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The energetic costs of chronic fish predation on reef-building corals

Thesis submitted by

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For the degree of Doctor of Philosophy in Marine Biology

ARC Centre of Excellence for Coral Reef Studies and the School of Marine and Tropical Biology

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Statement on the contribution of others

This thesis includes some collaborative work with Dr Morgan Pratchett, Dr Shaun Wilson, Professor Geoff Jones and Ms Rebecca Lawton. While undertaking these collaborations, I was responsible for the project design, data collection, data analysis and interpretation. My collaborators provided intellectual guidance, financial support, assistance with field work, technical instruction and editorial assistance. The chapters in this thesis have been presented as published, with exceptions for edits, updated references and standardised formatting.

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Abstract

Interactions between predators and prey organisms are of fundamental importance to ecological communities. While the ecological impacts that grazing predators can have in terrestrial and temperate marine systems are well established, the importance of coral grazers on tropical reefs has often been overlooked. Fishes that feed from live corals (corallivores) are a conspicuous component of healthy coral reef environments. Published records document that at least 128 corallivorous fish species from 11 different families feed at least in part upon scleractinian corals, with 69 of these belonging to the family Chaetodontidae. One third of all coral-feeding fishes feed almost entirely upon corals, with more than 80% of their diet based on live coral tissue. This thesis aims to assess the energetic cost and relative importance that predation from polyp-feeding fishes has on reef-building corals by: 1) determining how the frequency and intensity of predation is dispersed both among and within common species of reef-building corals, 2) quantifying the amount of coral tissue consumed by corallivorous butterflyfishes and determining the proportion of available coral tissue biomass and potential productivity of tabular acroporid corals this consumption represents, and 3) assessing the energetic cost that chronic tissue consumption by juvenile and adult corallivores has on the growth and condition of reef-building corals.

To assess how corallivore predation is dispersed both among and within coral species I used an observational study to quantify grazing rates on four common reef corals (*Acropora hyacinthus*, *Acropora millepora*, *Pocillopora damicornis*, and massive *Porites*). I also assessed the variation in predation intensity within *A. hyacinthus* and *A. millepora* by standardising grazing rates by colony surface area. Rates of grazing on individual colonies were highest (16.75 (± 0.30 SE) bites.20 minutes^{-1}) for *A. hyacinthus*. Within coral species, grazing rates showed a linear increase with increasing size of the colony, however the intensity of predation showed a negative relationship with increasing colony size. Predation intensity was highest for small to medium sized colonies with a peak intensity of 1.13 (± 0.17) bites 100cm^{-2}.20minutes^{-1}.colony^{-1} for *A. hyacinthus* colonies and 0.56 (± 0.09) bites 100cm^{-2}.20 minutes^{-1}.colony^{-1} for *A. millepora* colonies (200-600cm^{2}). In contrast, predation intensity was lowest for both very

small and very large colonies, with very small colonies (<200cm^2) rarely consumed by corallivorous fishes.

To assess the magnitude of coral tissue that is removed from the reef by corallivorous fishes I undertook aquarium based feeding trials to quantify the bite size of four prominent species of coral-feeding butterflyfishes. Sub-adult butterflyfishes (60-70mm TL, 6-11g wet weight) remove between 0.6 and 0.9g of live coral tissue per day, while larger adults (>110mm TL, 40-50g wet weight) remove between 1.5 and 3g of coral tissue each day. These individual consumption rates were extrpolated based on population sizes of corallivores at three exposed reef crest habitats at Lizard Island, Great Barrier Reef; these fishes consume between 14.6g (± 2.0) and 27.4g (± 1.5) 200m^{-2}.day^{-1} of coral tissue. When standardised to the biomass of butterflyfishes present, a combined reef wide removal rate of 4.2g (± 1.2) of coral tissue is consumed per 200m^{-2}.kg^{-1} of coral-feeding butterflyfishes. Feeding observations identified that between 61-68% of this consumption is directed towards tabular acroporid corals on exposed reef crest habitats at Lizard Island. This selective feeding resulted in an annual consumption of between 8.9-13.5% of the total available tissue biomass and between 52-79% of the annual productivity of these tabular acroporid corals.

