies was nearly double that found on bleached colonies, but only half that found on predominantly dead colonies. This was explained by the loss of obligate species and the proliferation of facultative species. Different coral species supported distinct assemblages of obligate coral-associated species, but once dead, different coral species supported overlapping communities of facultative species. Individual coral colonies with partial mortality (40-60 %) yielded the highest diversity and abundance of both obligate and facultative coral dwellers. However, as colony mortality increased, the community composition shifted from one dominated by a few obligate species to one marked by an abundance of facultative species. This study supports the hypothesis that moderate disturbances and spatial heterogeneity promote reef biodiversity, but phase shifts that lead to large-scale coral loss are a major extinction risk for specialised coral-dwelling invertebrates.

3.2 Introduction

Disturbance is a natural process that can influence ecological communities, either directly by impacting on species abundance or indirectly by altering interactions between species or modifying habitats (Dayton 1971, Sousa 1979, Svensson et al. 2012). Moderate disturbance may promote local biodiversity through a range of mechanisms, including preventing dominant competitors from monopolising habitat (Connell 1978, Huston 1979) or increasing spatial heterogeneity and microhabitat complexity (Jones and Syms 1998). However, severe disturbance due to habitat destruction is expected to result in declining biodiversity, as it threatens species dependent on pristine conditions (Hughes et al. 2003, Hoegh-Guldberg and Bruno 2010, Hooper et al. 2012). A decline in biodiversity can have subsequent effects on ecosystem function, disrupting nutrient cycling and reducing productivity through the loss of key species (Cardinale et al. 2012). However, not all species respond to disturbance and habitat change in the same way. Species that are highly specialised on habitat-forming organisms (obligate species) have the highest extinction risk should their habitat decline or disappear (Mckinney 1997, Munday 2004, Thomas et al. 2004). On the other hand, facultative habitat dwellers and generalist species may be unaffected, while those specialised on highly disturbed substrata may increase. The impact of different levels of disturbance on the overall biodiversity of communities is not always known. It is important to understand the point at which habitat degradation begins to negatively impact on species richness, as this is a fundamental concern when managing potentially threatened ecosystems.

Coral reefs encompass the highest biodiversity of any marine ecosystem (Sebens 1994, Gray 1997, Hoegh-Guldberg 1999), with the number of species ranging from 200,000 to 9 million (Reaka-Kudla 1997, Ruppert et al. 2004). Disturbance is considered one of the most important natural processes maintaining local diversity, and influencing the abundance and composition of coral communities (Gardner et al. 2003, Jenkins 2003, Bruno and Selig 2007). According to the well-established ‘intermediate disturbance hypothesis’, coral diversity may be low when disturbance is extreme due to the direct loss of rarer species and low when there is no disturbance, as fast growing species outcompete others to occupy all the space (Connell 1978, Rogers 1993). However, at intermediate levels of disturbance, diversity increases because inferior competitors can colonise, but disturbance is not severe enough to eliminate species.

The spatial heterogeneity in coral habitat created by small-scale disturbances also appears to promote the diversity of coral reef fishes, as it creates habitat for species that are reliant both on live and dead coral substrata (Jones and Syms 1998, Wilson et al. 2009). However, anthropogenic impacts are increasing on coral reefs, with an estimated 60% of reefs in a severely degraded state (Wilkinson 1999, Hughes et al. 2010, Pandolfi et al. 2003, Wilson et al. 2006, Carpenter et al. 2008). Such extreme levels of disturbance, with coral cover reduced to less than 5%, have resulted in declines in both coral (Hughes 1994, Aronson and Precht 1995, Hoegh-Guldberg et al. 2007, Pratchett et al. 2011) and reef fish (Jones et al. 2004, Graham et al. 2006, Pratchett et al. 2006, 2008, Wilson et al. 2006) biodiversity.

Although most reef biodiversity studies focus on coral and reef fish, it is the collective 32 phyla of invertebrates that comprise over 90 % of coral reef biodiversity (Reaka-Kudla 1997, Stella et al. 2011). However, the effects of different levels of disturbance and the threat of widespread reef degradation have not been tested for small, motile coral reef invertebrates. A large proportion of reef invertebrates live in close association with scleractinian corals, particularly bushy corals of the genera *Acropora* and *Pocillopora* (e.g. Abele and Patton 1976, Coles 1980, Edwards and Emberton 1980, Castro 1988) and of these, as many as 80% exhibit a preference for a single host (Stella et al. 2011). However, there are also many invertebrates associated with dead coral and algal turfs (Enochs 2012, Enochs and Manzello 2012, Kramer et al. 2014, Takada et al. 2014). Hence, spatial heterogeneity in coral communities has the potential to promote invertebrate biodiversity. However, obligate coral-dwelling species are unlikely to be able to cope with a severe decline in their habitat as a result of disturbance (‘the specialization-disturbance hypothesis, Vazquez and Simberloff 2002). Hence, it is important to understand how these communities respond to differing levels of disturbance and identify at what stage there is a risk of extinction of the more specialised species.

This study aimed to examine the response in diversity, abundance and species composition of small motile invertebrates to various levels of natural degradation of common host corals. I opportunistically exploited a moderate bleaching event in which host corals exhibited a range of bleaching severity. I compared invertebrate communities found on either healthy (non-bleached), bleached, and dead host corals in order to test the following predictions: (1) Extreme bleaching resulting in 100%

bleached tissue or death will result in a decline in the biodiversity due to the loss of obligate coral-dwelling specialists on the host coral species. (2) Extreme bleaching and coral death will result in a dramatic shift in invertebrate species composition, from obligate to facultative coral-dwelling species. (3) Healthy coral colonies of different coral species will form distinct invertebrate assemblages, but bleaching and coral death would lead to a convergence in community composition consisting of facultative species. (4) Partial coral bleaching or mortality will promote local biodiversity and abundance by creating spatial heterogeneity through a mix of live and dead substrata.

3.3 Methods

Sampling location, design and methodology

This study was conducted at Lizard Island (14°40’ S, 145°28’ E), in the northern Great Barrier Reef, Australia. Seventy individual coral colonies (ca. 20 cm diameter) of each of seven species of branching coral, *Acropora nasuta, A. spathulata* and *A. valida* (F. Acroporidae), *Pocillopora damicornis*, *P.verrucosa*, *Seriatopora hystrix* and *Stylophora pistillata* (F. Pocilloporidae), were identified following Veron (2000) and collected from shallow reef habitats (1.5-2.5m depth) within the Lizard Island lagoon. Corals ranged from 100-0 % live tissue and bleached tissue. All bleached corals were collected in 2010 at the onset of a natural bleaching event in the Lizard Island Lagoon (see Chapter 4). Individual coral colonies were collected by covering the entire colony with a plastic bag (to prevent any mobile animals from escaping) and then carefully chiseling the entire intact coral colony loose of the substrate. Coral colonies were transported in individual buckets of fresh seawater to the research station for processing.

Conspicuous invertebrates were initially removed using blunt probes and forceps. Corals were then washed with pressurized salt water over a bucket to dislodge any animals clinging to the coral surface. Corals were then submerged in 100% freshwater for up to thirty seconds as this was found to be an effective method for expelling any undetected animals still left in the coral. Fish quickly vacated the host when gently nudged with a blunt probe and were also collected in order to account for all species found within the colony. The water was then poured through a 1 mm X 1 mm mesh net and the animals were retrieved. Use of this method excluded both boring animals and those generally smaller than 1 mm. The corals were then carefully inspected for up to 30 minutes to maximize detection of small cryptic macrofauna. All animals were then anaesthetized with a clove oil solution and placed in a freezer for several minutes before being moved to a specimen jar of formalin. All specimens were then kept for later identification, whilst coral corals were returned to the lagoon and cemented back onto the substrate with marine epoxy.

Each individual animal was identified with the greatest possible taxonomic resolution based on all current literature and taxonomic descriptions available (e.g. the World Register of Marine Species) and with the assistance of taxonomic consultations (names in the acknowledgements). Where species level identification was not possible, species were identified to the genus or family. To estimate species richness, unidentifiable organisms were differentiated into a number of distinct species groups based on color patterns and/or morphology. Group assignment was extremely conservative (only based on clear and unambiguous differences), which is likely to result in underestimates of species richness. Species were also categorized as either obligate or facultative coral users based on current knowledge of coral-associated species (as reviewed by Stella et al. 2011).

Host Coral Characteristics

To account for differences in the size of each host coral, area was calculated for each colony. Firstly, maximum diameter and perpendicular diameter were measured. Diameter was obtained by averaging the two measurements. Circular area was then calculated in cm^2. For each colony, the proportion of live tissue, bleached tissue and/or dead skeleton was visually estimated as a percent of the entire colony to the nearest 5%.

Data Analysis

Overall biodiversity and abundance

Total species richness and abundance was examined in order to illustrate the phylogenetic diversity of coral-associated invertebrates and determine which phyla are the greatest contributors. Obligate species were determined by reviewing all current literature and their proportion was calculated. Data were then analysed to test the four hypotheses:

Hypothesis 1: Host coral bleaching and death will lead to a decline in invertebrate species richness and abundance

To determine if habitat quality affected diversity (species richness) and abundance of invertebrates, coral colonies (all host corals combined) were assigned one of three groups: live and healthy (colonies with 80 % or more live, non-bleached tissue), bleached (colonies with 80 % or more bleached tissue) and dead (colonies with less than 20 % live tissue). To ensure maximum differences in the quality of host corals, colonies that did not fit these criteria (for example 60 % live tissue) were not used in this analysis. Dead corals consisted of recently dead colonies, which were structurally intact with some turf algae present. Overall species richness and abundance (standardised to cm^2) characteristic of each category of coral was then examined using a one-way ANOVA and followed with a Tukey HSD test for pairwise comparisons.

Hypothesis 2: Host coral bleaching and death will lead to a change in invertebrate species composition from obligate to facultative species

Community composition was compared between all live, bleached and dead corals regardless of host coral species (using the same categories as above) to determine the response of invertebrate assemblages to host coral bleaching and death. Abundances of each species were square-root transformed to emphasize rare species and de-emphasize the importance of common species in the analysis (Legendre and Legendre 1998). In addition, known obligate species of the genera *Trapezia* (pocilloporid obligates) and *Tetralia* (acroporid obligates) were considered only at the genus level in order to reduce community variation between live host corals of the same family. Differences in invertebrate species composition using coral health category as the only factor were then examined with non-metric multidimensional scaling (nMDS). This 2D spatial representation describes similarities between samples in terms of their species composition based on Bray–Curtis similarity. Observed differences between assemblages were analysed with permutational multivariate analysis of variance (PERMANOVA) as this test is much more robust to correlations and heterogeneous variances (Anderson and Walsh 2013). Subsequently, the contribution of species to between-group similarity was assessed using a SIMPER analysis using 50 % contribution as a cut-off (similarity percentages) (Clarke and Warwick 1994). All analyses were performed using PRIMER v.6.1.12 pack-ages (Clarke and Gorley 2006).

Hypothesis 3: Different coral species will have distinct invertebrate assemblages, but bleaching and coral death will lead to a convergence in community composition

Differences in species composition between live, bleached and dead hosts (based on the same categories as above) of each of the seven coral species were investigated using three separate non-metric multidimensional scaling (nMDS) using host coral species as the single factor: 1) all live, healthy corals, 2) all bleached colonies and 3) all dead colonies. Observed differences between assemblages were analysed as above, with permutational multivariate analysis of variance (PERMANOVA) and SIMPER analysis with 50 % contribution cut-off.

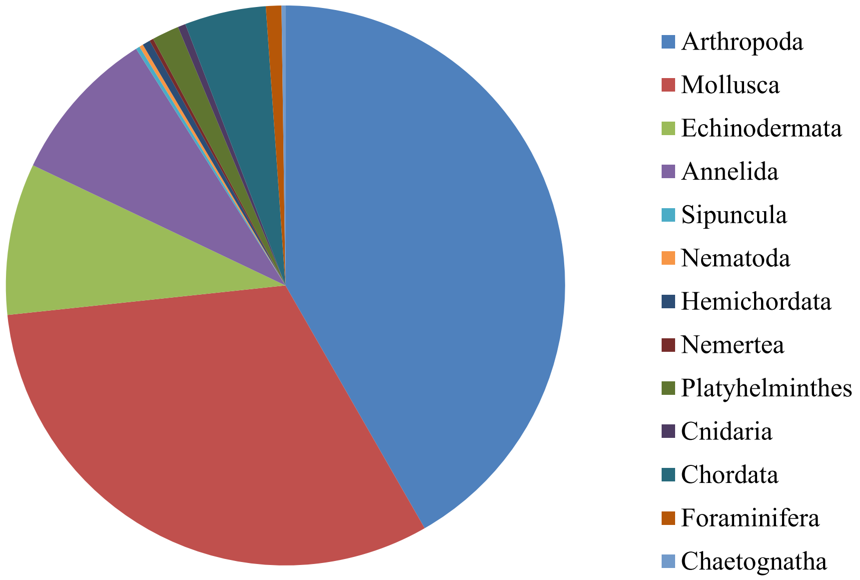
Hypothesis 4: Partial coral mortality will promote local biodiversity and abundance

The relationship between live coral tissue (as a percentage of the whole colony) and mean invertebrate species richness and abundance per colony was explored. Every coral colony sampled was assigned to one of 5 categories (in 20 % increments), based only on the percentage of live, healthy coral tissue. Therefore, coral colonies that were 100 % bleached (40 colonies in total) were excluded. A second degree polynomial line was fitted as a visualisation aid and to summarize the relationships between variables.

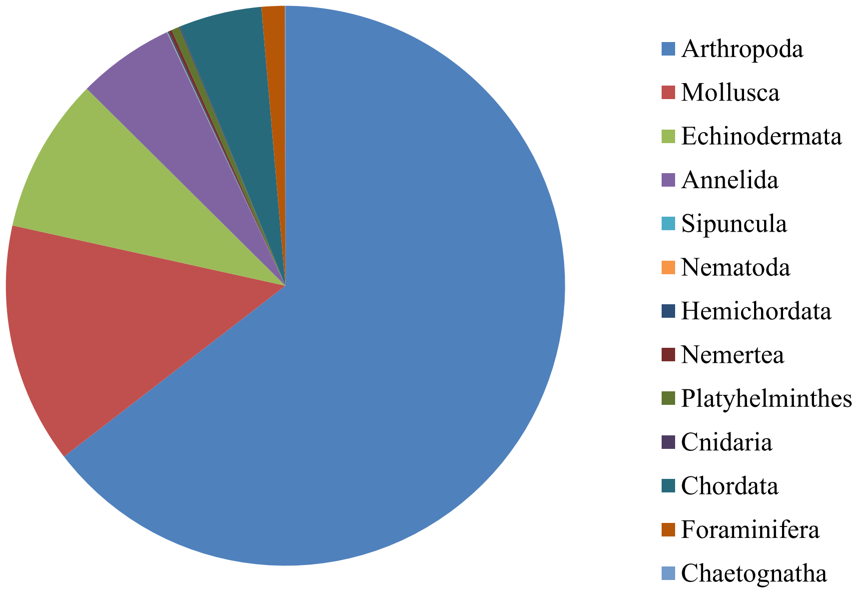
3.4 Results

Overall biodiversity and abundance

A total of 7,951 invertebrates were collected from the 490 colonies of coral. Across the 7 different host corals, 13 phyla were found to occur, comprised of 162 families, 273 genera and at least 422 species. Species richness ranged from 1 to 47 species within a single coral colony, and abundance ranged from 1 to 151 individuals. The most diverse group was the arthropods, contributing 186 species, followed by molluscs with 141 species (Figure 3.1a). Echinoderms contributed 39 species and polychaete worms, 38 species. Arthropods were also the most abundant group, with 5,340 individuals, followed by gastropods with 999, Echinoderms with 748, and polychaetes with 435 (Figure 3.1b). Of the 422 invertebrate species that occurred across all 7 host corals, 38 (~9 %) are known to be live coral obligates, only found on pocilloporid and acroporid host corals. Fish species accounted for 20 species from 6 families but the majority of individuals belonged to the family Gobiidae.



(a) Relative species richness



(b) Relative abundance

Figure 3.1 Relative species richness (a) and abundance (b) of coral-dwelling phyla associated with the branching corals *Acropora nasuta*, *Acropora spathulata*, *Acropora valida*, *Pocillopora damicornis*, *Pocillopora verrucosa*, *Seriatopora hystrix* and *Stylophora pistillata*.

Hypothesis 1: Host coral bleaching and death will lead to a decline in invertebrate species richness and abundance

There were significant differences in species richness (ANOVA $F_{(2,422)} = 8.80$, $P < 0.001$) and total abundance ($F_{(2,422)} = 10.58$, $p<0.001$) between corals that were predominantly healthy, bleached and predominantly dead (Figure 3.2). However, the prediction that dead corals would have the lowest species richness and abundance was not supported. Both mean species richness and abundance per coral were highest for predominantly dead corals, lowest for bleached corals, intermediate for live corals.

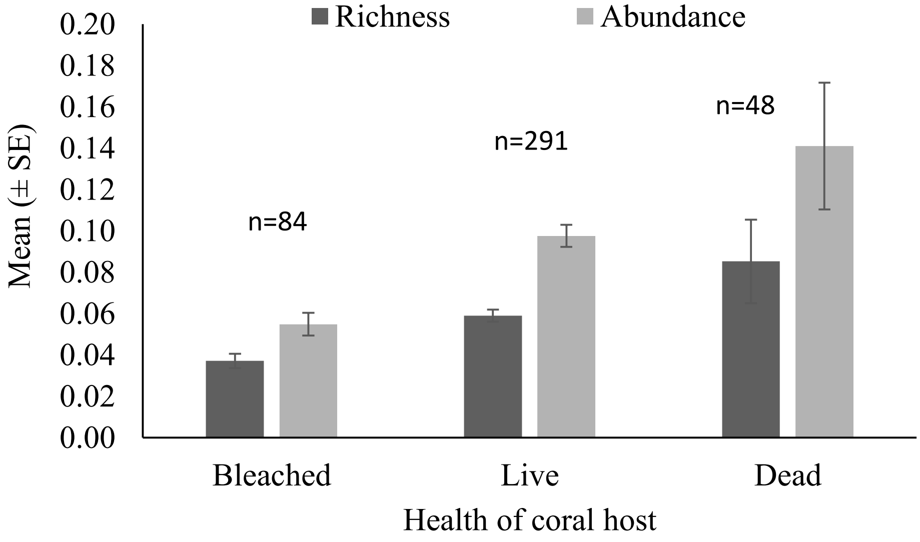


Figure 3.2 Mean species richness and abundance (per cm^2) characteristic of live (colonies with 80 % or more live, non-bleached tissue), bleached (colonies with 80 % or more bleached tissue) and dead (colonies with less than 20 % live tissue) branching corals of the species *Acropora nasuta, Acropora spathulata, Acropora valida, Pocillopora damicornis, Pocillopora verrucosa, Seriatopora hystrix* and *Stylophora pistillata.*

Hypothesis 2: Host coral bleaching and death will lead to a change in invertebrate species composition from obligate to facultative species

Host coral bleaching and mortality led to a distinct change in invertebrate species composition (PERMANOVA, p = 0.001 for each pairwise comparison). A SIMPER analysis revealed that the division between coral health by invertebrate species composition was due to differences in the presence and abundance of particular species.

Healthy and bleached corals were characterised by the presence of *Trapezia cymodoce* and *Tetralia glaberrima*, although the difference in abundance of these species between healthy and bleached corals was responsible for the division between assemblages. Dead corals were characterised by high abundances of *Periclimenella spinifera*, galatheids, xanthids and cerithids. An nMDS depicted a separation between healthy and dead host corals based on the composition of invertebrate assemblages, with bleached host corals broadly overlapping with the assemblages in live corals (Figure 3.3).

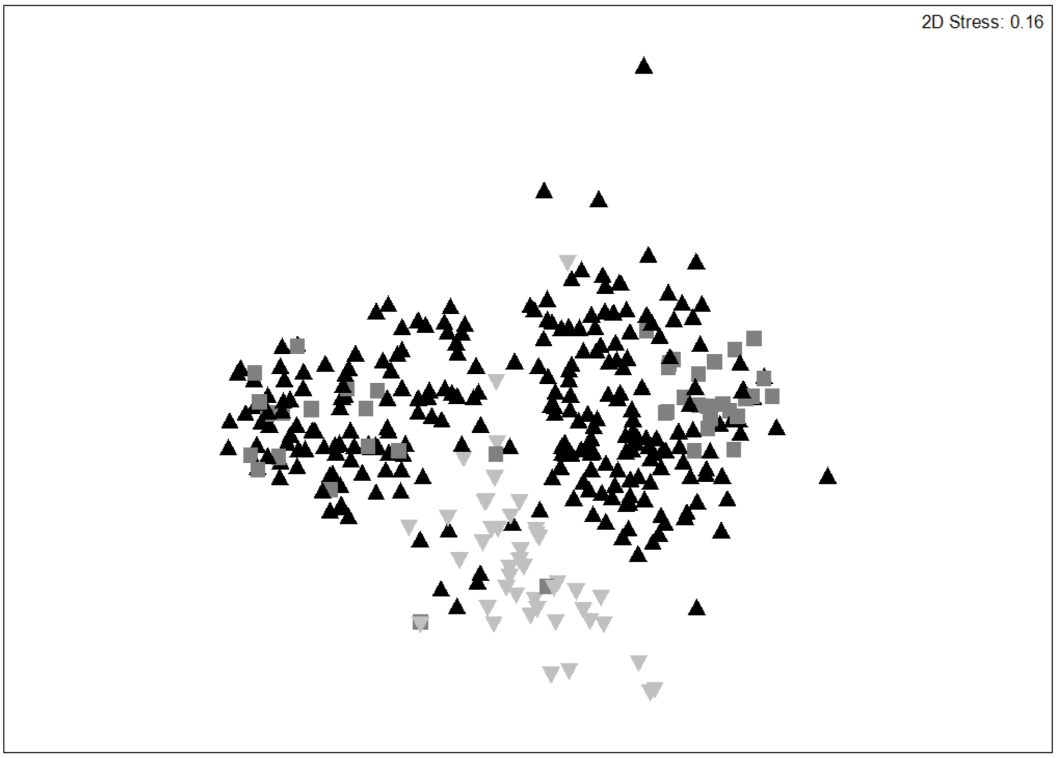
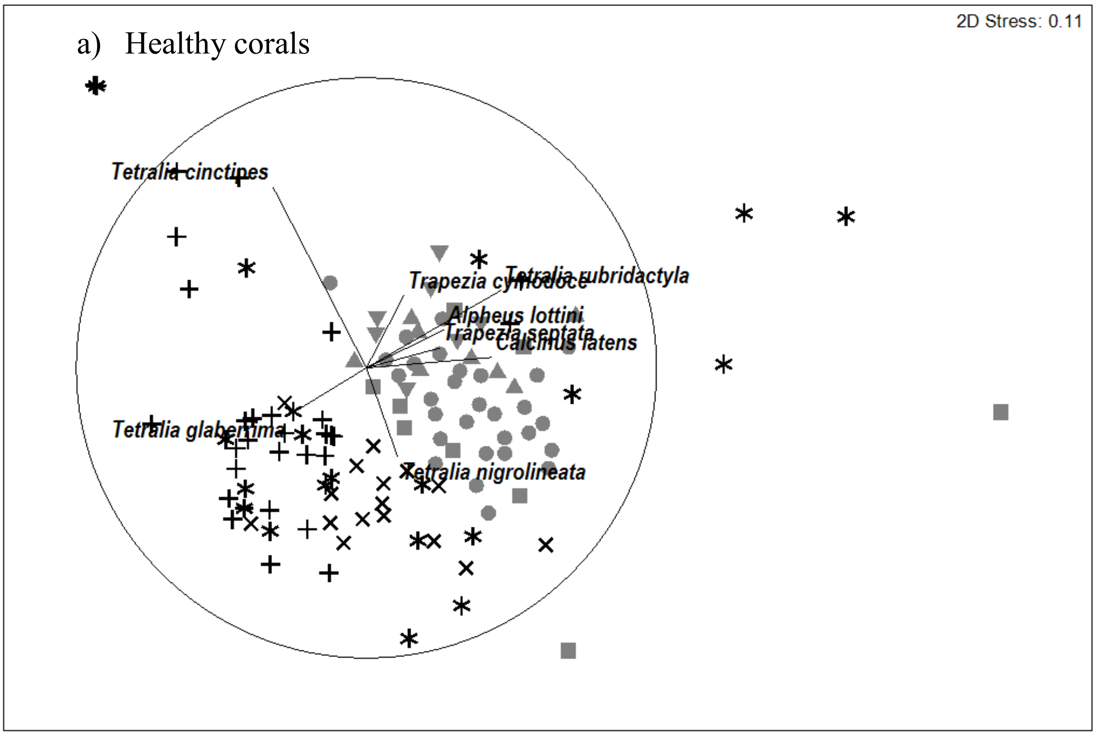
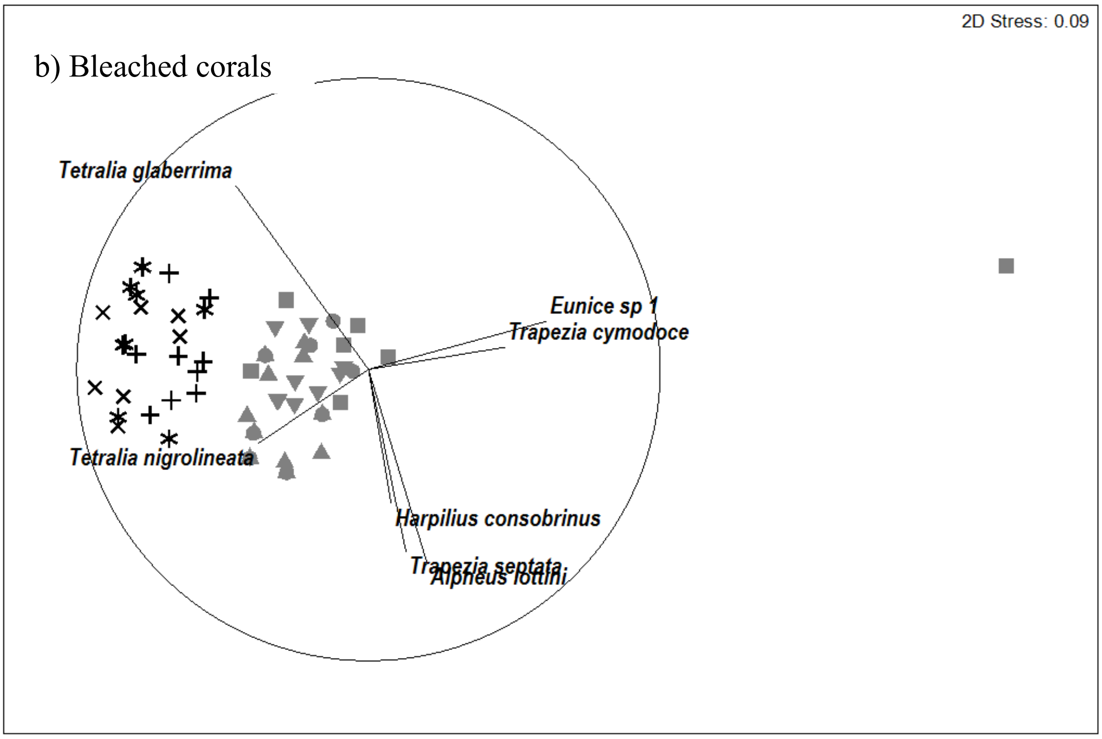


Figure 3.3 Non-metric multidimensional scaling (nMDS) results for invertebrate assemblages associated with healthy, bleached and dead host corals (▲=Live, ■=Bleached, ▼=Dead). The stress value represents the spatial dispersion based on resemblances among coral health. Groupings on the left correspond to acroporids, and right to pocilloporids.

Hypothesis 3: Different coral species will have distinct invertebrate assemblages, but bleaching and coral death will lead to a convergence in community composition

This hypothesis was supported by the comparison of community composition on different coral species, whether live, bleached or dead. Healthy colonies of each coral species were found to host distinct invertebrate assemblages (PERMANOVA, $p = 0.001$), with the exception of *P. damicornis* and *P. verrucosa*. An nMDS showed a clear separation between healthy coral species (Figure 3.4a), however the difference appeared to be greatest between the two coral families. A SIMPER analysis revealed that the division between coral species by invertebrate species composition was due to differences in the presence and abundance of different obligate species. *P. damicornis* were characterised by abundant *Alpheus lottini*, *S. hystrix* by *Trapezia cymodoce*, *P. verrucosa* by *A. lottini*, *Trapezia septata* and *Periclimenella spinifera*, *S. pistillata* by *T. cymodoce*, *Palaemonella* spp. and *Diodora galeata*, *A. nasuta* by *Tetralia glaberrima*, *A. spathulata* by almost exclusive presence of *T. glaberrima*, and *A. valida* by *T. glaberrima* and *Tetralia nigrolineata*.


2D Stress: 0.11
a) Healthy corals
Tetralia cinctipes
Trapezia cymodoce
Tetralia rubridactyla
Alpheus lottini
Trapezia septata
Calcinus latens
Tetralia glaberrima
Tetralia nigrolineata


2D Stress: 0.09
b) Bleached corals
Tetralia glaberrima
Eunice sp 1
Trapezia cymodoce
Tetralia nigrolineata
Harpilius consobrinus
Trapezia septata
Alpheus lottini

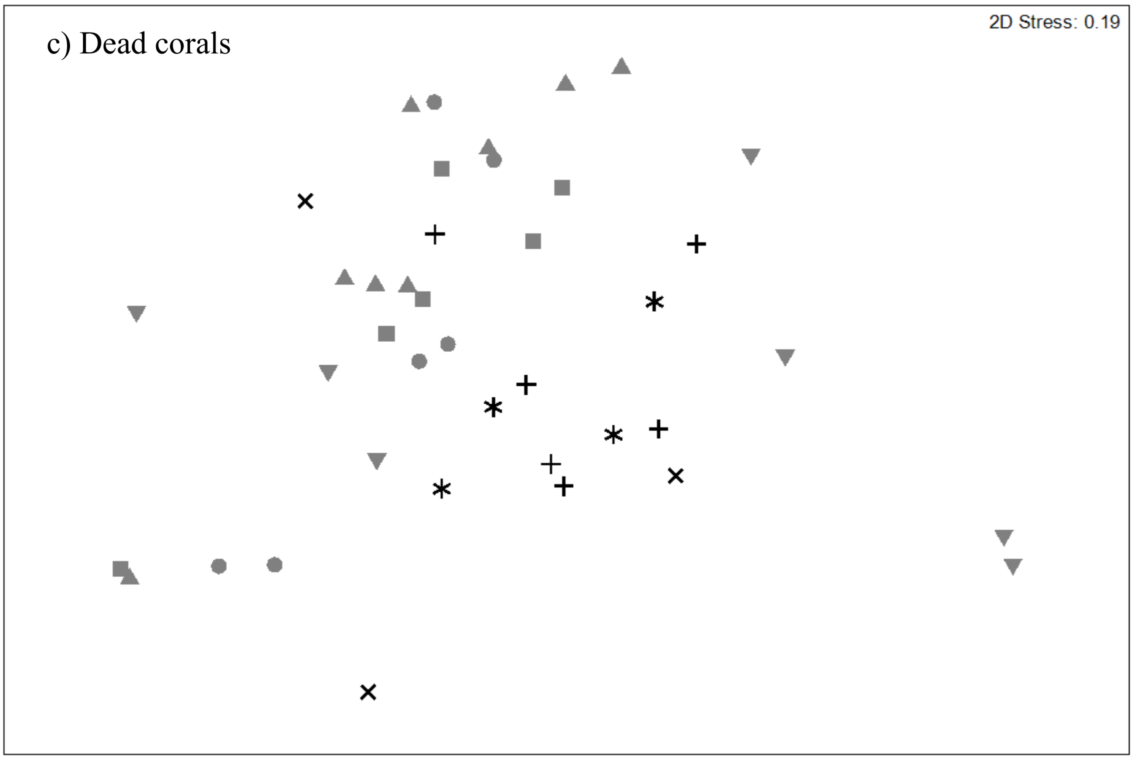


Figure 3.4 Non-metric multidimensional scaling (nMDS) results for invertebrate assemblages associated with (a) healthy host corals, (b) bleached corals and (c) dead corals. Acroporids are represented in black and pocilloporid corals are represented in grey (*****=*Acropora nasuta*, **+**=*Acropora spathulata*, **x**=*Acropora valida,* ▲=*Pocillopora damicornis*, ●=*Pocillopora verrusoca*,▼=*Seriatopora hystrix*, ■=*Stylophora pistillata*,). The stress value represents the spatial dispersion based on resemblances among host corals

Bleached colonies of each of the seven coral species were also significantly different (PERMANOVA, p = 0.001) (Figure 3.4b). The pairwise comparisons found all assemblages differed significantly from one another with the exception of *P. damicornis* and *P. verrucosa,* and *P. verrucosa* and *S. pistillata*. A SIMPER analysis found that species composition of the 7 bleached corals was a subset of obligate species normally associated with live, healthy corals.

Dead coral colonies of each of the seven coral species were also significantly different from one another, although the communities were less distinct than for live coral (PERMANOVA, p = 0.014) (Figure 3.4c). The pairwise comparisons found assemblages that differed significantly from one another were: *P. damicornis* and *S. hystrix* (p=0.002), *P. damicornis* and *A. nasuta* (p=0.023), *P. damicornis* and *A.*

spathulata (p=0.02), *P. damicornis* and *A. valida* (p=0.027), *S. hystrix* and *P. verrucosa* (p=0.029), and *S. hystrix* and *S. pistillata* (p=0.031). An nMDS did not show a clear separation between coral species or coral families based on the composition of invertebrate assemblages. A SIMPER analysis revealed that the differences were due to the varying combinations of several different generalist species, including *Periclimenella spinifera*, buccinids, cerithids, tanaids, *Etisus sp*., *Menaethius sp*. 2, galatheids, *Gonodactylaceus falcatus*, *Phasianella sp*. 1, *Domecia hispida*, *Alpheus leviusculus*, *Glabropilumnus dispar*, *cyclopoids*, *xanthids*, *Athanas parvus* and *pilumnids*.

Hypothesis 4: Partial coral bleaching or mortality will promote local biodiversity and abundance

Invertebrate species richness and abundance exhibited significant polynomial relationships with the proportion of healthy tissue per colony, both for obligate and facultative coral-associated species (Figure 3.5 a,b). The overall relationship between percentage healthy tissue and changes in invertebrate diversity was non-linear and best represented using a polynomial (facultative users $r^2 = 0.63$, obligate users $r^2 = 0.87$). Species richness was highest for both types of coral users when the coral colony exhibited partial mortality and lowest when the colony either exhibited no or low partial mortality or very high partial mortality (Figure 3.5a). For both obligate and generalist species, a threshold of 21 % live coral tissue was apparent, below which both groups exhibited a sharp decline (~ 50 %) in species richness.

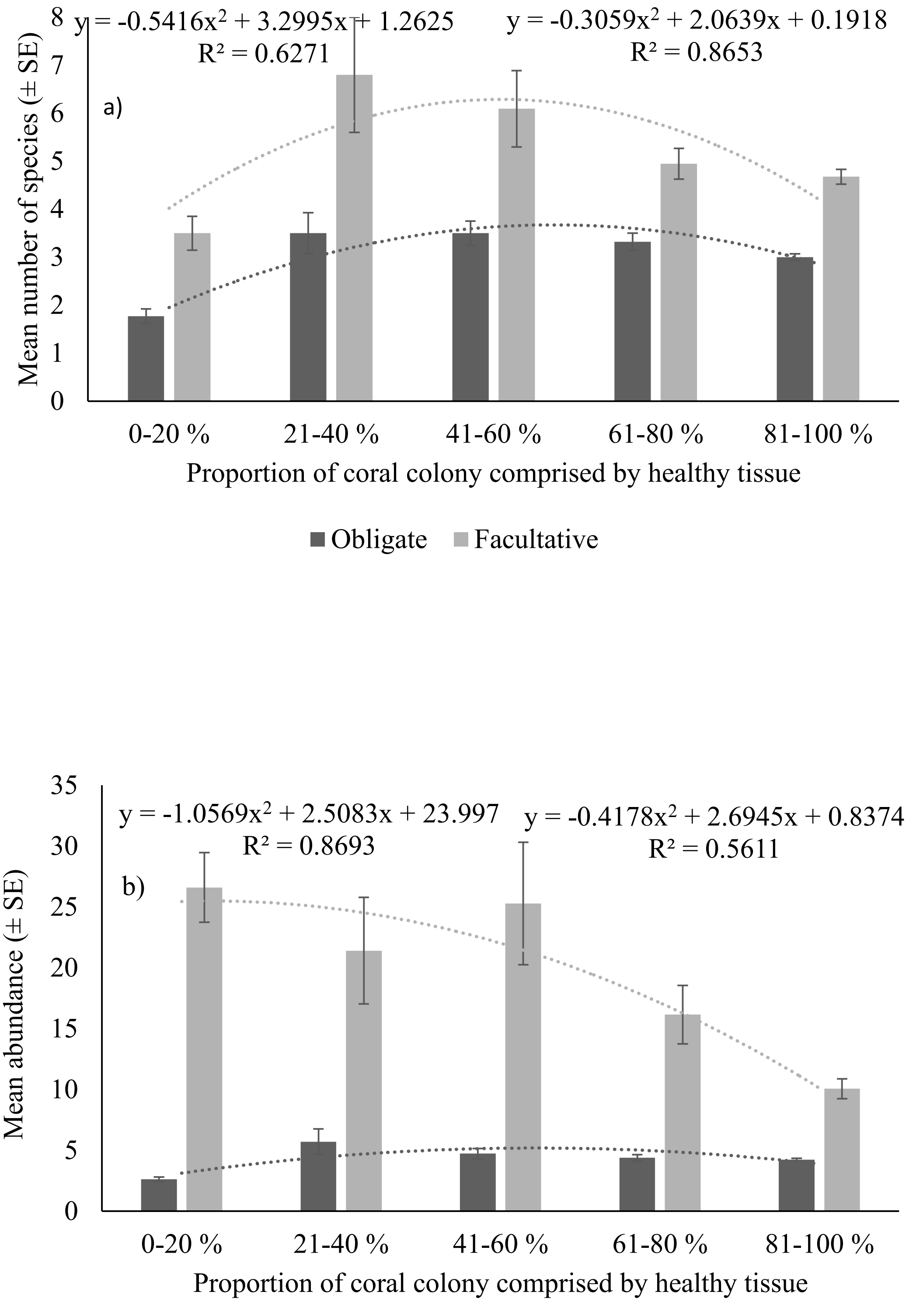


Figure 3.5 The relationship between percentage of live tissue per colony and (a) mean species richness per colony and (b) mean abundance per colony of both obligate facultative invertebrate species found on branching corals of the species *Pocillopora damicornis, Pocillopora verrucosa, Seriatopora hystrix, Stylophora pistillata, Acropora nasuta, Acropora spathulata* and *Acropora valida*. Polynomial equations on the left correspond to facultative species and on the right, obligate species.

The relationships between abundance and proportion of colony with healthy live tissue was also non-linear, but the patterns differed for obligate and facultative species (Figure 3.5b). The overall relationship between percentage healthy tissue and changes in invertebrate abundance was also non-linear and best represented using a polynomial (facultative users $r^2 = 0.87$, obligate users $r^2 = 0.56$), Abundance was highest at intermediate levels of habitat damage for obligate species, but was highest at medium to high levels of damage for facultative species. High levels of live coral tissue do not favour facultative species. Again, a threshold of 21 % live coral tissue seemed to exist but with contrasting effects: obligate abundance sharply declined by over 50 % whereas generalist abundance slight increased.

3.5 Discussion

Corals are vulnerable to many disturbances (e.g. crown-of-thorns predation, thermal bleaching and sedimentation) resulting in colony degradation (either full or partial colony mortality). Severe disturbances are predicted to cause a decline in invertebrate biodiversity through the loss of obligate coral-dwelling species. On the other hand, moderate levels of disturbance may promote invertebrate biodiversity by creating habitat suitable for both obligate and facultative species. Our comparisons of corals in different stages of bleaching and death confirmed some of these expectations, but not others. Severe bleaching caused a dramatic decline in species richness and abundance, but once corals were dead, diversity was higher than for live, healthy corals. This was explained by a shift towards facultative coral-dwelling species that were more numerous than obligate species. There was a high biodiversity of obligate coral-dwelling species across a range of different coral species that each supported distinct communities. These communities were maintained on bleached corals, but once dead, the biodiversity converged through the colonisation of facultative species. Overall, intermediate levels of disturbance promoted biodiversity, with highest species richness at 40-60% live coral tissue and lowest richness near 0 and 100 % healthy coral tissue. Together, these results suggest that impacts of coral disturbance on invertebrate species will depend on the severity of the disturbance and the degree of habitat specialisation.