The effects of this predation, however, were mixed. Juvenile butterflyfishes were found to settle directly into live coral and feed entirely upon a single colony for at least the first 6-8 weeks post settlement. This highly concentrated predation had negative effects on coral condition. In a field experiment coral tissue biomass declined by 26.7%, 44.5% and 53.4% in low, medium and high predation intensity treatments. Total lipid content of host corals declined by 29-38% across all treatments including controls and was not related to predation intensity; rather, this decline coincided with the mass spawning of corals and the loss of lipid-rich eggs. In contrast, the reef wide effect of predation by adult corallivores was less clear. Whole colony growth rates, tissue mass per unit area, total lipid content and fecundity were all higher for corals on experimental reefs with reduced predation, however these differences were small and only significant for the total lipid content of *Acropora hyacinthus*, which was 9.3% higher (52.6% ± 0.8 vs 48.1% ± 0.7) on reefs with reduced predation relative to controls. This result indicates that on healthy reef systems, where photosynthesis and energy acquisition is not impaired, corals have a high tolerance to the chronic damage caused by polyp-feeding fishes and the energy used to regenerate lost tissue does not result in an energy trade-off with other life history functions. However, on reefs already stressed by other factors where energy acquisition is impaired (e.g. during a coral bleaching event), chronic predation is more significant and can affect the survivorship of highly preferred prey corals.

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Chapter 1: General Introduction

Coral reefs are amongst the most diverse and unique ecosystems on the planet (Connell 1978, Veron 2000). Although corals can grow in temperate systems, it is only in the tropical zone extending roughly between 30°N and 30°S where conditions are conducive to create the iconic and highly productive ecosystems known as coral reefs (Wilkinson 1999, Kleypas et al. 1999). Numerous benthic organisms have colonised reef surfaces and contribute to their three dimensional structure including calcareous, turf and macroalgae, sponges and encrusting invertebrates, alcyonarian (soft) and scleractinian (hard) corals, among others. However, it is scleractinian corals which are singularly the most important component of coral reef systems. Scleractinian corals are vital to reef energetics, acting as a major trap of light energy and contributing substantially to the high gross primary productivity of coral reefs (Wild et al. 2004, 2005). Actual live coral tissue represents only a thin surface film, rarely more than a few millimeters thick. But through a relatively unique symbiosis with autotrophic dinoflagellates of the genus symbiodinum, these zooxanthelae symbionts provide the coral host with a constant source of energy in exchange for shelter, nutrients and a supply of carbon dioxide (Stat et al. 2008). This relationship has created an efficient system of nutrient re-cycling and has enabled the creation of modern reef systems which encompass an area greater than 255,000km^2 worldwide (Smith 1978, Spalding and Grenfell 1997, Wilkinson 1999).

In general, as the total cover and diversity of scleractinian corals increases, a corresponding increase in the diversity and abundance of the coral reef fish community occurs (Carpenter et al. 1982, Munday et al. 1997, 2008, Pratchett et al. 2011a). This increase is largely a result of the important ecosystem roles corals play in providing the predominant structural habitat that is of critical importance to reef-associated species (Jones et al. 2004, Graham et al. 2006, 2009, Wilson et al. 2006, Munday et al. 2008, Pratchett et al. 2008b, 2011a). At least 10% of fishes are directly reliant upon live corals for food and/or shelter (Pratchett et al. 2008b), and at least 40-65% of fish species utilise live corals during settlement when they transition from their pelagic larval stage to their benthic juvenile and adult life stages (e.g. Jones 2004, Holbrook et al. 2006, Feary et al. 2007a, Garpe and Öhman 2007, Wilson et al. 2008, 2010, Bonin et al. 2009). Moreover, the topographic complexity that live coral provides helps to mediate important biological interactions such as competition (Munday 2001, Holbrook and Schmitt 2002) and predation (Caley and St John 1996, Beukers and Jones 1997, Holbrook and Schmitt 2002, 2003, Almany 2004). The critical importance of live corals has recently been highlighted following the catastrophic loss of corals on many reef systems after severe coral reef bleaching events (reviewed by Wilson et al. 2006, Munday et al. 2008, Pratchett et al. 2007, 2008a). Extensive coral mortality and the subsequent reduction in topographic complexity has resulted in major population declines in up to 75% of coral reef fish species (Jones et al. 2004, Graham et al. 2006). These declines incorporate the full range of coral reef fishes and highlight the reliance upon corals by many reef fishes; even species which are not directly linked to corals as adults show large population declines following major disturbance events (Sebens 1994, Jones et al. 2004, Sano 2004, Wilson et al. 2006, Cheal et al. 2008, Graham et al. 2007, 2009, Pratchett et al. 2011a).