Coral bleaching and death clearly has a dramatic impact on the diversity and abundance of invertebrate species. Both were highest for predominantly dead corals, lowest for bleached corals, intermediate for live corals. Both live and bleached corals represent homogenous habitats, thus the lack in species diversity may mirror the lack in micro-habitat diversity. Bleached corals represented the least desirable habitat given the lowest values of species richness and abundance, perhaps because this habitat no longer provides critical resources to obligate species that normally associate with live coral. However, when corals die and lose their tissue, the bare skeleton is quickly colonised by other organisms, such as algae, sponges, bryozoans and ascidians. Therefore, the diversity of non-coral micro-habitats increases, which appears to promote the diversity of facultative species or non-coral specialists. As all dead coral were grouped together in this study regardless of the various colonising substrates, other species-habitat associations may be responsible for the variation observed in community assemblages of dead corals. A dead coral skeleton may, in fact, approach equilibrium and become a new homogenous micro-environment catering to entirely different obligate species. In addition, as generalist species are naturally more abundant (Devictor and Jiguet 2007, Devictor et al. 2007, 2008, Olden 2006), variation in community assemblages associated with dead corals could be entirely random. However, it is clear that bushy corals, whether alive or dead, represent an important habitat to a large diversity of small, motile invertebrates. Structurally intact coral skeletons still provide a valuable resource for invertebrates as a refuge from predation and mating site (Graham et al 2006, Madin et al. 2014). Therefore, reefs comprised of both healthy and dead corals may represent the best scenario for maintaining high biodiversity. This highlights the critical importance of structural complexity on reefs to biodiversity, rather than specifically on coral quality and cover as metrics for a healthy, well-functioning coral reef ecosystem. If conservation efforts focus on improving and maintaining structural integrity, overall reef biodiversity may be better preserved than by focusing solely on coral health.

A clear transition in species composition was found between live, bleached and dead coral colonies. Healthy and bleached host corals were primarily characterised by the abundance of species belonging to two obligate decapod genera, *Trapezia* and *Tetralia*. Although healthy coral colonies usually support a small community of species that coexist and often engage in cooperative behaviour (Glynn 1976, Lassig 1977, Vannini 1985, McKeon et al. 2012), a natural hierarchy of dominance may be activated upon thermal stress and/or host coral bleaching, altering the nature of mutualistic associations. This could result in increased antagonistic interactions among individuals in the colony, favouring the competitive dominant species and/or individuals (e.g. Chapter 5). The absence of other obligates on bleached corals, such as shrimps belonging to the families Alpheidae and Palaemonidae, indicates that these colonies are less convivial to community formation and instead are dominated by a small suite of obligate species. Dead corals were characterised by the absence of obligates and a higher abundance of commonly abundant species, particularly *Periclimenella spinifera*, galatheids, xanthids and cerithids. These animals occur to some degree on live coral but are also commonly found within crevices of the reef matrix and therefore may opportunistically exploit dead and dying corals. It is possible that the aggressive behaviours of obligate species inhibits other species from gaining access to live colonies (e.g. Lassig 1977, Vannini 1985), but as the coral dies and obligates disappear, the generalist species are no longer competitively excluded.

Live coral communities each harboured distinct species assemblages marked by occurrence and abundance of different obligates species. Observed differences in species composition were greatest between the two coral families. All pocilloporid corals were characterised by the abundance of *Trapezia* crabs (albeit different species), with *Pocillopora damicornis* and *P. verrucosa* also hosting an abundance of *Alpheus lottini*. *Seriatopora hystrix* and *Stylophora pistillata* also hosted palaemonid shrimp and the corallivorous snail *Diodora galeata* was found in abundance on the latter. The acroporids were characterised by smaller suite of species, with the different abundances of *Tetralia glaberrima* and *T. nigrolineata* responsible for community differences among acroporid species. Chapter 2 demonstrates that up to 15 % of coral-associated invertebrates exhibit strong preferences for one particular host corals (out of 4 host corals sampled). Species-specific preferences play an important role in the structure of invertebrate communities, however it is unknown how or why certain invertebrate species associate with only particular host corals. Whatever the mechanisms may be, these preferences allow niche partitioning among closely related invertebrate species and thus enable the support higher biodiversity overall.

Overall, as live corals died, the integrity of this structure broke down somewhat, with species assemblages tending towards a more homogenous and/or random composition. Notably, an observed decline in *Trapezia* spp., *Alpheus lottini* from pocilloporids and *Tetralia* spp. from acroporids was marked by an increase of *Periclimenella spinifera*, cerithid gastropods, xanthid crabs, galatheid squat lobsters, *Drupella* spp., and amphipods. Importantly, obligate species were sometimes found on coral colonies exhibiting the highest levels of mortality and it is unknown how long they had and would persist on a degraded host coral. For example, juvenile crabs of the genus *Trapezia* were found on 100 % dead corals in both this study and by Head et al. (2015). This indicates that either certain obligate species found on corals are somewhat robust to disturbance and would persist even when their resources were utterly exhausted or that the combative behaviour of *Trapezia* towards conspecifics would serve to exclude smaller, competitively inferior crabs, which are then forced to use less than optimal corals as a refuge (Chapter 4). As most crabs are opportunistic feeders, it is possible that these mutualistic coral-dwellers can exploit feeding modes other than corallivory during periods of limited resource availability. However, it is also possible that if attempts to migrate to more suitable colonies fail, these species simply resign to use dead corals as temporary refuge.

Importantly, bleached corals were found to harbour only a subset of species normally associated with live, healthy host corals. Although a decline of coral-dwelling fish on bleached host corals has identified an increased susceptibility to predation as a mechanism of decline (Coker et al. 2009), current research on the effects of bleaching on specialised crustacean fauna have implicated sub-lethal effects such as reduced fecundity and high emigration (Chapter 4) and increased agonistic behaviour by competitively dominant species as a mechanism for declining species richness (Chapter 5). As bleached corals produce less mucus relied upon by invertebrate inhabitants as food and are more prone to disease due to thermal stress, the reduction in resources can cause declines in the absence of predation via increased competition between formerly cooperative species. Avoidance of bleached corals could have strong implications for invertebrate larval recruitment during bleaching events and/or adult population structure during and after bleaching events.

Invertebrate species richness and abundance is influenced by the amount of live, healthy tissue present on their host coral. Species richness was highest for both types of coral users when the coral colony exhibited partial mortality (40-60% live tissue) and lowest when the colony either exhibited no or low partial mortality (<20%) or very high (>80%) partial mortality. The relationships between abundance and proportion of colony with healthy live tissue was also non-linear, but the patterns differed for obligate and facultative species (Figure 6b). Abundance was highest at intermediate levels of habitat damage for obligate species, but was highest at medium to high levels of damage for facultative species. High levels of live coral tissue do not favour facultative species.

The diversity and abundance of obligate and facultative species is influenced by colony mortality in fundamentally different ways. Species richness of obligate coral-dwellers appears to remain relatively constant (~ 3 species per colony) until colony mortality approached 80 % and species richness was halved. Facultative coral users, however, increase with increasing levels of colony mortality, but then also sharply decline at 80 % mortality. As larger live coral colonies have been known to host several different species of obligate trapeziids (Abele and Patton 1976), a decrease in live tissue area would limit resources and may increase inter-specific competition (Chapter 5). The greatest diversity overall occurs with intermediate colony mortality (on colonies comprised of 20-80 % live tissue), presumably coinciding with a more heterogeneous micro-habitat consisting of live coral tissue and various other substrates, such as algal turfs and sponges. Positive relationships have been observed between habitat diversity and species richness (Lawton 1983, Tews et al. 2004, Kissling et al. 2008, Hortal et al. 2009), with moderate levels of disturbance having negligible or even positive effects on the local diversity (Pratchett et al. 2011b), as colonies that can support both obligate and facultative users will boast a higher diversity than live corals alone. Abundance of obligate and facultative species also appeared to be influenced by colony mortality, with obligates again remaining at a somewhat constant abundance until colony mortality approached 80 % and facultative abundance increasing steadily with increasing coral mortality. Certain obligate species, such as *Trapezia* spp. are known to occur in strict mating pairs and often exhibit strong intra-specific aggression to maintain this dynamic (Castro 1976). A decline in abundance may be attributed to differential losses of individuals unable to meet metabolic requirements, such as ovigerous females (Chapter 5). Other species may live in eusocial groups (e.g. Duffy 1999) or exhibit a tendency to aggregate (e.g. hermit crabs, molluscs and amphipods, Mackay 1945, Hoeksema and van der Meij 2013). Whichever mechanism is involved in these patterns, it is clear that facultative species have a marked advantaged over obligate species during severe coral disturbance events.

Disturbance regimes in part, whether acute or gradual, shape the community composition of an ecosystem, whereas obligate species tend to occur in relatively stable environments, and generalist species will most likely dominate disturbed environments

(Kitahara et al. 2000, Kassen 2002, Devictor et al. 2008, Clavel et al. 2010). However, on coral reefs, over 80 % of species live in symbiosis with and rely on other species, thus their persistence through a disturbance is inexorably intertwined with that of their symbiotic partner. In addition, many invertebrate species are generally more sensitive to environmental changes than their host corals and could suffer mass mortality from an acute temperature rise or change in salinity that may only result in host coral bleaching (Abele 1976, Chapter 5). As this study did not examine the response of invertebrate species before and after an observed disturbance, it is unknown if the lack of obligates on degraded host corals resulted directly from mortality associated with a disturbance (such as an acute increase in temperature) or indirectly, due to the effects of the disturbance on the host coral itself (bleaching and mortality due to increased temperatures). All disturbances are not equal in their effect on individual coral colonies. Bleaching, predation and disease affect coral health, and consequently the amount of live tissue, but leave the skeleton intact. However, mechanical damage as a result of cyclones may have the most adverse effect on reef diversity, as overall complexity within the reef system declines (Hughes et al. 1999, Loya et al. 2001, Willis et al. 2004, Pratchett 2007, Fabricius et al. 2011, De'ath et al. 2012, Madin et al. 2014). Although fish communities may exhibit temporal lags in response to disturbance (e.g. Graham et al. 2007), the effects on invertebrates living within the branches of a host coral may be more acute. As climate change threatens more frequent and severe disturbances, branching corals will most likely be the first to exhibit catastrophic declines. With the demise of these few coral species, it is expected that an astonishing number of invertebrate species (38 in this study) are at a high risk of extinction. How the loss of these species will reverberate through the coral reef ecosystem is unknown.

As the relationship between species diversity and ecosystem function is very complex, we have very little insight into how any changes in one affects the other or at which scale (local or landscape) these impacts can be important (Pasari et al. 2013). There may be gradual and reversible decreases in function with decreased biodiversity or no noticeable effect until a tipping point is reached (Hoegh-Guldberg et al. 2007). As invertebrates are small and cryptic, yet vastly abundant and ecologically important, the loss of some species may occur inconspicuously and have reverberations up the food web or upon the population of bushy corals that rely upon important ecological services provided by their symbiotic fauna. Some species exert a disproportionately large effect on their ecosystem relative to their biomass and abundance (Zook 2002), therefore small reef invertebrates may be keystone species within the reef ecosystem. Habitat degradation threatens the diversity of every ecosystem on Earth and is occurring at a rate faster than ever before. Community-wide effects have already been documented in highly diverse ecosystems such as coral reefs. Research addressing the effects of habitat degradation on animal biodiversity would ideally encompass the greatest component of diversity; the invertebrates. Participative management and restrictions on the collection of micro-habitats known to support numerous invertebrate species could help to protect overall coral reef biodiversity. By protecting resources critically important to marine invertebrates, a main component of the coral reef food web will also be preserved, with possible benefits to a vast number of other reef species.

Chapter 4: Effects of coral bleaching on the obligate coral-dwelling crab *Trapezia cymodoce*

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4.1 Abstract

Corals are an essential and threatened habitat for a diverse range of reef-associated animals. Episodes of coral bleaching are predicted to increase in frequency and intensity over coming decades, yet the effects of host coral bleaching on the associated animal communities remain poorly understood. The present study investigated the effects of host-colony bleaching on the obligate coral-dwelling crab, *Trapezia cymodoce*, during a natural bleaching event in the lagoon of Lizard Island, Australia. Branching corals, which harbour the highest diversity of coral-associates, comprised 13 % of live coral cover at the study site, with 83 % affected by bleaching. Crabs on healthy and bleached colonies of *Pocillopora damicornis* were monitored over a 5 week period to determine if coral bleaching affected crab density and movement patterns. All coral colonies initially contained one breeding pair of crabs. There was a significant decline in crab density on bleached corals after 5 weeks, with many corals losing one or both crabs, yet all healthy colonies retained a mating pair. Fecundity of crabs collected from bleached and healthy colonies of *P. damicornis* was also compared. The size of egg clutches of crabs collected from bleached hosts was 40 % smaller than those from healthy hosts, indicating a significant reduction in fecundity. A lab experiment on movement patterns found that host-colony bleaching also prompted crabs to emigrate in search of more suitable colonies. Emigrant crabs engaged in aggressive interactions with occupants of healthy hosts, with larger crabs always usurping occupants of a smaller size. Decreased densities and clutch sizes, along with increased competitive interactions could potentially result in a population decline of these important coral-associates with cascading effects on coral health.

4.2 Introduction

The high biodiversity of coral reefs is facilitated by the extraordinary diversity of habitats and topographic complexity provided by scleractinian corals (Luckhurst and Luckhurst 1978, Jennings et al. 1996, Öhman and Rajasuriya 1998, Lindahl et al. 2001). The close association between small mobile animals and corals has resulted in the evolution of numerous symbiotic associations (Castro 1988, Stella et al. 2011). Although coral reefs experience natural disturbances (e.g., storms) that help maintain local diversity (Abele 1976, Connell 1978, Karlson and Hurd 1993), an escalation of anthropogenic disturbances is having serious negative effects on reef diversity (Hughes et al. 2003, Bellwood et al. 2004) and may disrupt these symbiotic relationships (Caley et al. 2001). Coral bleaching is one such disturbance that is predicted to become more frequent and intense over coming decades due to anthropogenic climate change (Hoegh-Guldberg 1999, Sheppard 2003, Donner et al. 2005). Bleaching events cause significant coral mortality and consequently alter the abundance and community composition of animals that are symbiotic, or closely associated with coral (Glynn 1983a, Munday 2004, Bellwood et al. 2006, Pratchett et al. 2008, Bonin 2012, Coker et al. 2012). However, many coral colonies recover from bleaching and may retain their symbiotic animal communities throughout the bleaching event. Even though corals may recover, such non-lethal bleaching may still have negative impacts on populations of symbiotic species.

Many symbioses are formed between tightly branching corals and other reef invertebrates, such as crustaceans and molluscs (Abele and Patton 1976, Austin et al. 1980, Coles 1980, Castro 1988 Patton 1966, 1994, Chapter 1, Stella et al. 2011). Branching corals provide symbiotic animals with a range of resources including a large surface area on which to live, a complex architecture that provides a refuges from predation, food in the form of coral tissue, mucus and its associated detritus, and a hard skeleton used as a substratum by specialised burrowers and gall-forming animals (Castro 1988). In turn, many branching corals are reliant upon certain invertebrates for protection from predators and cleaning (Glynn 1983c, Stewart et al. 2006), thus forming recognizable mutually beneficial partnerships.

There is often a differential response among coral species to bleaching, with branching corals consistently being the most susceptible to bleaching and consequent colony mortality (Brown and Suharsono 1990, Gleason 1993, Marshall and Baird 2000, Loya et al. 2001, McClanahan et al. 2004, Graham et al. 2015). This differential response can lead to marked shifts in the community composition of coral reefs, with branching corals slowly being replaced by bleaching-resistant corals, such as massive and encrusting forms, which offer little structural complexity (Marshall and Baird 2000, Loya et al. 2001, McClanahan et al. 2004, 2007). As live coral is an important resource for a large diversity of reef organisms and branching corals are the most preferred (Pratchett et al. 2009, Stella et al. 2011), any reduction in branching coral cover could have severe implications for reef biodiversity and vital ecological processes.

A high degree of dependence on branching corals has been documented for some coral-reef fish, with consequent effects of coral loss on reef fish abundance and diversity (Jones et al. 2004, Garpe et al. 2006, Wilson et al. 2006, Pratchett et al. 2008) with the most coral-reliant species exhibiting the greatest declines (Munday 2004, Wilson et al. 2008). However, measures of abundance do not always provide a clear picture of the full effects of coral loss on coral-dependent species. Coral bleaching and habitat degradation can also affect the individual fitness of coral-dependent animals (Kokita and Nakazono 2001, Munday 2001, Pratchett et al. 2004, Brooker et al. 2014). For example, Kokita and Nakazono (2001) documented a dramatic decrease in survival, growth and reproduction of the obligate corallivorous filefish, *Oxymonacanthus longirostris*, within a month of coral bleaching. A few months after the bleaching event, the local population had entirely disappeared. The corallivorous butterflyfish *Chaetodon lunulatus* responded to a mass bleaching event by switching to a more abundant coral prey that was less affected by bleaching. Total abundance was not affected, however, the physiological condition of the fish declined (Pratchett et al. 2004), with possible long-term consequences for reproductive success. Although coral-associated invertebrates may be more dependent on coral than many reef fish, their response to coral loss is almost completely unknown. As a large proportion of coral-associated invertebrates demonstrate a high reliance on live host corals in conjunction with a preference for host corals that are most susceptible to coral bleaching and mortality (Pratchett et al. 2009, Stella et al. 2011), these animals will likely be predisposed to increased rates of extinction via a decline in fitness and subsequent population declines if reef degradation continues unabated.

Coral crabs of the genus *Trapezia* are perhaps some of the most coral-reliant reef animals, specialised to certain host corals upon which they depend for habitat, food in the form of coral mucus, polyps and eggs, and as a breeding site (Knudsen 1967, Patton 1974, Castro 1988, Stimson 1990). The relationship between trapeziids and corals appears to have been established by the Eocene (Schweitzer 2005) and there is evidence to support co-evolution (Glynn 1983b). Trapeziids are ecologically important to their host corals. Occurring in excess of 90% on pocilloporid corals (Huber and Coles 1986, Chapter 2), *Trapezia* crabs have been shown to enhance coral skeletal growth (Glynn 1983c), clean host corals of sediments (Stewart et al. 2006) and mucus nets of the vermetid gastropods (Stier et al. 2010) that would otherwise be detrimental to coral growth and survival (Shima et al. 2010), and actively defend their hosts from coral predators such as the starfish, *Acanthaster planci* (Weber and Woodhead 1970, Glynn 1980, Pratchett 2001). Indeed, the relationship between host coral and *Trapezia* crabs is such that the crabs are only found in association with a host coral and the corals undergo high rates of colony mortality if the crabs are removed (Glynn 1983c, Stewart et al. 2006).

The abundance of pocilloporid colonies, coral colony size and living space within branches are all limiting factors to *Trapezia* (Castro 1978). Therefore, competition for space may increase as coral cover declines (Glynn 1976). Trapeziids are territorial and naturally occur in strict mating pairs among colonies (Patton 1974, Castro 1978). They are aggressive towards other associates, including conspecifics of the same sex (Castro 1978) and rely solely on their relatively large chelipeds for defence (Glynn 1980, Pratchett et al. 2000). As species of *Trapezia* are known to move among colonies at night with the possible aim of securing a larger colony or mate (Castro 1978), conspecific interactions can occur frequently. Interactions between conspecifics of the same sex usually elicit a strong aggressive response and fights can result in the loss of limbs (Vannini 1985). The outcome of these interactions appears to relate to body size, with larger crabs successfully expelling smaller intruding crabs or taking over colonies from smaller crabs (Tsuchiya and Yonaha 1992). Due to the crabs' aggressive nature and healthy colony numbers acting as a limiting factor, an acute reduction in healthy host corals due to coral bleaching could increase competitive interactions among the crab population as suitable resources dwindle.

The aim of this study was to examine the immediate effects of coral bleaching on the persistence, reproduction and competitive interactions of the obligate coral-associated crab, *Trapezia cymodoce*. I documented the consequences for crabs of a prolonged bleaching event in the lagoon of Lizard Island (Great Barrier Reef, Australia). Coral bleaching was first documented in order to describe the severity and extent of bleaching, and also to distinguish which coral growth forms were most affected. Individual corals were then monitored along with the persistence and social organisation of the crabs in bleached and healthy corals. Fecundity was compared among crabs inhabiting bleached and healthy corals to assess effects of bleaching on reproductive success. Finally, competition for healthy hosts was experimentally tested, in order to assess how the crabs' behaviour during a bleaching event might further affect their fitness.

4.3 Methods

Study Site

This study was conducted during a natural coral bleaching event in the lagoon of Lizard Island, Australia from April to May 2010, at a depth range of 2-5 meters. A temperature anomaly was recorded from March 6th 2010-March 10th 2010 at a depth of 2 meters, with maximum daily temperatures ranging from 32ºC – 32.9ºC (Figure 4.1). This temperature anomaly coincided with the onset of coral bleaching around mid-March (L. Vail pers. comm.). The maximum temperatures sustained over the 5 day period were ~3-4 ºC higher than the long term average summer temperature of 29ºC for Lizard Island (Lough 1999).

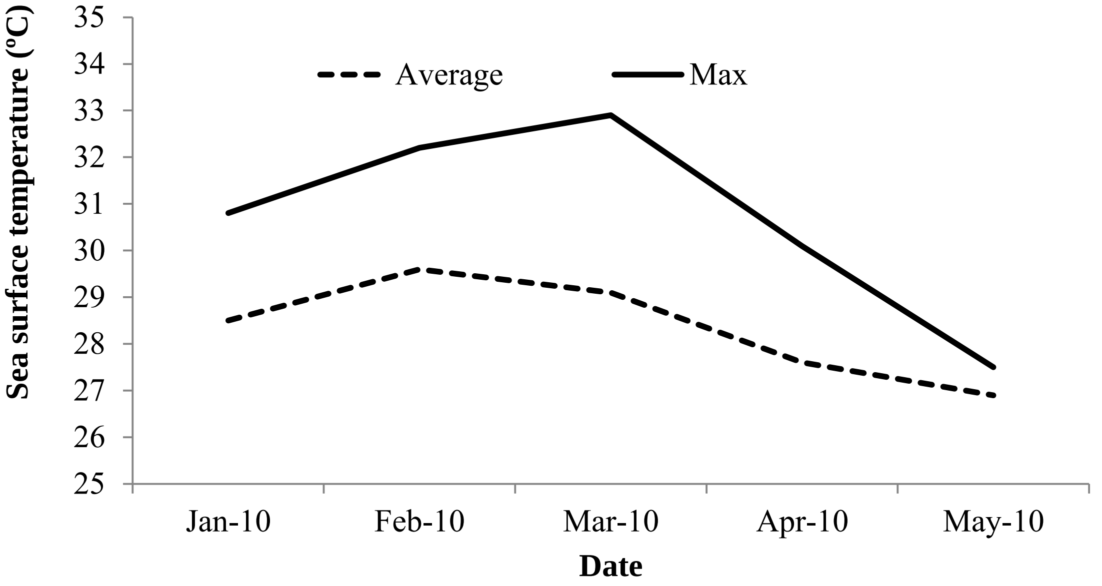

Figure 4.1 Average and maximum 2010 summer sea-surface (depth of 2 m) temperatures for Lizard Island (data courtesy of the Australian Institute of Marine Science)

Extent of Bleaching

Coral bleaching was most prominent in shallow depths (1-5m) and nearly constrained within the lagoon. Therefore, 2 sites were chosen in the lagoon to document coral cover and the extent of bleaching. Coral cover was determined by conducting 4 replicate 25 m line-intercept transects at each of the sites and benthic substratum was identified under 50 random points along each transect. Where live corals corresponded with a random point, the growth form and genus were recorded. Corals were also categorised as either healthy (e.g., normal pigmentation) or affected by bleaching (pale or white).

Percent hard coral cover, branching coral cover, and percent bleaching at each site was calculated from the transect data. The total number of bleached colonies was also compared to the total number of colonies in order to estimate the proportion of bleaching at the whole colony level.

Effects of host bleaching on crab density and persistence

To assess the effects of host-colony bleaching on the persistence of the obligate coral-associate *Trapezia cymodoce*, 20 unbleached and 20 bleached colonies of *Pocillopora* *damicornis* that hosted a mating pair of crabs were tagged in the lagoon and monitored over a 5 week period. *Pocillopora damicornis* was chosen because both healthy and bleached colonies were approximately equally abundant, making it ideal for this type of study. Bleaching was categorized using the 4-point scale developed by Marshall and Baird (2000) where: (1) healthy = no visible loss of colour, (2) moderately bleached = 1 to 50% of colony affected or entire colony pale, (3) severely bleached = 51 to 100% of colony with strong pigmentation loss (colony appears white), (4) dead = 80 to 100% of colony covered by light algal overgrowth. Tagged colonies were censused once per week by visually inspecting the inter-branch spaces for the presence of the crabs. Recovery from bleaching, bleaching progress, or mortality of the host colony was monitored by reassigning a score using the 4-point scale and proportional mortality was estimated to the nearest 5%.

As bleaching severity did not differ among bleached host corals over the census period, host colony health was then categorized as either “healthy” or “bleached” for crab density comparisons. Changes in the number of crabs on healthy and bleached colonies of *P. damicornis* were examined using the Freeman-Halton extension (Freeman and Halton 1951) to Fisher's exact test in which the frequency of all possible combinations (0 crabs, 1 crab or 2 crabs) was compared between healthy and bleached colonies at the start and end of the monitoring period.

Effects of host bleaching on crab fecundity

To determine the effects of host-colony bleaching on the fecundity of *T. cymodoce*, the number and size of eggs were measured for crabs collected from 30 bleached and 30 unbleached colonies of *P. damicornis* of approximately equal diameters (~20 cm). Because fecundity is likely to be affected by crab body size, I selected a similar size range of crabs from both healthy (5.5 mm – 17 mm carapace width) and bleached (6.9 mm – 16 mm) host corals to help control for this. Coral colonies were removed from the reef and carefully transported to the laboratory in bins full of seawater. The crabs were removed from their host coral by gently nudging them to the outer perimeter of the colony with a blunt probe. All crabs were weighed to the nearest 0.001g and carapace width measured to the nearest 0.1 mm. Body condition was noted if the crabs were missing any claws. Female crabs were anesthetized using a mild solution of clove oil (~1-2 drops of clove oil per 250mL of seawater). The egg clutches were then gently scraped out of the abdomen using tweezers, added to a petri dish with seawater, photographed under a dissecting microscope and counted using UTHSCSA ImageTool (IT). The diameter of eggs from a subset of each clutch was also measured using ImageTool. The crabs were then returned to their original host coral and the colony cemented back onto the substratum.

ANCOVA was used to determine the effect of coral health on clutch size. Crab size was included as a covariate because female size can have a significant effect on fecundity. (Gotelli et al. 1985, Tsuchiya and Yonaha 1992). Carapace width was used as the measure of crab size. The assumption of homogeneity of slopes between the covariate (crab size) and main effect (coral health) was confirmed prior to running the ANCOVA. As the relationship between fecundity and body size for decapod crustaceans usually takes the form of a power function (Somers 1991), data were log transformed for the analyses. Egg diameter was measured for 10 eggs per clutch. The mean diameter of each clutch was calculated and ANOVA was then used to determine if group means differed between crabs from healthy or bleached host corals.

Effects of host bleaching on crab emigration and competitive interactions

To ascertain whether host bleaching prompts *T. cymodoce* to seek an alternate host and if crab size is a factor in emigration success, movement of crabs from bleached to unbleached colonies of *P. damicornis* were observed in a manipulative experiment. In the laboratory, crab pairs were removed from 44 colonies (22 healthy and 22 bleached) of *P. damicornis* and the carapace of each individual measured to the nearest 0.1 mm with vernier callipers. Crab pairs were then returned to a host colony of either 1) the same quality (i.e., from bleached to bleached or healthy to healthy, or 2) a different quality (i.e., from bleached to healthy). To account for possible colony fidelity, no crabs were returned to, nor offered in the experiment, their original host coral. Coral colonies were then paired based on nearest size and similar inter-branch space, and having crab occupants with at least a 2 mm difference in carapace size to the occupants of the paired colony. Of the 44 colonies, 14 healthy colonies were paired, 14 bleached colonies were paired and 16 colonies of differing health were paired (8 bleached and 8 healthy). The larger pair of crabs was placed on the bleached colonies in the latter treatment. Each pair of colonies was then placed into an aquarium measuring 40 × 30 × 30 cm, with a continuous flow of sea water (approximately 2 l min^{-1}). Corals were placed approximately 5 cm apart. After 2 days, all crabs were removed from the corals and re-measured in order to detect movement among colonies, as crab size was used to identify the original occupants of the colony.

To determine if degraded host colony healthy would cause crabs to seek out a new host, the number of crabs that moved to an alternate host of the same quality (either from healthy to healthy or bleached to bleached) was compared with the number that moved to an alternate host of improved quality (from bleached to healthy). The frequencies were compared using a 2-tailed Fisher's exact test.

4.4 Results

Extent of coral bleaching

Mean hard coral cover pooled among sites was 21 % (± 2.7 %) of the benthos. Branching coral constituted 64.7 % (± 5.7 %) of total hard coral cover. The mean proportion of hard corals affected by bleaching pooled was 60.4 % (± 4.8 %). Of the hard corals that exhibited bleaching, 86.8 % (± 4.7 %) were branching corals.

Effects of host bleaching on crab density and persistence

Of the 20 healthy colonies tagged at the start of the census period, 75% remained unaffected by bleaching or mortality. Four colonies were affected by mild bleaching on the branch tips. Two colonies experienced partial mortality of 20% and 10%; however the remaining tissue was healthy. Of the bleached colonies initially tagged, 70% remained bleached, 10% experienced mortality of more than 50% of the colony and 20% showed some signs of recovery. Crab density remained at a constant of 2 per colony for all tagged colonies during the first two weeks after the initial census (Figure 4.2). However, three weeks after the initial census, crab density began to decline on the bleached colonies (Figure 4.2). Fisher's exact tests revealed that crab densities found on bleached colonies differed significantly from that found on healthy colonies after 5 weeks ($p = 0.004$). Of the 20 bleached colonies, seven colonies lost one or both crabs. While crab densities remained constant on healthy colonies, there was some fluctuation on the bleached colonies between census weeks, with both emigration and immigration occurring (Figure 4.2).

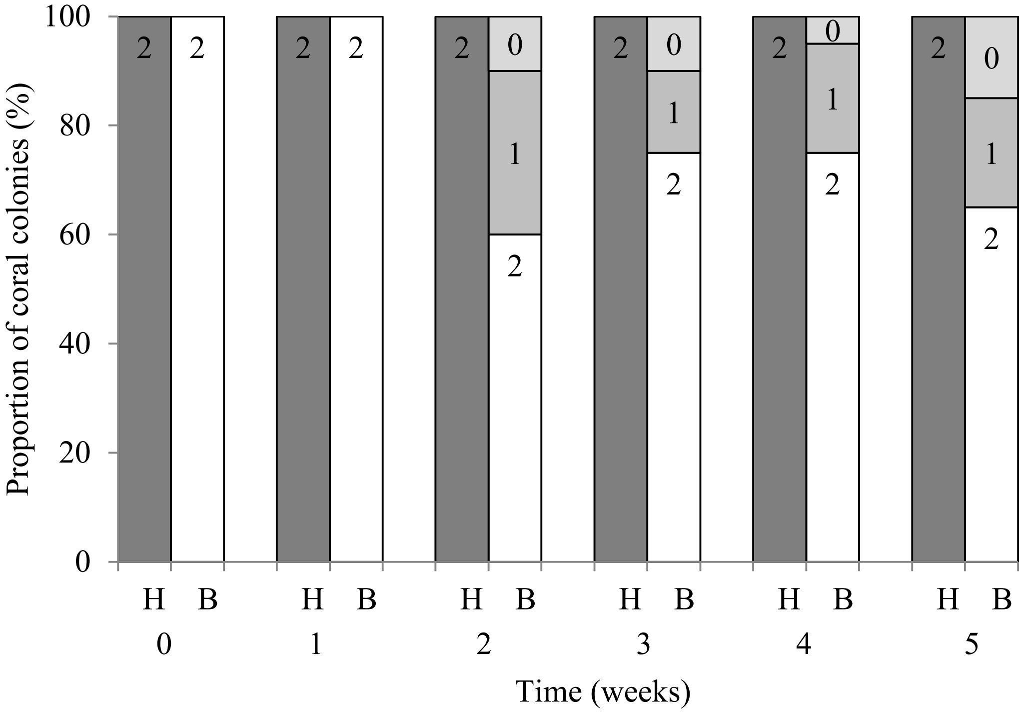

Figure 4.2 Proportion of colonies of *Pocillopora damicornis* with 2 *Trapezia cymodoce* crabs, 1 crab or no crabs on healthy (H) and bleached (B) colonies

Effects of host bleaching on crab fecundity

As a similar size range of crabs from both healthy (5.5 mm – 17 mm carapace width) and bleached (6.9 mm – 16 mm) host corals was selected to help control for effects of crab size on fecundity, mean carapace size of females collected from healthy host corals (10.5 mm ±0.43) did not differ significantly from those collected from bleached host corals (10.67 mm ± 0.39). There was a positive significant relationship between female carapace size and clutch size living on both healthy ($F_{1,\,28} = 24.37$, $r^2 = 0.46$, $p < 0.001$) and bleached corals ($F_{1,\,28} = 9.52$, $r^2 = 0.25$, $p = 0.004$) (Figure 4.3). After adjusting the group means for carapace size, there was a significant effect of coral health on mean clutch size (ANCOVA: $F_{1,\,57} = 11.02$, $p = 0.001$). The average clutch size of *T. cymodoce* collected from bleached colonies of *P. damicornis* was 876 eggs (± 128.7); 40% less than clutch size of crabs collected from healthy colonies (1410 eggs per clutch ± 165). Sampling a subset of each clutch revealed that mean size of eggs from healthy corals was 0.358 mm ± 0.008 and eggs from bleached corals were 0.343 mm ± 0.009, however this was not significant (ANOVA: $F_{1,56} = 2.167$, $p = 0.14$). Observations made on body condition of both female and male crabs, noted that 10 of the 60 crabs (4 females and 6 males) from healthy corals were missing one claw. Of the 60 crabs collected from bleached corals, 9 were missing one claw (5 females and 4 males) and 1 female was missing both.

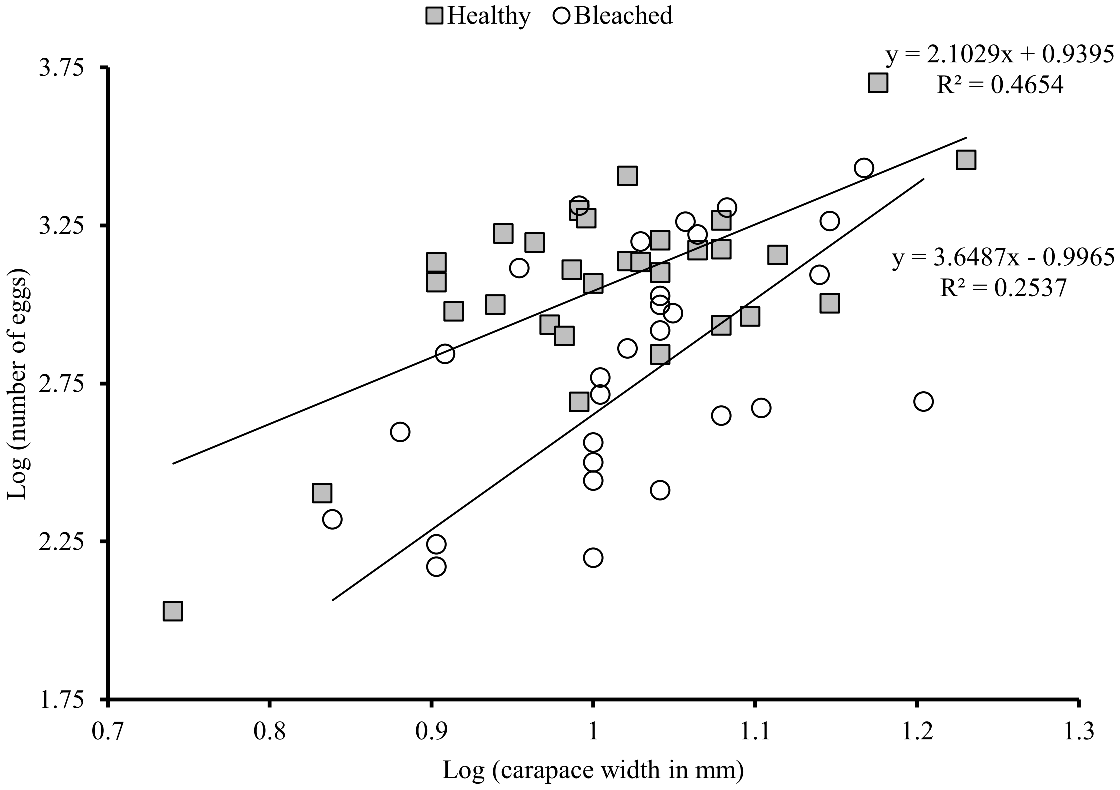

Figure 4.3 Relationship between the carapace width (mm) and fecundity (number of eggs) of *Trapezia cymodoce* females collected from either healthy or bleached colonies of *Pocillopora damicornis*

Effects of host bleaching on crab emigration

The frequency of movement of crabs from bleached host colonies to healthy host colonies was significantly different from movement among colonies of the same quality (2-tailed Fisher's exact: $p < 0.001$). In the 8 trials where coral health differed, all larger crabs moved from bleached colonies to healthy colonies and usurped the smaller occupants, which moved onto the bleached colonies. In the trials where the two corals were of the same quality, only 3 individuals out of 28 moved to an alternate host (Figure 4.4).

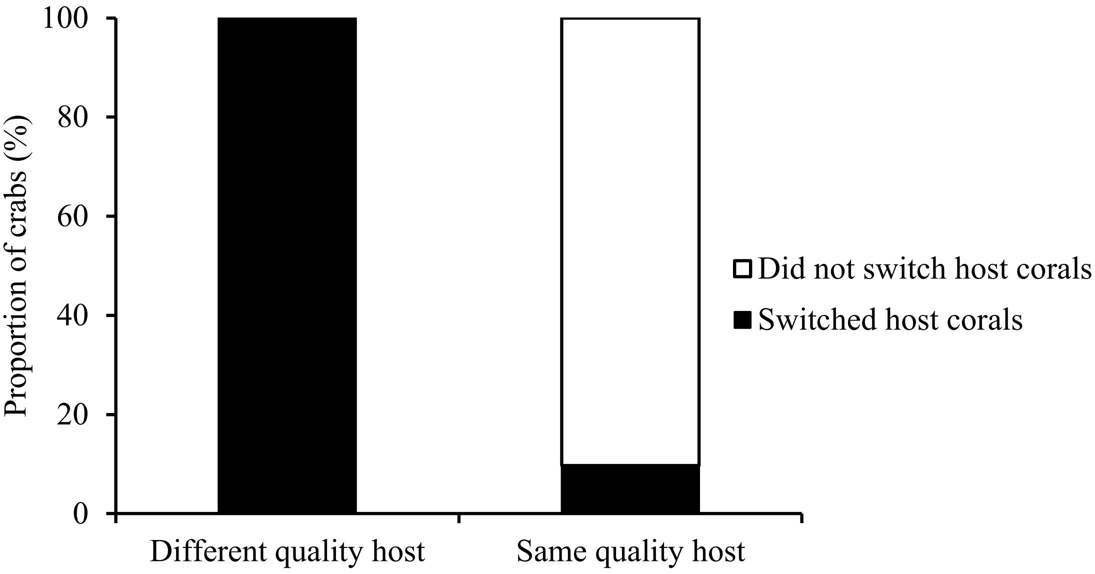

Figure 4.4 Proportion of *Trapezia cymodoce* crabs that moved to an alternate host coral of *Pocillopora damicornis* of either the same quality (i.e. from healthy to healthy or bleached to bleached) or different quality (from bleached to healthy)

4.5 Discussion

Coral bleaching events are occurring more frequently and can result in a severe decline of live coral cover (Glynn 1983a, Hoegh-Guldberg 1999) and impacts on fishes have been widely reported (Jones et al. 2004, Munday 2004, Wilson et al. 2006, Pratchett et al. 2008, Pratchett et al. 2011). This study is one of the first to directly assess the effects of a natural bleaching event on an obligate coral-associated invertebrate. The bleaching event that took place was relatively moderate, with a low incidence of coral mortality following the onset of bleaching. However, branching corals comprised the majority of affected corals and most corals remained bleached for an extensive period (at least 5 weeks). The coral crabs, *Trapezia cymodoce*, that are obligate associates of the branching coral *Pocillopora damicornis* were, in turn, detrimentally affected by host-colony bleaching. There was both a reduction in the density and fecundity of crabs associated with bleached colonies and evidence for increased movement of crabs occupying bleached corals. As these crab associates have been shown to be vital to coral health, bleached corals with fewer or less fit trapeziid crabs may be more susceptible to further disturbance and predation.