Coral reefs have always been subject to ongoing natural stresses and disturbances from both physical and biological sources (reviewed by Wilkinson 1999). For instance, competition for space is an important mechanism affecting the community structure of benthic assemblages, whereby many slow growing corals utilise specialised tentacles (e.g. sweeper tentacles, mesenterial filaments) to directly kill areas of neighboring corals (Lang 1973, Chornesky 1983, Lang and Chornesky 1990). Likewise, fast growing corals can overtop and shade out slower growing competitors (Stimson 1985, Baird and Hughes 2000, Connolly and Muko 2003). Storms and cyclones also play a role in shaping coral communities, where frequent storm damage can have a disproportionate effect on the relative cover of fast growing weedy coral species (e.g. branching *Acropora* spp.) (Harmelin-Vivien 1994, Connell et al. 1997, 2004, Lirman et al. 2001). Similarly the influx of fresh water from extensive monsoonal rain and subsequent flooding can lead to salinity shock-related mortality (Goreau, 1964, Van Woesik et al. 1995, Kerswell and Jones 2003). Corals are also subject to predation, sometimes on a reef-wide scale (Glynn 1990, Carpenter 1997). For example outbreaks of crown of thorns starfish (*Acanthaster plancii*) can rapidly deplete the cover of live corals and leave reefs in a state of low coral cover for several years (e.g. Moran et al. 1988, Carpenter

1997, Baine 2006, Pratchett et al. 2009). Corals have evolved under a history of relatively small scale disturbances of varying intensities. These disturbances can all be considered part of the natural dynamics of coral reef systems and contribute to natural cycles of growth and mortality of coral reefs. They also help to create the abundance and distribution patterns observed on coral reef systems (Connell 1978, Petraitis et al. 1989, Karlson and Hurd 1993, Brown 1997a, Nyström et al. 2000, Connell et al. 2004).