Host-colony bleaching affected the normal pattern of occurrence of *T. cymodoce*, with bleached colonies losing one or both crabs in a breeding pair within a few weeks. Crab numbers remained constant on the healthy colonies, but the densities fluctuated among colonies of bleached *P. damicornis*, indicating that crabs were both emigrating and immigrating, perhaps in search of more suitable hosts. As only the few predators morphologically equipped to penetrate the matrix of coral branches are capable of picking crabs out of their host coral (such as the bird wrasse *Gomphosus varius* with its protractile snout and the moray eel *Gymnothorax buroensis* with its flexible body) (Hiatt and Strasburg 1960), predation of *Trapezia* by other fish may occur opportunistically as the crabs move among host corals at night (Castro 1978). The reduction of suitable hosts, therefore, could increase the exposure of these animals to predation due to increased movement between coral colonies (Preston 1973). As *Trapezia* crabs are specialised on live coral and have not been recorded from other habitats, it is extremely unlikely that these crabs would persist without a host coral. The decrease in density of *Trapezia* on bleached host corals could also have implications for the host coral. These crabs help protect the host corals from predators (Weber and Woodhead 1970, Glynn 1980, Pratchett 2001, McKeon et al. 2012), enhance coral growth (Glynn 1983c), and prevent smothering of the colony by sedimentation (Stewart et al. 2006). Consequently, a decline in abundance of crabs could further debilitate bleached corals, making them more susceptible to further disturbance and reducing their recovery potential.

The marked difference in clutch size of crabs associated with healthy or bleached corals indicates that coral health, either directly via a change in nutritional quality or indirectly via a change in energy expenditure on competition over less abundant suitable hosts, has a strong influence on the health of obligate associates. If it is assumed that clutch size is a direct function of reproductive ability, female crabs with a larger clutch size would generate more viable offspring than ones with a smaller clutch size (Childress 1972). There was a 40 % reduction in fecundity relative to crabs on healthy corals, which could potentially have an effect on the fitness of these individuals. The significant increase in movement from bleached corals observed in the experiment supports the notion that residing in a healthy coral has a significant fitness advantage. In one of the only other studies to investigate the effects of coral bleaching on the fecundity of coral associates, Glynn et al. (1985) found only 1 in 8 females collected from bleached corals were ovigerous during an El Niño warming event that caused coral bleaching in Panamá. A decline in lipid levels in the coral *Pocillopora damicornis* spurred a simultaneous decline of lipids in trapeziids, with consequences on crab reproductive output (Glynn et al. 1985). A considerable amount of energy is assumed to be allocated for reproductive output in trapeziids, as females usually produce a new clutch 1-2 days after each clutch hatches (Huber and Coles 1986). Living on a healthy host coral, with an adequate food supply in the form of coral mucus, may allow such a high investment of energy into reproduction. An abundance of suitable hosts may also reduce the frequency of intra-specific agnostic interactions, allowing more energy to be allocated to reproduction rather than competition.

The manipulative experiment showed the crabs on bleached corals will attempt to move and occupy a healthy coral if their host coral bleaches. This is supported by the evidence for increased movement by crabs occupying bleached corals in the field. To gain access to a healthy coral, crabs must first defeat and evict the current occupants. The smaller individuals will inevitably be forced to leave the coral in search of another. Although crabs usually only move between colonies at night (Castro 1978), the search for suitable host corals will likely enhance susceptibility to predation (Preston 1973). Bleaching events and a decline in suitable habitat could, therefore, affect crab population structure by increasing the mortality rate of small crabs, because they are less likely to gain access to a healthy coral and more likely to be evicted by larger crabs if they already occupy a healthy coral.

The strict pair forming social organisation of *Trapezia* is thought to be the result of strong intraspecific competition for habitat space (Huber 1987). Intraspecific competitive interactions among crustaceans are for the most part limited to displays and do not usually result in injury or limb autonomy (Hyatt and Salmon 1978). For trapeziids, however, nearly all encounters between conspecifics of the same sex result in long, violent fights with injury and/or cheliped autonomy a common occurrence (Huber 1987). Irrespective of sex or host-colony condition, many crabs in this study were missing one or both claws, indicative of previous agonistic encounters. Elevated agonistic interactions caused by more frequent movements to healthy corals would likely increase the occurrence of cheliped loss among crabs. Limb loss is likely to affect the reproductive success of crabs as it involves a significant energy cost for regrowth (Norman and Jones 1993, Stella et al. 2014), and could reduce the ability of crabs to defend their hosts from coral predators. Consequently, increased movement of crabs caused by coral bleaching could influence both the condition and fitness of the crabs and their host corals.

With bleaching events predicted to be more frequent and severe in the future due to continued global warming, the fate of bleaching susceptible branching corals is of considerable concern. The loss of even just a few branching coral species could dramatically impact reef biodiversity, potentially causing the extirpation of other species, that are reliant on live coral, such as coral-associated crabs and gobies. As coral health declines, the fecundity of coral associates will decline which could ultimately affect recruitment and population persistence. Reduced health of symbiotic associates could potentially impair their ability to perform important functional roles, such as cleaning and protecting corals from predators. Further research is required to determine how persistent and severe bleaching events will affect the population dynamics of coral associates, and ultimately, what feedbacks would occur to coral populations as a result of a reduction in the abundance or physical condition of their associated faunal communities.

Chapter 5: From cooperation to combat: adverse effect of thermal stress in a symbiotic coral-crustacean community

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5.1 Abstract

Although mutualisms are ubiquitous in nature, our understanding of the potential impacts of climate change on these important ecological interactions is deficient. Here, I report on a thermal-stress related shift from cooperation to antagonism between members of a mutualistic coral-dwelling community. Increased mortality of coral-defending crustacean symbionts *Trapezia cymodoce* (coral crab) and *Alpheus lottini* (snapping shrimp) was observed in response to experimentally elevated temperatures and reduced host coral (*Pocillopora damicornis*) condition. However, strong differential numerical effects occurred among crustaceans as a function of species and sex, with shrimp (75 %), and female crabs (55 %), exhibiting the fastest and greatest declines in numbers. These declines were due to forceful eviction from the host coral by male crabs. Furthermore, surviving female crabs were impacted by a dramatic decline (85 %) in egg production, which could have deleterious consequences for population sustainability. Our results suggest that elevated temperature switches the fundamental nature of this interaction from cooperation to competition, leading to asymmetrical effects on species and/or sexes. Our study illustrates the importance of evaluating not only individual responses to climate change, but also potentially fragile interactions within and among susceptible species.

5.2 Introduction

Climate change is arguably the greatest looming threat to global biodiversity in the coming decades (Walther et al. 2002, Hughes et al. 2003, Parmesan and Yohe 2003, Thomas et al. 2004). However, our understanding of the likely consequences of climate change is incomplete due to our limited knowledge of how temperature effects ecological interactions within and among species (Ives 1995, Harley et al. 2006, Montoya et al. 2006, Tylianakis et al. 2008, Kiers et al. 2010). While many studies have examined the effects of rising temperature and other climate change stressors at the level of the individual (Parmesan and Yohe 2003, Harley et al. 2006,), fewer have tested the effects on ecological interactions among individuals (Walther 2010). It is recognised that key interactions such as predation, parasitism, competition and mutualism are basic determinants of the structure of ecological communities (Lubchenco et al. 1991, Ives and Gilchrist 1993, Montoya et al. 2006, Bascompte and Stouffer 2009). If higher temperatures alter the fundamental ways in which individuals interact, the structure of communities could be irrevocably altered.

Mutualistic interactions, which are defined as inter-specific relationships that yield net fitness gains to individuals of both interacting species, are especially important to the generation and maintenance of biodiversity in many ecosystems (Bronstein et al. 2004, Montoya et al. 2006, Bascompte and Jordano 2007). Indeed, every species known on earth is involved directly or indirectly in one or more mutualistic partnerships (Elton 1927. Reprint) and some are involved in hundreds (Bronstein et al. 2004). While mutualistic interactions act to enhance survivorship and facilitate the acquisition of otherwise unobtainable resources, strong fitness-dependence can seal mutualists to a shared fate during rapid environmental change (May 1976, Briand and Yodzis 1982). Changes in biotic and abiotic conditions can alter the costs and benefits of cooperative behaviour, prompting individuals to abandon mutualistic associations (Sachs and Simms 2006, West et al. 2007, Kiers et al. 2010). The disruption of mutualistic interactions by climate change may exacerbate the loss of biodiversity and alter key ecosystem processes and services (Kiers et al. 2010).

Coral reefs support the highest number of mutualistic associations in the marine environment (Castro 1988, Stachowicz 2001). Aside from the well-known mutualism between corals and their endo-symbiotic dinoflagellates, *Symbiodinium* spp. (Odum and Odum 1955, Trench 1979), corals also host a variety of mutualistic exosymbionts that rely on corals for shelter, food and reproduction (Knudsen 1967, Patton 1974, Chapter 2, Stella et al. 2011). In return, a number of these exosymbionts, chiefly crustaceans, are ecologically important to their host corals, providing cleaning services, defence against predators and disease mitigation (Glynn 1976, Stewart et al. 2006Pollock et al. 2012). These mutualists have the potential to either buffer or exacerbate the impacts of thermal stress on corals and their symbiotic communities, depending on how thermal stress affects cooperative interactions among the community of symbiotic species. Elevated temperatures may reduce resource availability and therefore may exacerbate competition at the expense of cooperation, which may have subsequent effects on individual fitness (Bonin et al. 2009, Feary et al. 2009, Chapter 4). In turn, reduced fitness via thermal stress may affect competitive ability to secure resources. Adverse effects of thermal stress have had an observed effect on coral exosymbiont life history characteristics, such as fecundity, density and survivorship (Glynn and D'Croz 1990, Tsuchiya et al. 1992), yet the effects on behavioural interactions between individuals within and among exosymbiont species are yet to be explored.

Some coral-dwelling crustaceans exhibit antagonistic behaviour towards conspecifics that typically restricts occupancy to one breeding pair per coral (Castro 1976). Nevertheless, cooperation between mutualistic species has been recorded (Glynn 1976), with a dominance hierarchy often observed among cohabiting species (Lassig 1977, Vannini 1985, McKeon et al. 2012). Theoretical models predict that antagonism should become more intense as valuable resources diminish (Maynard-Smith 1982), and that some individuals will be more capable of securing or retaining resources than others (resource holding potential or RHP, (Parker 1974)). Among cooperative coral crustaceans, RHP can differ greatly, with one species or sex being subordinate to another (Parker 1974, Briffa and Dallaway 2007). Resource depletion due to climate change may result in increased competition within and among species utilizing the same resource (e.g. host coral), with subordinate species and sexes being highly disadvantaged. Consequently, the effects of environmental change are not only dependent upon the direct effects of the environment on an individual’s survival and fecundity, but also on any changes to interactions with other species in the community (Connell 1961, Ives and Gilchrist 1993, Wootton 1994). Incorporating species interactions with individual responses will help determine the ultimate response of populations to environmental changes.

The purpose of this study was to test the effects of thermal stress (and subsequent coral bleaching) on fecundity, survival and behavioural interactions among individuals within a common coral-crustacean mutualistic community. I experimentally bleached host corals by exposure to elevated temperatures and then monitored egg production, survival, and host coral occupancy by males and females of two co-existing crustacean species. The study system comprised a previously demonstrated mutualistic association between the host coral *Pocillopora damicornis* (Linnaeus, 1758**)**, the coral crab *Trapezia cymodoce* (Herbst, 1801) and the snapping shrimp *Alpheus lottini* (Guérin Méneville, 1828), a species complex of alpheid shrimp (Williams and Knowlton 2001). I tested the hypothesis that increasing temperature would erode the advantages of cooperation and increase the levels of antagonism within and among the two symbiotic crustacean species, with disproportionate negative effects on subordinate individuals.

5.3 Methods

The focal symbiotic community

In the wild, the crustacean symbionts *T. cymodoce* and *A. lottini* typically co-inhabit the coral *Pocillopora damicornis* as one monogamous pair per crustacean species per coral colony (Huber and Coles 1986, Lassig 1977, Vannini 1985). However, corals with just *T. cymodoce* also occur in the wild. These crab and shrimp are often collectively referred to as 'coral guardians' (Glynn 1983a). Both species defend their coral home from coral predators such as crown-of-thorns starfish *Acanthaster planci* (Glynn 1976, Pratchett 2001), and increase coral vitality by keeping their coral free of sediment and organic debris (Glynn 1983b, Stewart et al. 2006, Stier et al. 2010). Both species use live coral habitat as a breeding site, as a refuge from predation, and as a primary food source in the form of coral mucus (Knudsen 1967, Patton 1974) and fat bodies produced only in the presence of coral crabs (Stimson 1990). Whilst coral crabs are extremely aggressive towards both same-sex conspecifics and individuals of some other species, they frequently form lasting social bonds with snapping shrimp (Castro 1976, Lassig 1977, Castro 1978). Evidence suggests that shrimp are competitively subordinate to crabs, but are allowed to co-habit corals because they provide cleaning services for the crabs in addition to assistance with coral defence and coral cleaning (Lassig 1977, Vannini 1985).

Specimen collection for thermal experiment

This study was conducted in late summer at Lizard Island, Great Barrier Reef, Australia (14^{o}400'S, 145^{o}270'E). Forty colonies of *Pocillopora damicornis* (ca. 20 cm diameter) were randomly collected from the Lizard Island lagoon. All colonies were apparently healthy (i.e. with no partial mortality). Twenty-four of the collected coral colonies were found to contain a monogamous pair of *T. cymodoce* crabs and a monogamous pair of *A. lottini* shrimp, and sixteen colonies were found to contain a monogamous pair *T. cymodoce* crab only. Colonies were enclosed in a plastic bag to retain all organisms, gently removed from the substrate, and then transported to Lizard Island Research Station (LIRS) in a seawater bath. At the LIRS aquarium laboratory, individual *Trapezia cymodoce* and *Alpheus lottini* were counted and sexed. All crustacean individuals appeared to be in good health, and possessed all of their appendages. All known corallivores (*Coralliophila* spp., (Brawley and Adey 1982); *Drupella* spp., (Robertson 1970); *Diodora galeata*, (Stella 2012)) were removed from colonies to avoid the confounding effect of variable coral predation on crustacean symbiont behaviour. No crustacean predators were found to be occupying host corals. Remaining coral community group members (consisting of Ophiuroids, Holothurians and no known Pocilloporid obligates) were recorded by visual survey and left undisturbed. Ten days after collection, both symbionts were carefully removed from each colony using a blunt probe to gently nudge the animal to the outer branches. Both sexes of crabs and shrimp were then anesthetized with a mild solution of clove oil (2 ppt), weighed to the nearest 0.001g and measured to the nearest 0.1 mm (carapace width for the crabs and total length for the shrimp). Egg clutches were removed from ovigerous female crabs and shrimp by gently scraping them out of the abdomen using tweezers. Egg clutches were added to a petri dish with seawater, photographed under a dissecting microscope and counted using UTHSCSA ImageTool (IT). All animals were then returned to their original colony. Coral colonies were measured and approximate living space calculated for each using the following equation ((LxWxH)-V). Volume was measured by the displacement of 6,000 cm^3 of water.

Experimental design

To test the effects of elevated temperature on coral symbiont communities I randomly allocated the 40 coral communities to temperature treatments (elevated temperature and control). Shrimp pairs were kept with the same pair of crabs in order to reduce possible aggression associated with presence of unfamiliar individuals. Coral communities were housed in individual insulated aquaria (40cm L × 30cm W × 25cm H; $n = 40$), and each tank received a continuous flow of filtered and aerated lagoonal water (flow ca. 0.5 $L.min^{-1}$; aeration = ca. 2 $L.min^{-1}$). Ambient temperature in all tanks was maintained at 29.5 ºC ± 0.02 ºC for 10 days prior to the start of the experiment to allow corals and symbionts to acclimate to aquarium conditions. Upon commencement of the experiment, I simulated a thermally-induced bleaching event: tank temperatures in the elevated temperature treatment group were increased by an average of 0.1-0.3 ºC per day using electric heaters until 32.5 ºC was reached. This temperature regime was adapted from a natural bleaching event which took place on Lizard Island in 2010 in which a temperature anomaly was recorded for one week with maximum daily temperatures ranging from 32 to 32.9 ºC (Chapter 4). The maximum temperatures sustained over the week long period were ~3–4 ºC higher than the long-term average summer temperature of 29 ºC for Lizard Island (Lough 1999) and also coincide with projected increases in tropical sea surface temperatures of up to 3 ºC by 2100 (Lough 2007; Munday et al. 2009).Once coral bleaching occurred, the temperature was slowly reduced (by 0.2 ºC ± 0.1 ºC per day) to initial ambient temperature conditions. The control group was maintained at 29.5 ºC ± 0.02 ºC throughout the experiment, using a chiller when necessary. Temperatures were recorded 3 times per day (8am, 12pm, and 6pm) for 81 days (Supp data). Twenty-four of the collected coral colonies were found to contain a monogamous pair of *T. cymodoce* crab and a monogamous pair of *Alpheus lottini* shrimp, and sixteen colonies were found to contain a monogamous pair of *T. cymodoce* crab only. Thus two sub-groups were created among each treatment groups, crab-only communities (8 per treatment) and crab+shrimp communities (12 per treatment).

a) Coral bleaching

All corals were assessed and photographed weekly to record changes in colour and subsequent level of bleaching. Bleaching progress of coral tissue was measured using a coral colour reference card (Siebeck et al. 2006). This method involves matching the colour and hue of coral tissue with that of a palette of colours and hues on a plastic chart. The numbered scale ranges from 1 (all white, indicate bleaching) to 6 (darkest hue, indicating good coral condition). To estimate colour score, the plastic chart was held alongside each colony and the best matching colour score was recorded for that colony. If and when colonies bleached, they were scored daily thereafter as "alive" or "dead" based on the presence (alive) or absence (dead) of a polyp-retraction response upon tactile stimulation using a blunt probe. A score of “0” was assigned to indicate a dead colony.

b) Species and sex-specific patterns of eviction

Coral colonies were visually inspected daily to record any changes in species- and sex-specific crustacean symbiont abundance. Individuals were scored as being either within the coral or outside of the coral, and whether they were alive or dead. Forceful eviction was evidenced as the loss of limbs (such as pereopods and/or chelpids), which is the typical outcome of inter- and intra-specific combat among marine decapods crustaceans (Hyatt & Salmon 1987) and, specifically, the current focal species (Huber 1987).

I used a General Linear Model (GLM) with a binomial error distribution to test for differential numerical crustacean loss throughout the experiment as a function of thermal treatment group, species, and sex. As all mortalities were preceded by evictions, but not all evictions resulted in immediate mortality, I calculated crustacean loss as the number of losses by evictions.

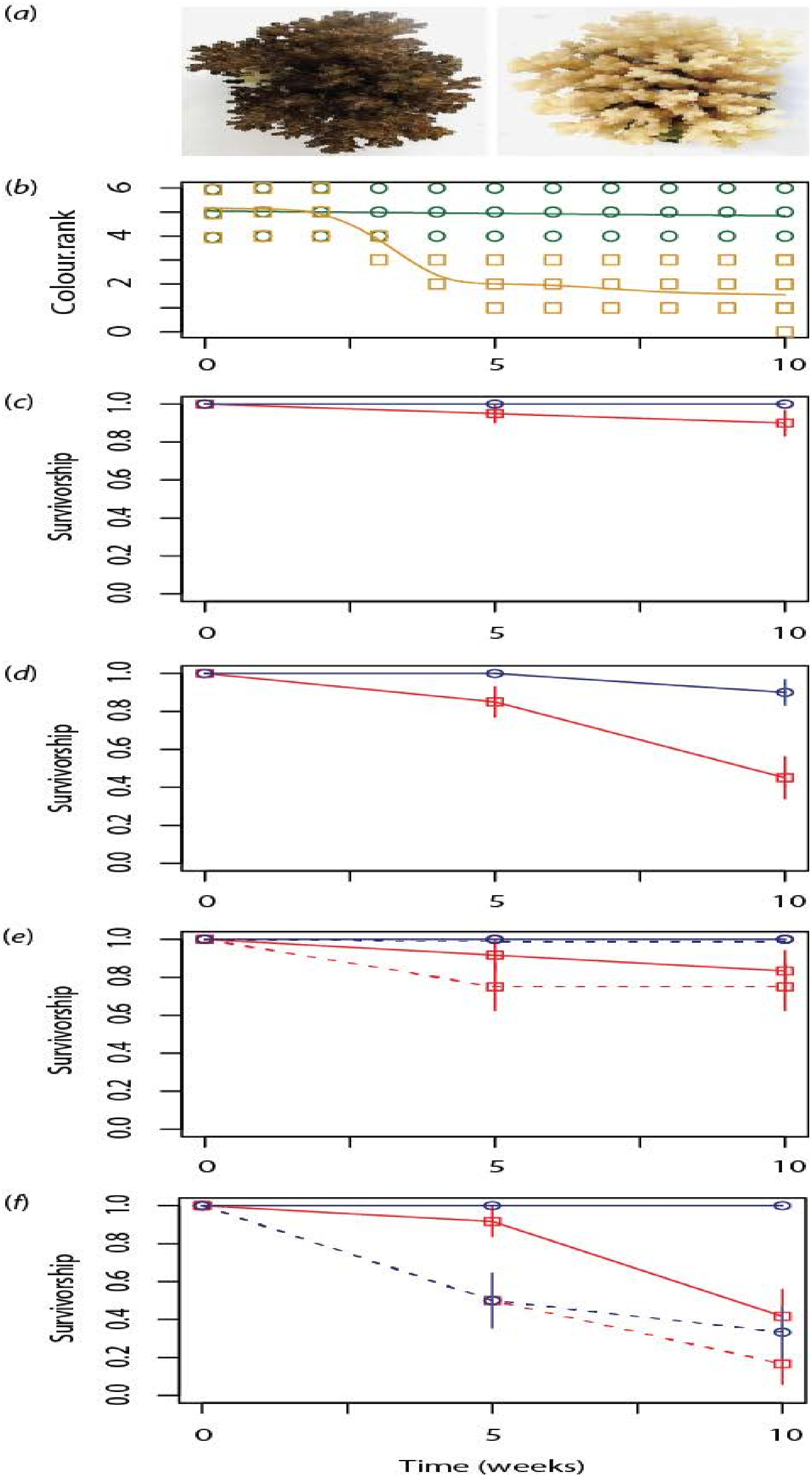
c) Female crab fecundity

Batch fecundity of all live female crabs and shrimps was recorded for both the thermal stress and control treatment groups at three intervals throughout the experiment; at the beginning of the experiment; at the onset of host coral bleaching (approximately 30 days after thermal stress began), and; at 32-40 days after coral bleaching occurred in the thermal stress treatment group. To sample batch fecundity, individual crustaceans were anesthetised with clove oil (as above), and eggs were then collected from ovigerous females by gently dislodging them from the female's abdomen (where the eggs are held externally) using blunt tweezers. Egg clutches were then added to a petri dish containing seawater, photographed under a dissecting microscope and counted using UTHSCSA ImageTool (IT). All animals were then returned to their original colony following recovery from anaesthesia. I used Repeated Measures Analysis of Variance (R-M ANOVA) to test for differential temporal shifts in batch fecundity between thermal stress and control treatments groups. Although mean carapace size did not differ between the control and treatment groups for either sex (control group was 12.96 mm ± 0.35 for females and 12.39 mm ± .34 for males and the thermally bleached group was 13.05 mm ± 0.36 for females and 12.20 mm ± .37 for males (mean ± SE, $n = 20$ crabs), batch fecundity was calculated as number of eggs/carapace width (mm). Individuals who died during the experiment were case-wise deleted prior to statistical analysis.

5.4 Results

Available resource, bleaching and death of corals

Available resources to coral obligates as measured by living space of corals was slightly higher in thermally stressed group (3105.55 cm^3 ± 382.84 for thermally stressed and 2957.2 cm^3 ± 346.31 for control) (mean ± SE) but was not significant (ANOVA, $F_1 = 1.652$, $P=0.21$). In the thermal stress treatment group, all coral colonies (n=20) were pale in appearance by the end of week 2, and bleaching of all colonies occurred by week 4 (Figure 5.1a, b, c). Two of the 20 colonies died during week 9. All control colonies (n=20) retained their colour and none experienced any mortality for the duration of the experiment.


(a)
(b)
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2
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(c)
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(d)
Survivorship
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(e)
Survivorship
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0
5
10
(f)
Survivorship
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
Time (weeks)

Figure 5.1 a) Representative examples of live healthy coral (*left*) and **(a)** bleached coral (*right*) from the control and thermally stressed treatment groups, respectively, at the end of the experiment, **b)** colour scores of *Pocillopora damicornis* corals throughout the experimental period for control (green, $n = 20$) and thermally stressed (brown, $n = 20$) treatment groups, fitted to generalized additive models smoothing functions. Coral colour rank: 0 (dead), 1 (alive; white), 6 (alive; darkest hue). **c–f)** Cumulative loss of individuals ± SE (binomial) throughout the experiment as a function of community type, species, and sex: **c** crab-only communities, control treatment group ($n = 8$); **d)** crab-only communities, thermally stressed treatment group $n = 8$); **e** crab plus shrimp communities, control treatment group ($n = 12$); **f)** crab plus shrimp communities, thermally stressed treatment group ($n = 12$). *Circles* males, *squares* females, *continuous lines* crabs, *dotted lines* shrimp

Species-specific eviction

Throughout the experiment, every crustacean symbiont not within the branches of its host coral was found in the basal part of the colony or in the corner of the aquarium, and whether dead or alive, was missing two or more appendages (pereopods and/or chelipeds). Therefore, migration off the colony appears to be due to eviction from the coral colony by another occupant. Once evicted, the crab and/or shrimp remained outside of the coral and most, but not all, died within 1-2 weeks. Corals sustained crab and shrimp losses via eviction in both the control and thermal stress treatment groups, however, by the end of the experiment, numerical losses were markedly greater for thermally stressed corals (48%) compared to control corals (7%) for both the crab-only communities (GLM; Treatment: $z = 2.98$, $P < 0.01$), and the crab+shrimp communities (GLM; Treatment: $z = 4.2$, $p < 0.01$) (Figure 5.1).

Sex-specific eviction

Different occurrences of eviction were observed as a function of sex for both species and community types (GLM, Crab-only community; Sex: $z = 2.98$, $P < 0.01$. GLM, crab+shrimp community; Sex: $z = 3.36$, $p < 0.01$), with females more frequently evicted than males, particularly among crabs (Figure 5.1). Different occurrences of eviction were also observed as a function of species within crab+shrimp communities, with shrimp being more heavily evicted compared to crabs (GLM, crab+shrimp community; Species: $z = 2.99$, $p < 0.01$). The structure of the surviving resident community at the end of the experiment differed between thermally stressed and control treatment corals for both community types. Control corals were characterised by relatively high abundances and near-equal representation of sexes and species. In contrast, thermally stressed corals were characterised by relatively low abundances and dominated by male crabs (Figure5.1). Eighteen out of 20 bleached colonies (with or without shrimp) contained a male crab at the end of the experiment. The high thermal-stress associated loss of crustacean symbionts, chiefly females and shrimp, contrasts sharply with mortality rates experienced by host corals: 0% in the control treatment group; 10% in the thermal stress treatment group.

Fecundity of female crabs

A significant decline in batch fecundity of female crabs was also observed as a function of thermal treatment group (MR-ANOVA; Treatment*Time: $F_{2,56}$=6.13, p=0.003). At the beginning of the experiment thermal stress treatment and control treatment crabs displayed statistically similar mean batch fecundity (Figure5.2). However, by the end of the experiment thermally stressed female crabs displayed a mean batch fecundity that was just 14% of the mean batch fecundity of control crabs (Figure 5.2). Batch fecundity of female shrimp was not examined due to the near 100% mortality rate experienced during the experiment. All treatment colonies that had started with a pair of shrimp had lost one shrimp by the time coral bleaching began and many colonies lost both shrimp by the end of the experiment, so it was not possible to compare fecundity changes of shrimp between the two groups.

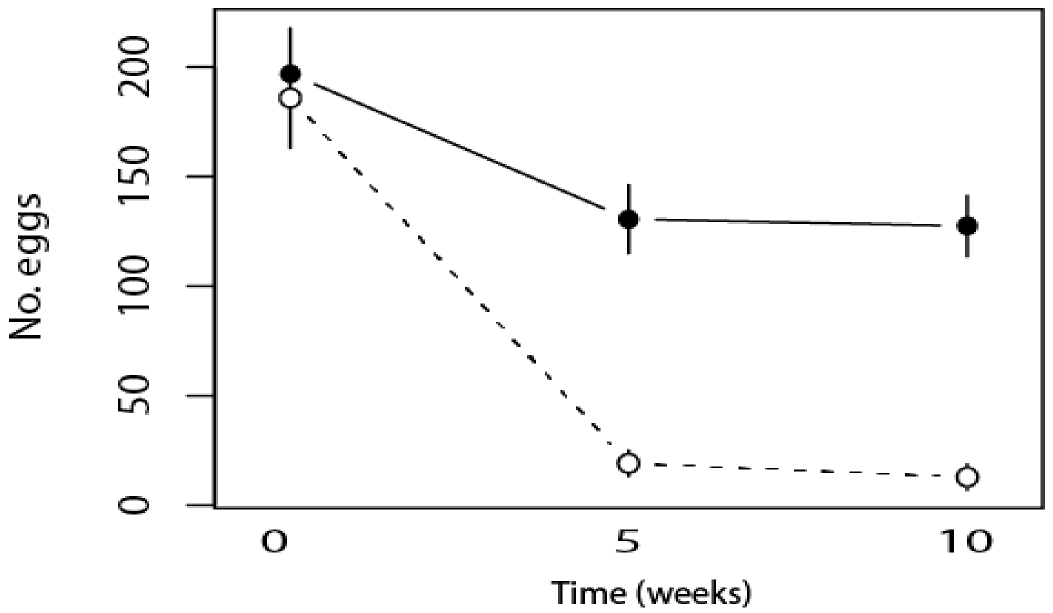

Figure 5.2 Standardised batch fecundity (number of eggs/carapace width) per female of *Trapezia cymodoce* living on a *Pocillopora damicornis* host coral throughout the experimental period for a control group (*continuous line*, *n* = 20) or thermally stressed (*dotted line*, *n* = 20) treatment groups at three time intervals

5.5 Discussion

Our results indicate that the coral reef mutualistic network comprised of the coral *Pocillopora damicornis* and symbiotic crabs and shrimp may be severely impacted by rising ocean temperatures. Both the crab and shrimp were found to suffer a significant decline in numbers via forceful eviction in response to thermal stress, with a 40 % greater decline on thermally stressed corals compared to non-stressed corals. Differential effects of thermal-stress were observed as a function of crustacean symbiont species and sex. Shrimps were eliminated by the competitively superior crabs and female crabs were evicted by male crabs. The observed eviction of female crabs and the massive decline in egg production in surviving females could have a catastrophic effect on the long-term persistence of crab populations subject to increasing temperatures.

All mortality throughout the experiment was associated with loss of limbs, the majority of which were pereopods (walking legs) and occasionally chelipeds (claws), indicating forceful eviction from coral colonies (Huber 1987, Tsuchiya and Yonaha

1992). Forceful eviction from coral colonies suggests thermal stress is eroding the conditions for co-existence and increasing the importance of antagonistic interactions among individuals in the colony, favouring the competitive dominants. Shrimp suffered the fastest and greatest declines in numbers via forceful eviction among thermally bleached corals. Many alpheid shrimp, including the current species, are known to engage in complex behavioural and communicative interactions with other coral reef animals and the mutualism is often intimate, lifelong and fundamental for the shrimp's survival (i.e. obligate mutualism) (Karplus 1987, Marin et al. 2005).

The typically peaceful, and often cooperative, crab-shrimp interactions that exist during stable environmental conditions, (Lassig 1977, McKeon et al. 2012) appear to have been disrupted by the thermal-stress event, presumably because competition for a limiting resource became more intense. I suggest that temperature, via a set of interactions between individual fitness, behaviour, and asymmetries in RHP, results in rapid loss of crustacean symbiont abundance and reproductive potential. As the shrimp require a host coral to survive, yet al.so require the acceptance of crab residents in order to access a host coral (Lassig 1977, Vannini 1985), they are reliant upon positive interactions with both the crabs and the host coral for their survival. This interpretation is consistent with previous studies that provide evidence for asymmetric RHP between symbiotic shrimp and crabs (Lassig 1977, Vannini 1985). Obligate coral mutualism, coupled with low RHP against symbiotic coral crabs, indicates that shrimps are the most susceptible to a breakdown in cooperative interactions within the symbiotic community.

The differential mortality of female crabs and the marked decline in clutch size highlights the potential for climate change to have a greater impact on one sex of a species than the other. Elevated temperature had a strong influence on the health of obligate crabs and can be attributed to one or all of three factors: 1) direct physiological stress; 2) agonistic interactions with male crabs resulting in an overall increase in energy expenditure, both during the encounter as well as via limb loss and subsequent regeneration (Norman and Jones 1993); or 3) a reduction in the nutritional quality of the host coral due to bleaching. Smaller clutch sizes in trapeziid crabs associated with bleached corals have been reported during past bleaching events (Tsuchiya 1999, Chapter 4) and have been attributed to a reduction of food, primarily coral mucus (Knudsen 1967), provided by the coral colony as bleached corals exhibit a substantial decline in both the amount and nutritional quality of mucus secreted (Brown and

Bythell 2005). Direct physiological effects of high temperature on egg production and increased agonistic interactions with males could have contributed further to the dramatic decline in female fecundity. As bearing eggs can potentially raise the metabolic rate in ovigerous female crabs and thus impact their fitness (Taylor and Leelapiyanart 2001), a small decrease in oxygen availability could have had detrimental effects on the metabolism of female crabs, leaving male crabs competitively superior.

The relatively high reproductive output of *T. cymodoce* during stable environmental conditions might be associated with high larval mortality rates, as is the case for most high fecundity marine organisms (Williams 1975, Miller et al. 1988). Even small changes in reproductive output can strongly influence recruitment success (Hughes et al. 2000). As 55 % of female crabs were evicted from their host corals, and those that were not evicted exhibited an 86% reduction in egg production, female crabs clearly suffer a massive loss of fitness due to elevated temperatures, potentially leading to recruitment limitation and a long-term decline in population abundance.

This study is the first illustration of intersex RHP asymmetries, and thermal-stress associated intersexual conflict, within crustacean symbiont species. Intersexual aggression has also been observed among hermit crabs, where males and females often fight for access to preferred gastropod shells (Briffa and Dallaway 2007). While evidence suggests that intersexual conflict over resources may be common in nature (Briffa and Dallaway 2007), and has important individual fitness consequences, it is a far less studied aspect of competition compared to intrasexual and interspecies conflict (Rausher and Fowler 1979, Briffa and Dallaway 2007). Our results suggest a higher RHP for male crabs during periods of thermal stress. The benefit of this behaviour presumably rests on successful re-colonisation by female recruits from unaffected populations following the environmental disturbance event (i.e. for future reproduction) (Tsuchiya et al. 1989). However, accelerated rates of change in thermal stress frequency, intensity, and extent expected due to climate change, may prove maladaptive for crab populations, and the coral symbiotic community in general. Our study illustrates the importance of considering differential sex-specific behaviour when examining biological responses to thermal change.

Both coral symbionts began to decline in abundance during thermal stress just prior to host colony bleaching, indicating that symbionts may be more sensitive to thermal stress than their host corals. Although their host coral remained in a bleached state for over a month, only 10% of colonies died, whereas 75% of shrimp and 33% of crabs died. In understanding how disturbance events affect community ecology, the sequence of events, and not just the severity and frequency, can be very important (Fukami 2001). Bleaching events are preceded by higher than normal sea surface temperatures (Glynn and D'Croz 1990, Glynn 1991). Disturbance events that kill symbionts may only cause partial mortality to the corals (Abele 1976, Glynn et al. 1985). The fitness benefits to corals of crab and shrimp occupancy under a normal thermal environment have been shown to be additive, whereby corals receive the most cleaning and predator-defence services when both crustacean symbiotic species are present (Glynn 1980, McKeon et al. 2012); consequently the loss of these symbionts could have significant repercussions for the corals that rely on them. Bleached corals no longer protected by crustacean symbionts are expected to face increased mortality from predation and sedimentation, reducing the chance of coral recovery. In addition, rapid loss of mutualists may enhance the prospect of invasion by opportunistic generalist species that are not intimately associated with coral health, and which may further exacerbate coral community-level effects of climate and global change (Marvier et al. 2004, LaJeunesse et al. 2009).

In conclusion, our study highlights a poorly understood interaction between behaviour and temperature and illustrates the need to focus research efforts on the vulnerability of cooperative interactions to environmental stress. Whether populations will persist through climate change is not only determined by individual organism response, but may rely heavily on the preservation of important species interactions. The development of theoretical frameworks for behaviour-based symbiotic community dynamics (and community dynamics in general) that consider shifts in individual social behaviour is vital to understanding and predicting the effects of climate change on biotic systems.

Chapter 6: General Discussion

Biodiversity loss associated with climate change is predicted to be catastrophic for coral reef ecosystems because they are highly sensitive to temperature changes (Walther et al. 2002, Hughes et al. 2003, Hoegh-Guldberg et al. 2007). This biodiversity loss is already underway, with extinction threatening nearly one third of corals (Carpenter et al. 2008) and the likely extinctions of several marine fish, largely due to habitat loss (Dulvey et al. 2003). Despite the urgency, relatively little attention has been paid to reef invertebrates, by far the most abundant and diverse array of animals on coral reefs (Reakla-Kudla 1997, Bouchet 2006, Chapman 2009). The threat to their biodiversity is extreme given their close association with corals, particularly branching corals (Knowlton et al. 2010, Glynn and Enochs 2011, Stella et al. 2011, Prather et al. 2013). As branching corals are particularly susceptible to climate change, via thermal stress and extreme storm events, those species that exhibit strong coral dependency face an increased risk of extinction risk should their coral habitat be compromised (McKinney 1997, Loya et al. 2001). In addition to the threat of habitat loss, invertebrate species must also cope with the direct effects of climate change in order to persist in their ecosystem. An understanding of how this diverse group of coral-associated animals will respond to climate change is critical to predicting what the future of coral reef diversity will look like. By exploring these associations and assessing the effects of thermal stress and habitat degradation on specialised species, this study found an astonishing concentration of invertebrates that associate with branching coral, with specialised species at high risk of extinction via habitat degradation and thermal stress.

Diversity

Compact branching corals belonging to the families Pocilloporidae and Acroporidae are epicentres for coral reef invertebrate biodiversity (Chapters 2-3). Up to 13 phyla are found within these branching corals which is greater than the phylogenetic diversity of rainforest animals. This immense diversity includes at least 420 species, belonging to 162 families and 273 genera, dwarfing the diversity of the four fish families known to be coral-dwellers (Wong et al. 2013). Although other host corals also support distinct communities of invertebrates, total diversity is relatively low compared to this study (e.g. 95 species associated with 50 fungid species, Hoeksema et al. 2013). Assemblages of coral-associated invertebrates among host corals were quite distinct, with the greatest variation occurring between acroporids and pocilloporids, and these strong preferences could be indicative of host specialisation (Patton 1974, 1994, Sin 1999, Vytopil and Willis 2001, Stella et al. 2011). Approximately 9-15 % of invertebrates found are considered obligate coral users (Chapters 2-3, Stella et al. 2011). The implication of this research is that a proportion of coral reef species either have strong preferences for, or may be specialised to, a narrow range of coral species that are themselves facing an elevated extinction risk (Carpenter et al. 2008). As this was one of first studies to comprehensively assess and compare the diversity of invertebrates associated with multiple coral species, it highlights a substantial deficit in our understanding of the threats to overall coral reef biodiversity. Including a wider range of host corals, such as favids and agariicids (Hoeksema et al. 2012, Hoeksema and van der Meij 2013), would provide better insight to not only estimates of total invertebrate diversity, but also to identify the diversity associated with corals considered to be less susceptible to disturbance.