More recently, coral reefs are experiencing intense pressure in the form of anthropogenic stressors (Hoegh-Guldberg et al. 1999, 2007, Nyström et al. 2000). In the latest review on the status of the world's reefs, Wilkinson (2008) estimates that 19% of the world's coral reefs have been effectively lost, with these reefs suffering reductions in live coral cover of more than 90%. These reefs no longer function as productive ecosystems and have poor prospects for recovery. A further 35% of the world's reefs are expected to show similar declines in live coral by 2050. The most significant factor influencing the degradation of these reefs and the declines in live coral are anthropogenic pressures, with the reefs nearest to large human population centers generally exhibiting the most pronounced degradation (Wilkinson 2008). The direct causes of this reef degradation are variable but include pollution, eutrophication, sedimentation, overfishing and/or destructive fishing practices, among others (Davis 1977, Pastorok and Bilyard 1985, Brown 1997a, Jackson et al. 2001, Hughes et al. 2005, Dubinsky and Stambler 2006, Wilkinson 2008). These types of direct anthropogenic stressors are important, but generally impact reefs at relatively small, local scales (Brown 1997a, Done 1999, Wilkinson 1999). More concerning is the compounding effect of the much larger and more significant indirect anthropogenic stressors of global climate change, where changes in greenhouse gas concentrations in the atmosphere result in increased sea water temperatures and reduced alkalinity of the world's oceans (Wilkinson 1999, Nyström et al. 2000, Hughes et al. 2003, 2010, Hoegh-Guldberg et al. 2007). When sea surface temperatures rise above a critical threshold (typically 1-3°C above the long term summer average) the coral-zooxanthellae symbiosis breaks down and results in coral bleaching (Glynn 1993, 1996, Brown 1997b, Birkelmans and Willis 1999, Hoegh-Guldberg et al. 1999, Donner et al. 2005). During a bleaching event corals are unable to photosynthesize and are entirely reliant upon stored energy reserves to meet their daily metabolic costs, which often leads to high rates of coral mortality on a reef- or region-wide scale (Brown 1997b, Hoegh-Guldberg 1999, Douglas 2003, but see Grottoli et al. 2006). Over the longer term, coral growth rates are expected to decline as the acidified oceans make the energetic cost of calcification more expensive, with the potential scenario where erosion begins to overtake calcification rates (Kleypas et al. 1999, 2006, Kuffner et al. 2008, Anthony et al. 2008, Doney et al. 2009). The most alarming effect of global climate change is the much larger spatial scale of direct effects relative to previous man-made effects (e.g. pollution, sedimentation, etc.) (Glynn 1993, Wilkinson 1999, Hoegh-Guldberg 1999, 2007, Nyström et al. 2000, Donner et al. 2005, Hughes et al. 2010). These direct effects (e.g. mass coral bleaching events) are already a major contributor to the regional-scale degradation of many reef systems around the world (Glynn 1996, Greenstien et al. 1998, Gardner et al. 2003, Hughes et al. 2003, Bellwood et al. 2004, Bruno and Selig 2007, Graham et al. 2008, Carpenter et al. 2008, Alvarez-Filip et al. 2009).

There is currently an active effort to attribute coral mortality to various sources (Osbourne et al. 2011, Sweatman et al. 2011, Hughes et al. 2011), although many of these studies only consider the acute effects of periodic disturbances (e.g. cyclones, diseases, coral bleaching, outbreaks of crown-of-thorns starfish, etc.). However, attributing the direct cause of mortality during annual snapshot surveys is often difficult, especially on coral reefs where several factors can all interact to create the observed patterns of mortality (Hughes and Connell 1999). Further, these causes of mortality need to be considered in the context of other natural long term stressors which result in tissue loss (e.g. predation), whose direct effects are rarely apparent but are likely to be an important component of the background level of stress operating on coral reef systems. An important question for the future health of coral reef systems will be how the subtle effects of natural chronic stressors will interact with and potentially be compounded by the more recent, superimposed impacts from global climate change (e.g. Glynn 1996, Nyström et al. 2000, Hughes et al. 2003, Baker et al. 2008). Preliminary information suggests that following a disturbance event (e.g. coral bleaching) which results in coral mortality, the intensity of predation upon the remaining corals increases and can result in elevated levels of coral mortality (e.g. Bellwood et al. 2006, Cole et al. 2009, Gochfeld 2010). However, before we can begin to properly assess the interaction between anthropogenic and natural stressors, we first need a thorough understanding of the effects that chronic predation currently have on healthy reef systems.

1.1 Corallivores

Numerous coral reef organisms (including many species of fish and invertebrates) feed on corals, but unlike the crown-of-thorns starfish, most tend to remove only a small proportion of the living tissue from any given colony (Glynn 1988). Most fishes take only a few bites at a time from any given colony before moving on to the next colony within their home range, thus they are referred to throughout this thesis as “chronic” or “grazing” predators. These grazing predators rarely cause whole-colony mortality, but the continual removal of tissue by predators is expected to represent a substantial energetic cost. Few trophic studies of coral reef fish communities ascribe corallivores a significant role in reef processes (e.g. Connell 1973, Hatcher 1988). Previous studies of coral predation have focused mainly on the acute effects of periodically abundant corallivores, such as *Acanthaster planci* and *Drupella* spp., which can have devastating impacts on coral communities over very short time periods (Glynn 1974, Boucher 1986, Glynn and Krupp 1986, Williams 1986, Glynn 1994, Turner 1994, Reyes-Bonilla and Calderon-Aguilera 1999, McClanahan 1997). These invertebrate corallivores are characterized by periodic explosions in population sizes, and during outbreaks the density of *A. planci* can exceed 4-6 individuals per square meter, with each individual starfish capable of consuming 5-6m^2 of live coral annually (Carpenter 1997).