Habitat degradation effects on diversity and abundance

Pocilloporid and acroporid corals harbour an immense diversity of invertebrates (Chapters 2-3) and are also among the most susceptible to disturbances (e.g. high wave action, predation by fish and crown-of-thorns starfish, flood plumes, and thermal bleaching) (Brown and Suharsano 1990, Gleason 1993, Marshall and Baird 2000, Loya et al. 2001, Floros et al. 2004, McClanahan et al. 2004, Pratchett et al. 2010). My research found that host coral bleaching and mortality has dramatic effects on the diversity and abundance of associated invertebrates, with bleached host corals representing the least desirable habitat. However, dead corals support a higher diversity and abundance than healthy corals, indicating that structurally intact coral skeletons are important to invertebrate diversity, as has been shown for fish (e.g. Gratwicke & Speight 2005, Garpe et al. 2006, Wilson et al. 2007). Differences in diversity and abundance among healthy, bleached and dead host corals can be attributed to a shift in the number of obligate and facultative coral-dwellers. This implies that severe disturbances will impact invertebrate biodiversity mainly through the loss of obligate coral-dwellers. Thirty-eight known obligate species were found on 7 host coral species, all facing an elevated extinction risk if their host coral species declines. Importantly, this research highlighted the effect of moderate levels of disturbance, which appears to be a natural process promoting invertebrate biodiversity by creating habitat suitable for both obligate and facultative species. As a similar pattern has been documented for fish (Jones & Syms 1998, Wilson et al. 2009) and coral diversity (Aronson and Precht 1995), these results suggest that structural complexity may be one of the most important factors in maintaining coral reef diversity (Wilson et al. 2007, Sueiro et al 2010, Kovalenko et al. 2011, Fabricius et al. 2014, St. Pierre and Kovalenko 2014). Impacts of coral disturbance on invertebrate species will depend on the severity of the disturbance and the degree of habitat specialisation. If structural integrity is retained, it is possible the diversity will be maintained, however it is clear that facultative species will have a marked advantaged over obligate species during severe coral disturbance events.

Direct effects of thermal stress and host coral bleaching

Obligate coral-associated invertebrates are often so reliant upon their host, that their fitness may be inexorably intertwined to the health of the coral. A natural bleaching event following an acute sea surface temperature anomaly provided an opportunity to directly assess the effects on an obligate coral-associated invertebrate (Chapter 4). The coral crabs, *Trapezia cymodoce*, exhibited many detrimental effects after thermal stress and subsequent bleaching of their host coral *Pocillopora damicornis*. Thermal bleaching caused a marked reduction in the fecundity and density of obligate crabs. A drastic decline in egg production of crabs associated with bleached corals indicates that host coral health is strongly linked with the fitness health of obligate associates. Coral bleaching and habitat degradation have had similar effects on the fitness of coral-dependent fish (Kokita and Nakazono 2001, Munday 2001, Pratchett et al. 2004) with lower survival, growth and reproduction. Bleaching also elicited a strong behavioural response; crabs moved on and off bleached host corals, increasing their risk to predation. An increase in intra-specific competition over healthy host corals resulted in high occurrences of limb loss, further affecting fitness levels. Larger crabs were more successful in migrating to and dominating healthy corals, indicating that bigger is truly better. These behaviours support the notion that healthy host corals lend obligate coral users a significant fitness advantage. Together, these results highlight the sub-lethal effects of bleaching on obligate species' fitness, impacting both their physiology and behaviour in ways that may be detrimental to their persistence through frequent bleaching events.

Direct and indirect effects of thermal stress and/or host coral bleaching: species interactions

The density of invertebrates occurring in branching corals potentially facilitates a multitude of species interactions, some of which may be critical to one or more species' survival. Research to date mainly examines effects of rising temperature and other climate change stressors at the level of the individual (Harley et al. 2006, Parmesan and Yohe 2003). My study was one of the first to holistically consider the effects of climate change on a mutualistic coral-dwelling community and to document differential effects of thermal stress as a function of species and sex (Chapter 5). It supports the existence of a hierarchy within obligate coral-dwellers (Lassig 1977, Vannini 1985) as shrimps were eliminated from bleached corals by the competitively superior crabs. This thesis is the first to illustrate intersexual conflict associated with thermal-stress on obligate crustacean species as female crabs were evicted from bleached corals by male crabs. I also found that host corals appear to be more resilient to thermal stress than their symbiotic crustaceans. This observation has been documented before (Abele1976, 1979, Glynn and D'Croz 1999) and has serious implications for host corals stripped of their mutualistic partners and the subsequent loss of vital ecological services. These results imply that species interactions may be severely impacted by rising ocean temperatures having catastrophic effects on the long-term persistence of mutualistic species. Overall, my research highlights a possible significant link between behaviour and temperature and illustrates the necessity to focus research efforts on the vulnerability of cooperative interactions to environmental stress. Whether populations will persist through climate change is not only determined by individual organism response, but may rely heavily on the preservation of important species interactions.

Future directions

One of the biggest challenges in assessing the biodiversity of coral reefs is that the largest proportion of it is inherently hard to measure due to being small and cryptic. A multitude of invertebrate species may go extinct without ever having been discovered. Ecological studies of corals should begin to incorporate symbiotic invertebrate assemblages, as it would greatly supplement gaps in our knowledge regarding their importance in coral reef trophic networks and ecosystem function (even at the level of individual coral health, e.g. Pollock et al. 2012). Systematic intensive surveys of a more comprehensive set of microhabitats would be invaluable in promoting our knowledge of invertebrate diversity, however they are costly and usually restricted to small spatial and/or temporal scales. Applying molecular methods such as genetic barcoding has been employed to reduce reliance on a shrinking pool of taxonomic expertise (Hebert et al.2003). Although to date this has had only moderate success at matching existing genetic sequences (e.g. Plaisance et al. 2009), repeated and systematic global sampling would build an invaluable knowledge base and develop more precise techniques. Recent improvements in sharing and compiling data, such as the creation of an open access inventory of marine species names in the World Register of Marine Species (WoRMS), has helped to address a multitude of problems with taxonomic inaccuracies (Appeltans et al. 2012, Costello et al. 2013). Collaborative international initiatives will be vital to expand our knowledge of marine invertebrate species, enhance taxonomic accuracy, identify biodiversity hotspots, and reveal important ecological insights. Knowing where biodiversity is concentrated, flourishing, maintaining or declining will help target hotspots for conservation focus. With climate change occurring rapidly and half of the world's coral reefs already highly impacted by human activities (Halpern et al. 2008), it may be more prudent to conserve hotspots of diversity that are also under threat (Hughes et al. 2014), whether on the spatial scale of a region, a reef, or a micro-habitat, rather than assessing the extinction risk for individual species. This thesis clearly demonstrates that two families of coral are hotspots for coral reef diversity, dead or alive, and their associated obligate species are not likely to persist without them. Regions or reefs with high abundances of these branching corals would be key areas for conservation priority, as their protection would in turn protect the greater proportion of coral reef diversity.

Concluding remarks

This thesis has broadened our understanding of invertebrate diversity on coral reefs by assessing communities intimately associated with compact acroporid and pocilloporid branching corals. It has also demonstrated that many invertebrate species are heavily reliant upon a host coral and that thermal stress and/or host bleaching elicits physiological and behavioural responses that can alter the dynamics and structure of these invertebrate communities, eroding mutualistic relationships and lowering reproductive success, both of which can threaten population persistence. As coral-associated invertebrates are ecologically important to their host corals, engage in a disproportionate number of symbiotic associations and occupy a variety of trophic levels, their loss will likely have large indirect impacts on coral reef ecosystems under global change (Castro 1988, Traill et al. 2010, Stella et al. 2011, Prather et al. 2013). Further investigations into the importance of these communities to the wider ecosystem and their functional roles are required before a true understanding of the threats to coral reef biodiversity due to climate change can be realised. In addition to management actions aimed to preserve and promote coral diversity, maintaining healthy populations of pocilloporid and acroporid corals could help to protect a large proportion of coral reef biodiversity.

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Appendices

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CORAL-ASSOCIATED INVERTEBRATES: DIVERSITY, ECOLOGICAL IMPORTANCE AND VULNERABILITY TO DISTURBANCE

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Abstract The biodiversity of coral reefs is dominated by invertebrates. Many of these invertebrates live in close association with scleractinian corals, relying on corals for food, habitat or settlement cues. Given their strong dependence on corals, it is of great concern that our knowledge of coral-associated invertebrates is so limited, especially in light of severe and ongoing degradation of coral reef habitats and the potential for species extinctions. This review examines the taxonomic extent of coral-associated invertebrates, the levels of dependence on coral hosts, the nature of associations between invertebrates and corals, and the factors that threaten coral-associated invertebrates now and in the future. There are at least 860 invertebrate species that have been described as coral associated, of which 310 are decapod crustaceans. Over half of coral-associated invertebrates appear to have an obligate dependence on live corals. Many exhibit a high degree of preference for one or two coral species, with species in the genera *Pocillopora*, *Acropora* and *Stylophora* commonly preferred. This level of habitat specialization may place coral-associated invertebrates at a great risk of extinction, particularly because preferred coral genera are those most susceptible to coral bleaching and mortality. In turn, many corals are also reliant on the services of particular invertebrates, leading to strong feedbacks between abundance of corals and their associated invertebrates. The loss of even a few preferred coral taxa could lead to a substantial decline in invertebrate biodiversity and have far-reaching effects on coral reef ecosystem function. A full appreciation of the consequences of further coral reef degradation for invertebrate biodiversity awaits a more complete description of the diversity of coral-associated invertebrates, the roles they play in coral reef ecosystems, their contribution to reef resilience and their conservation needs.

Reef sites

Evidence of corallivory by the keyhole limpet *Diodora galeata*

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Discovery of the Corallivorous Polyclad Flatworm, *Amakusaplana acroporae*, on the Great Barrier Reef, Australia – the First Report from the Wild

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Abstract

The role of corallivory is becoming increasingly recognised as an important factor in coral health at a time when coral reefs around the world face a number of other stressors. The polyclad flatworm, *Amakusaplana acroporae*, is a voracious predator of Indo-Pacific acroporid corals in captivity, and its inadvertent introduction into aquaria has lead to the death of entire coral colonies. While this flatworm has been a pest to the coral aquaculture community for over a decade, it has only been found in aquaria and has never been described from the wild. Understanding its biology and ecology in its natural environment is crucial for identifying viable biological controls for more successful rearing of *Acropora* colonies in aquaria, and for our understanding of what biotic interactions are important to coral growth and fitness on reefs. Using morphological, histological and molecular techniques we determine that a polyclad found on *Acropora valida* from Lizard Island, Australia is *A. acroporae*. The presence of extracellular *Symbiodinium* in the gut and parenchyma and spirocysts in the gut indicates that it is a corallivore in the wild. The examination of a size-range of individuals shows maturation of the sexual apparatus and increases in the number of eyes with increased body length. Conservative estimates of abundance show that *A. acroporae* occurred on 7 of the 10 coral colonies collected, with an average of 2.6±0.65 (mean ±SE) animals per colony. This represents the first report of *A. acroporae* in the wild, and sets the stage for future studies of *A. acroporae* ecology and life history in its natural habitat.

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Introduction

The role of corallivory on coral reefs is becoming increasingly important to coral reef ecology given the number of other stressors coral reefs worldwide currently face [1]. Invertebrates are the majority of corallivores, outnumbering their fish counterparts nearly 3 to 1 [2,3]. However, most invertebrate species have long been overlooked due to their small size and cryptic nature [4]. Corallivorous invertebrates may play an important role in coral health, inflicting minor or lethal damage on their coral hosts, which may subsequently have deleterious effects on coral growth and fitness [1]. They have also been implicated in transmitting or increasing vulnerability to coral disease [5], which indirectly contributes to coral loss or shifts in community composition. As scleractinian corals are the major reef builders, more attention is required to identify their predators and determine the roles they might play in maintaining or conserving coral reef ecosystems.

Two species of polyclad flatworms are known to prey on scleractinian corals [6,7], yet very little is known about their impacts on coral reefs. As they are small and difficult to detect due to their excellent camouflage against the coral host, they may have been overlooked thus far in most studies of coral-associated animals. One such cryptic polyclad, the *Acropora*-eating flatworm (commonly known as the AEFW), was recently identified and classified as *Amakusaplana acroporae* Rawlinson et al., 2011 [7]. Known only from aquaria as a notorious pest of *Acropora* coral, this species has never been found in the wild. In fact, the taxonomic assignment was based on multiple specimens collected from two aquaria in the United States. Although most small animals that live and feed on corals have negligible, if any, ill effects on the coral host [8], infestations of *A. acroporae* on acroporids in captivity can result in rapid and complete colony death [9]. *A. acroporae* is a destructive predator of at least nine aquarium-reared Indo-Pacific acroporids (*Acropora valida, A. pulchra, A. millepora, A. tortuosa, A. nana, A. tenuis, A. formosa, A. echinata and A. yongei*), individuals lay multiple egg batches on an *Acropora* host and the hatchlings have a low dispersal capability [7]. These life history characteristics, combined with high prey specificity to *Acropora*, lend this species the potential to be a significant corallivore of *Acropora* corals.

Corallivory on *Acropora* corals is of particular interest to conservation management as *Acropora* is one of the most ecologically important coral genera to coral reefs worldwide. It is the largest extant coral genus, occurring in all tropical oceans as the dominant reef building coral [10]. Acroporids are a source of critical habitat and food for an immense diversity (~150 species) of coral-associated animals [3,11,12]. They are extremely abundant and fast-growing branching corals yet are among the most susceptible corals to bleaching [13] and disease [14]. Furthermore, many corallivores actively select species of *Acropora* as their preferred prey [1,2], such as the crown-of-thorns sea star, *Acanthaster planci* [15] and the gastropod *Drupella conus* [16]. Acroporids are also commercially important, being among the top three genera collected for the aquarium trade [17]. Thus acroporids are often the focus of conservation efforts, such as reef restoration [18], and an understanding of what biotic and abiotic interactions affect the growth, survival and distribution of acroporid corals is critical to their effective conservation.

Given *Amakusaplana acroporae*'s preference for Indo-Pacific *Acropora* species it is assumed that the worm is endemic to that region. Its cryptic coloration and relatively small size would make it difficult to detect *in situ,* hence its easy introduction into aquaria as *Acropora* epifauna. Locating *A. acroporae* in its natural environment would permit further study of its biology and ecological interactions, and this, in turn, could lead to the discovery of effective biological controls for this corallivore in captivity. This study aimed to determine whether an as-yet unidentified polyclad flatworm found on *Acropora valida* colonies from Lizard Island, Australia, was *Amakusaplana acroporae.*

Materials and Methods

Animal Collection and Fixation

Animals were collected from Lizard Island, in the northern Great Barrier Reef, Australia (Fig. 1a) (under the Great Barrier Reef Marine Park Authority Permit: G09/32695.1). Sampling was conducted in November 2011, with average water temperatures ranging from 28.5–29.5°C. Ten colonies (ca. 20 cm diameter) of *Acropora valida* were collected at random from a shallow reef habitat (2–4 m depth) within the Lizard Island lagoon (Fig. 1b) (14°41′13.04 S, 145°27′20.06 E). All corals appeared to be in good health and did not show any signs of tissue damage. Coral colonies were first covered with a plastic bag to ensure animal retention, carefully chiseled off the substrate and transported in fresh seawater to the laboratory. Due to the cryptic nature of the polyclad associates, visual inspection did not yield any animals. Other macrofauna were visually identified and recorded. Corals were held over an empty container and the entire surface area, including all inter-branch space, was washed with high-pressured jets of seawater for approximately one minute. The water in the container was sieved through a 1×1 mm mesh, which was then inverted over a container of fresh seawater. This method proved to be successful at both dislodging the animals and maintaining them alive and in good condition. For histological and whole mount analysis, individuals were fixed on 4% frozen formaldehyde in seawater and left overnight at room temperature. Animals were then rinsed in seawater multiple times before being transferred to 70% ethanol for storage. For molecular analysis, adult specimens were preserved in 95% undenatured ethanol.

Morphological Analysis

Histological and whole mount protocols are described in Rawlinson et al. [7]. For species identification paraffin-embedded histological sections (5 μM) were stained following a Masson's trichrome protocol. The presence and distribution of *Symbiodinium* in the worm was confirmed by observing their autofluorescence with a Zeiss Axioscope fluorescent compound microscope on sections stained with DAPI (4′, 6-Diamidino-2-phenylindole, Sigma). Five individuals were sectioned in the transverse plane, three individuals were sectioned in the sagittal plane, and two individuals mounted as whole mounts. All material, including whole specimens, has been deposited in the Museum of Tropical Queensland.

Molecular Analysis

Genomic DNA was extracted from one adult specimen (G20079) and the D1–D2 region of the 28 S rDNA gene was amplified using a novel forward (3′–5′) and reverse (3′–5′) primer pair designed for *Amakusaplana acroporae* based on conserved regions within aligned polyclad 28S rDNA sequences [7]. PCR was carried out using the following cycle temperatures/times: 4 min at 94°C; 45 cycles of 20 s at 94°C, 20 s at 52.5°C and 90 s at 72°C; 8 min at 72°C for a final extension. PCR was electrophoresed in a 1% agarose gel, and the product was excised and purified using the Qiagen MinElute Gel Extraction kit. The amplified fragment was cloned and sequenced in both directions using the pGem-T easy vector system (Promega). The 28 S rDNA D1-D2 region of G20079 (Genbank accession number JQ791553) was aligned using the ClustalW algorithm in MacVector with the polyclad sequences used in Rawlinson et al [7] (outgroup *Macrostomum lignano*). Phylogenetic trees were constructed using Bayesian Inference (BI) in MrBayes 3.2 [19]. The analysis was performed for 2,000,000 generations with a sampling frequency of 100. Node support was determined by posterior probabilities.

Results

Morphological Analysis

Analysis of the gross morphology was conducted on eighteen individuals, eight of which were sectioned for histological analysis of anatomy. We identified this animal to the family Prosthiostomidae (sub-order Cotylea) based on the following characters: absence of tentacles, a mouth at the anterior end of pharyngeal chamber, a tubular pharynx, a large muscular seminal vesicle adjacent to a pair of thick-walled accessory vesicles, a penis papilla and stylet enclosed in a penis pocket, a short vagina that is looped anteriorly and uterine canals arranged in an H-shaped figure [20]. Diagnosis to the genus *Amakusaplana* was established by the lack of a ventral sucker, a slight median depression in the anterior margin and irregularly scattered eyes in the anterior region of the body [21]. We determined that this animal is *Amakusaplana acroporae* (and not *Amakusaplana ohshimai*, the type and only other species of *Amakusaplana*) based on eye arrangement (distinct clusters of marginal and cerebral eyes in *A. acroporae*) and eye number (less than half the number of eyes in A. acroporae compared with *A. ohshimai*) and features of the reproductive systems (a bulbous female atrium and distinct egg chamber in *A. acroporae*) (see below and [7]).

Individuals of *Amakusaplana acroporae* collected from Lizard Island ranged in size from 3–6 mm in length and 1.5–3.5 mm in width when fixed. Examination of gross morphology and histological sections of animals with different body lengths revealed two trends in characters of taxonomic importance. Firstly, the number of eyes increases with body length. The two clusters of ventral marginal eyes increased from 5 eyes per cluster in a 3.2 mm long animal (Fig. 2a) to 10 eyes per cluster in a 5 mm long animal (Fig. 2b). The number of cerebral eyes clustered around the brain also increased from 27 to 35 in these two individuals (Fig. 2a & b). Secondly, the male reproductive system matures before the female reproductive system. The 4 individuals examined with a body length <4 mm had mature male but immature female reproductive systems. The male

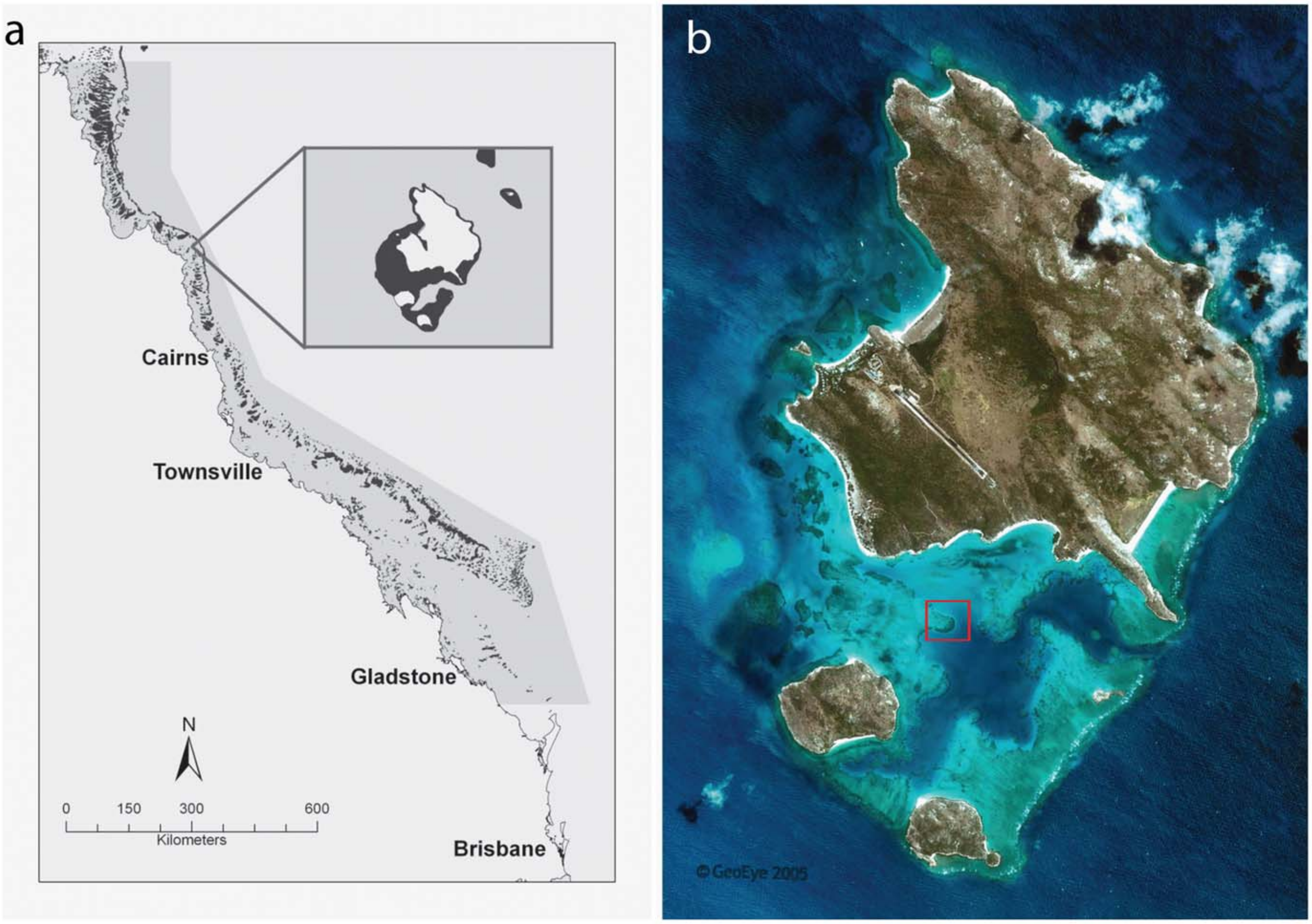

Figure 1. The collection site of *Amakusaplana acroporae.* (a) Map of the Northern Great Barrier Reef, Australia with inset of Lizard Island. (b) Photo of Lizard Island with collection site (red square) of *Amakusaplana acroporae* from its host coral *Acropora valida*. Photo credit ''GeoEye satellite image''.
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reproductive system consists of a penis armed with long sclerotized stylet (Fig. 2c), which sits in the penis sheath and protrudes into the male atrium. The penis is connected via the ejaculatory duct to two accessory vesicles and a large seminal vesicle, each bound by a muscular sheath (Fig. 2c). Prostatic glands empty into the penis sheath and prostatic secretions and sperm are visible in the male atrium (Fig. 2c). While the female reproductive system in these individuals was immature, a female gonopore was present (Fig. 2d) but no eggs were visible in the uteri (Fig. 2a) and no shell glands were developed. Individuals ≥4 mm in length had mature male and female reproductive systems. Eggs were present in the ovaries and the paired uteri (Fig. 2b), well-developed shell glands surrounded the distended female atrium and distinct oval egg chamber (Fig. 2f), and sperm were present in the vas deferens and seminal vesicle. These developments in reproductive maturity with increased body length indicate that this animal is a sequential and then a simultaneous hermaphrodite.

Amakusaplana acroporae from Lizard Island differed from individuals collected from aquaria in two morphological traits. Firstly, in the number of marginal eyes clustered on each side of the anterior margin depression. Mature individuals from Lizard Island have 9.83±0.98 (mean ±SD; n = 6) marginal eyes per cluster instead of 2–3 in mature animals from aquaria. Secondly, when examined in cross section the tubular pharynx of *A. acroporae* is cleft [7]. This cleft appears only at the distal tip of the pharynx in the four animals examined in cross section from Lizard Island (Fig. 2g), whereas it extends further towards the gut in the specimen examined from captivity.

Molecular Analysis

The Bayesian analysis of 28S rDNA sequence data (Fig. 3) resolves an individual from Lizard Island (G20079) to within the well supported clade (BI: 100%) of *Amakusaplana acroporae* collected from two different aquaria in the USA (Virginia and New York). This analysis is consistent with the morphology-based assignment of this individual to *A. acroporae*.

Rates of Occurrence and Evidence of Corallivory

Amakusaplana acroporae occurred on 7 of the 10 coral colonies collected. Between 1 and 5 animals were found on each colony, with an average of 2.6±0.65 (mean ±SE) animals per colony. All eight individuals of *A. acroporae* that were examined histologically had *Symbiodinium* in the gut and parenchyma distributed throughout the body (Fig. 2h & i). The *Symbiodinium* were not observed intracellularly and their autofluorescence distinguished them from polyclad cells (Fig. 2h). Large (~24 μm), unfired spirocysts were particularly abundant in the main intestinal trunk, less abundant in the intestinal branches and absent in the dorsal epidermis.

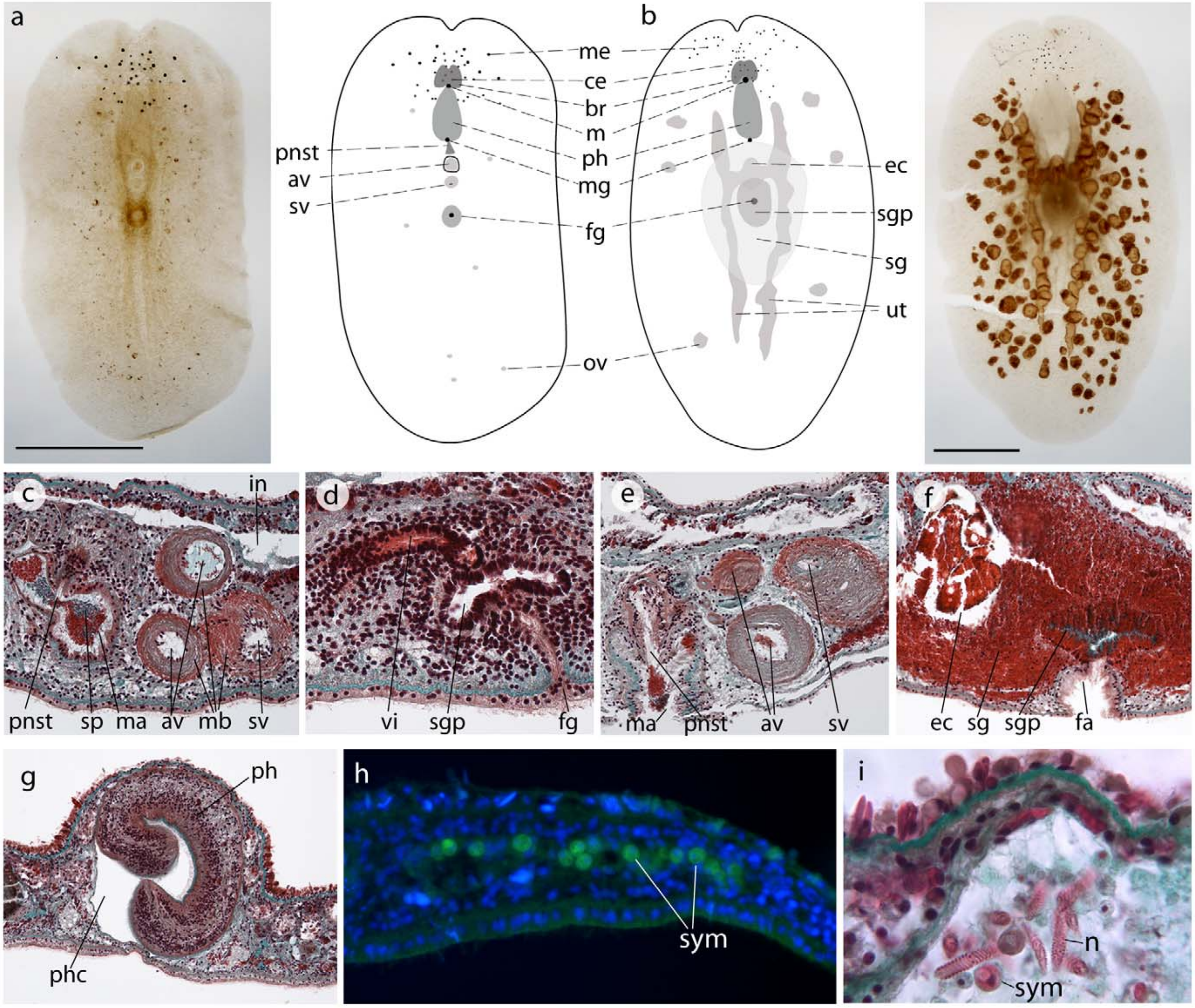

Figure 2. Anatomy and morphology of *Amakusaplana acroporae* from Lizard Island, Australia. Wholemounts and schematic representations of (a) a 3.2 mm and (b) a 5.0 mm long *A. acroporae* (scale = 1 mm) showing gross morphology and development of the female reproductive structures. Individuals <4 mm in length possess (c) a mature male reproductive system, but (d) an immature female system. Individuals >4 mm in length possess mature (e) male and (f) female reproductive systems. (g) A cross section through the distal portion of the pharynx reveals its cleft morphology. *Symbiodinium* are present in the gut and parenchyma of *A. acroporae*, and may be observed (h) by autofluorescence and (i) light microscopy, spirocysts are also visible in the gut lumen. *av* accessory vesicle, *br* brain, *ce* cerebral eye, *ec* egg chamber, *fa* female atrium, *fg* female gonopore, *in* intestine, *m* mouth, *ma* male atrium, *mb* muscle bulb, *me* marginal eye, *mg* male gonopore, *ov* ovary, *ph* pharynx, *phc* pharyngeal cavity, *pnst* penis stylet, *sc* spirocysts, *sg* shell glands, *sgp* shell gland pouch, *sp* sperm, *sv* seminal vesicle, *sym Symbiodinium*, *ut* uteri, *vi vagina interna*.
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Other amorphous material in the gut may have consisted of coral mucus and tissue.

Other Macrofauna Present on the *Acropora Valida* Colonies

Each of the ten colonies contained other macrofauna, including a breeding pair of coral crabs (identified as *Tetralia nigrolineata*), 2 gobies (*Gobiodon brochus*) and 2 palaemonid shrimp (*Coralliocaris graminea*).

Discussion

This study identifies a polyclad flatworm found on *Acropora valida* colonies around Lizard Island as *Amakusaplana acroporae* and represents the first report of this animal in the wild. Evidence that *A. acroporae* is a corallivore in its natural habitat, as it is in aquaria, is supported by the presence of *Symbiodinium* and cnidarian spirocysts in the gut and parenchyma. In addition, the extracellular distribution of *Symbiodinium* implies that they were ingested and are not symbionts living within *A. acroporae*. Discovering *A. acroporae* in its natural environment and documenting a method of extracting the animals from their coral host alive will aid further research into the abundance, distribution and ecology of this corallivore.

Polyclad flatworms are morphologically quite homogeneous and over the past two centuries species descriptions and classifications have been based on a limited number of taxonomic characters [20,22,23]. These characters, used at all taxonomic

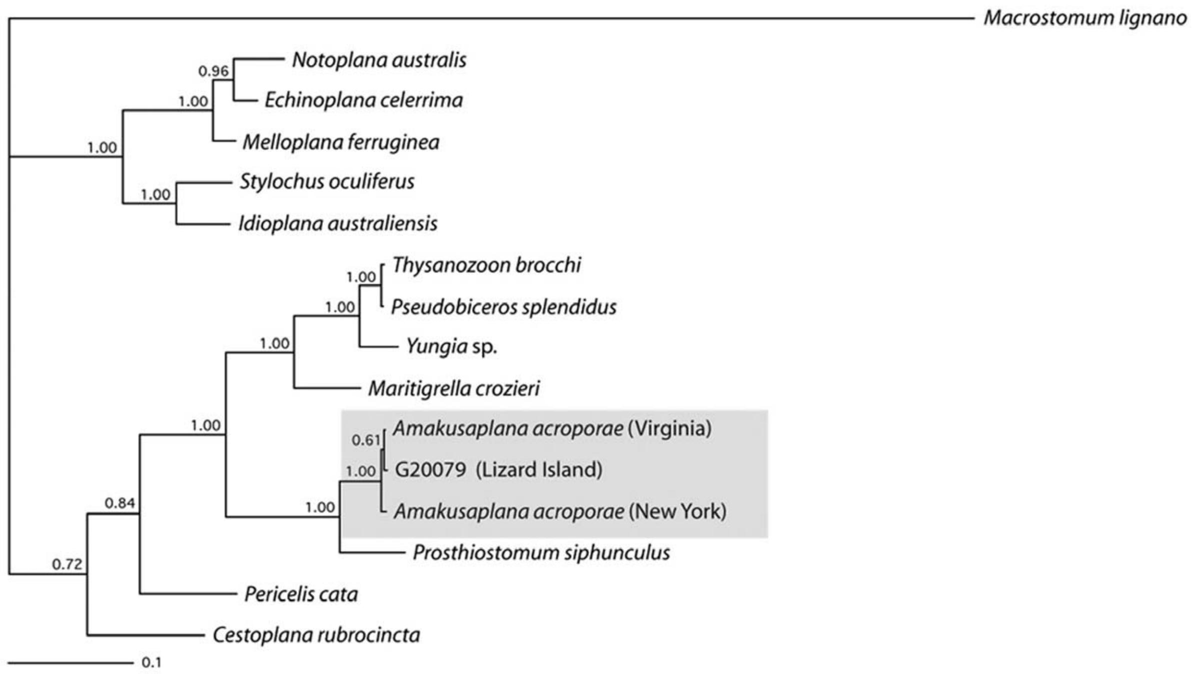

Figure 3. Consensus phylogenetic tree resulting from the Bayesian analysis of 28S rDNA sequence data. Clade support indicated by Bayesian posterior probabilities. The Lizard Island polyclad (G20079) falls out within a well–supported clade of *Amakusaplana acroporae* from captivity.
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levels, are described from the animal's gross morphology and anatomy; for example the presence of a ventral sucker, the type and position of the pharynx, the presence of tentacles, details of the reproductive system and patterns of eyes. However, these last two sources of taxonomic characters, which are important for species level identification within the Prosthiostomidae, demonstrate plasticity during maturation as observed in this study and Kato [24] (in *Prosthiostomum (L.) purum)*. Therefore, without access to *Amakusaplana ohshimai* material for comparative morphological and molecular analysis we cannot rule out the possibility that *Amakusaplana acroporae* is synonymous with *A. ohshimai*, given that the characters that distinguish the two species (eye arrangement and number, morphometrics of the male and female reproductive systems and the presence of an egg chamber) vary with body length and maturation. This highlights the need to include in future species descriptions changes in morphological characters during development, and within and between populations, where possible. Nevertheless, from our morphological and molecular diagnoses we are confident that the polyclads collected from Lizard Island are the same species as that described from aquaria [7].

The presence of *Symbiodinium* and cnidarian spirocysts in the gut and parenchyma provides evidence that *Amakusaplana acroporae* is a corallivore in its natural habitat. No other prey items were observed in the gut of *A. acroporae* indicating that perhaps they are obligate corallivores (as has been demonstrated in the only other known scleractinian-eating polyclad *Prosthiostomum (Prosthiostomum) montiporae* [25]). As spirocyst morphology is fairly homogeneous within the Anthozoa [26] more direct evidence that *A. acropora* is feeding on *A. valida* would involve comparisons of molecular fingerprints of coral tissue in the gut contents with tissue from the coral host. Unlike some polyclad species that sequester nematocysts from their cnidarian prey in the lateral and posterior margins of their dorsal epidermis [27–29], there was no evidence of spirocysts being sequestered in *A. acroporae* in this study. While some corallivores have morphological adaptations that provide them with protections from coral nematocysts [30], how *A. acroporae* overcomes *Acropora* nematocysts is unknown.

As *Amakusaplana acroporae* is quite small, cryptic and possesses excellent camouflage against its acroporid coral host, this species is easy to overlook and thus far, their corallivory in the wild has probably been attributed to another species or even coral disease [30]. Moreover, until now this species has been unknown to marine ecologists, hampering any potential to learn about its role in coral health. Although Sweet et al. [31] reported that previous studies had found *A. acroporae* (or AEFW, as it would have been known at the time) in Indonesia and the Red Sea (citing [32–34]), Haapkylä et al. [33] actually refer to the acoel worm from the genus *Waminoa* which is a known coral-associate [35], and the other two studies do not mention flatworms. Although it is highly likely that the distribution of *A. acroporae* mirrors that of its *Acropora* species prey, and it could therefore be found in Indonesia and the Red Sea, visual surveying methods alone would probably not be sufficient to see *A. acroporae in situ* (Stella pers obs), although bite marks in the coral tissue and egg capsules on the bare coral skeleton might be visible on a heavily infested colony. As *A. acroporae* has been found in association with other Indo-Pacific *Acropora* species in aquaria (*A. pulchra, A. millepora, A. tortuosa, A. nana, A. tenuis, A. formosa, A. echinata and A. yongei* [7]), it is possible these species would be suitable natural hosts as well and might serve as a logical basis for learning more about these animals under natural conditions.

Gaining knowledge of the natural rates of occurrence and ecology of these polyclad worms will be vital to understanding its ecological role on coral reefs. No obvious tissue damage was evident on the *Acropora valida* colonies sampled in this study. That may, in part, be due to the small abundances (averaging less than three worms per colony) or the presence of natural predators within the coral colony. The estimates of abundance per colony in this study are somewhat underrepresented given that our sample size was small and the method was biased towards individuals greater than 1 mm^2. *Amakusaplana acroporae* hatchling size is 250–300 μm [7] and these juvenile stages would have escaped collection. In aquaria some wrasse species have been observed to eat dislodged adult worms in the water column [7,9]. Embryonic and hatchling life history stages may be vulnerable to a different set of predators, such as gastropods and decapods, which are highly diverse on acroporid corals [12]. Coral crabs, belonging to the genus *Tetralia,* have high occurrence rates on tightly branching acroporids [11] and are known to provide the coral host with cleaning services [36]. It is possible that these crabs may eat the adult worms and egg capsules, thus controlling the worms' numbers. It is also possible that *A. acroporae* only becomes a serious pest in disturbed coral systems and aquarium environments, as is the case with *P. (P.) montiporae* [9,25]. Further observations of *A. acroporae* in the field are needed to determine rates of coral tissue consumption (and subsequent colony mortality), identify its natural predators and quantify spatio-temporal patterns in its abundance.

Scleractinian corals are the most functionally important corals to reef processes, thus it is essential to understand what factors affect their growth and survival. Corallivores represent a biotic stressor that can detrimentally affect coral growth and fitness. In order to effectively manage conservation efforts of *Acropora* on coral reefs and to successfully rear colonies in aquaria, it is critically important to understand what biotic interactions are important to coral growth and fitness. This discovery of *Amakusaplana acroporae* in the wild and at Lizard Island will facilitate easy access to populations of this coral symbiont, enabling investigation of *A. acroporae* ecology, biology and life history in its natural habitat.

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Author Contributions

Conceived and designed the experiments: JSS KAR. Performed the experiments: JSS KAR. Analyzed the data: JSS KAR. Contributed reagents/materials/analysis tools: JSS KAR. Wrote the paper: JSS KAR.

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