By comparison, the effects of chronic predation by corallivorous fishes are rarely apparent, often delayed and indirect (Glynn 1988). Nevertheless, experimental studies have demonstrated that corallivorous fishes that damage the coral skeleton when feeding can influence the abundance and distribution of corals (Neudecker 1979, Wellington 1982, Cox 1986, Littler et al. 1989, Miller and Hay 1998) and can also modify the outcome of competitive interactions between coral species (Cox 1986). For example, Cox (1986) found that predation by *Chaetodon unimaculatus* reduced the vertical growth rates of its preferred coral prey, *Montipora verrucosa*, and restricted the distribution of this coral to shallow reef tops of patch reefs in Hawaii where the abundance of *C. unimaculatus* was low (Cox 1986). Predation was also found to reverse the competitive hierarchy of the coral community, whereby the competitively inferior *Porites compressa* was capable of overgrowing *M. verrucosa* (Cox 1986). In another study, Neudecker (1979) transplanted colonies of *Pocillopora damicornis* from the reef flat to depths of 15 and 30m and found that within a week corallivores had removed one quarter of the colony wet weight of these corals. However, caged controls grew well at these depths (Neudecker 1977). Likewise, the zonation patterns of *Porites* corals on Belizean barrier reefs are largely caused by predation from the stoplight parrotfish, *Sparisoma viride*. *Porites porites* is naturally found up on the reef flat where parrotfish grazing is low. When *P. porites* was transplanted to the reef crest, rapid and intense predation occurred and entire transplants were consumed within 24 hours. In contrast, caged controls were able to survive and grow well on the reef crest (Miller and Hay 1989, see also Littler et al. 1998).

These studies which have demonstrated a direct effect of corallivory have all focused on fishes which physically damage the coral skeleton when feeding. In contrast, small bodied corallivores (e.g. butterflyfishes, tubelip wrasses, etc.) typically remove individual coral polyps and tissue without harming the underlying corallite. As such, they leave no visible evidence of damage. These polyp-feeders have consequently often been dismissed as largely unimportant to coral reef trophy-dynamics on the assumptions that too few fishes actually feed from live corals and that the amount of coral consumed as a proportion of the total coral available is minimal (Harmelin-Vivien and Bouchon-Navaro 1982, 1983, Hatcher 1988, Hixon 1997). These assumptions were further compounded by relative differences in the structure of the corallivore guild between the Caribbean and Indo-Pacific regions. In the Caribbean, only one species of polyp-feeder butterflyfish occurs (*Chaetodon capistratus*) (Birkeland and Neudecker 1981, Pitts 1991), with large skleletal-feeding scarids being the primary corallivores in this region (Miller and Hay 1998, Rotjan and Lewis 2005, 2006, 2008). In contrast, the Indo-Pacific is dominated by small-bodied corallivores (e.g. butterflyfishes, tubelip wrasses) (Harmelin-Vivien and Bouchon-Navaro 1983, Findley and Findley 1985, Hourigan et al. 1988, Sano 1989, Tricas 1989a, Fowler 1990, Pratchett 2005, Berumen et al. 2005), with the larger skeletal-feeding corallivores generally either occurring in low densities (Glynn et al. 1972, Bellwood and

Choat 1990, Jayewardene et al. 2009, but see Bonaldo et al. 2011) or ranging over much larger distances (e.g. *Bulbometopon muricatum*) (e.g. Bellwood et al. 2003, Hoey and Bellwood 2008). Despite these observed differences between regions, the full range of corallivorous species remains unknown. For example, recent work has identified three genera of labrid corallivores (tubelip wrasses) which are also heavy consumers of hard coral in the Indo-Pacific (Cole et al. 2010). These small bodied corallivores feed continuously throughout the day, with typical densities of these fishes ranging between 12-25 individuals per 200m^2 (Fowler 1990, Berumen et al. 2005, Cole et al. 2010). As such, it is likely that the size of the trophic link, the total amount of coral tissue consumed and subsequently the relative importance of polyp-feeding fishes on Indo-Pacific reefs is much higher than previously assumed.

The majority of previous studies which have looked at the interaction between polyp-feeders and the coral community have focused on answering ecological questions arising from the fishes' perspective (reviewed in chapter 2). These studies have provided a significant amount of information on their feeding rates and behavior (Hiatt and Strasburg 1960, Reese 1977, 1981, Tricas 1985, 1989a, Harmelin-Vivien and Bouchon-Navaro 1983, Harmelin-Vivien 1989, Irons 1989, Sano 1989, Wylie and Paul 1989, Alwany et al. 2003, Pratchett 2005, 2007, Graham 2007, Niedermüller et al. 2009), home range sizes, social organizations and competitive hierarchies (Pitts 1991, Wrathal et al. 1992, Roberts and Ormond 1992, Cox 1994, Zekeria et al. 2002, 2005, Brokovich and Baranes 2005, Pratchett 2005, Berumen and Pratchett 2006a) and the dietary preferences of these fishes (Cox 1994, Alwany 2003, Pratchett 2005, Berumen et al. 2005, Pratchett 2007 Berumen and Pratchett 2008, Lawton et al. *In press* a, b). For example, most species of polyp-feeders show highly convergent patterns of prey use and preferentially consume *Acropora hyacinthus* and *Pocillopora damicornis* over all other coral species (Pratchett 2007). Despite this information we know very little about how this predation relates back to the reef itself. Likewise, we do not know whether the relative intensity of predation is the same for all colonies within a species, or whether certain colonies are favoured over others depending on factors like colony condition or size (e.g. Niedermüller et al. 2009). This information is important as relative differences in the amount of predation received by different corals will have large consequences for the amount of energy that is needed to be spent on tissue regeneration.

The other major factor that will determine the potential effect that chronic tissue consumption has on reef-building corals is the amount of coral tissue that is removed by polyp-feeders. Only one study has tried to quantify the amount of predation removed from the reef. Harmelin-Vivien and Bouchon-Navaro (1983) used an equation which linked the mean weight of coral found inside the stomachs of speared fishes, along with estimates of fish biomass and the assumption that stomachs would be filled twice daily. From this equation they estimated a reef-wide consumption rate of 27.6g (± 21.0) $1000m^{-1}.day^{-2}$; although a peak of 62.5g was estimated for the outer slope at 10m. The authors concluded from these estimates that polyp-feeders were unlikely to have any meaningful impact on coral growth. However, since their early study, a large body of literature has accumulated which convincingly demonstrates that polyp-feeding fishes take between 400-700 bites an hour, with more than 90% of their time spent in feeding related activities (e.g. Tricas 1989a, Gregson et al. 2008). It is likely that the amount of coral removed from the reef is substantially higher than previously thought. The importance of this consumption will depend to a large extent on the amount of tissue lost relative to the rate of production (Harmelin-Vivien and Bouchon-Navaro 1983, Hay 1991). If the amount of coral tissue consumed is high relative to the rate of production, I expect significant sub-lethal effects to occur, whereby the cost of continually replacing grazed tissue reduces energy available for other energetic processes.

The relative intensity of predation received by different colonies will be an important determinant of the total amount of tissue lost to predation and the subsequent energetic cost of tissue regeneration. The intensity of predation received by a given colony may actually be highest for colonies which host juvenile corallivores. Live coral is of critical importance to juvenile corallivores who not only use individual coral colonies as settlement habitat but also as an exclusive food source immediately post settlement (Harmelin-Vivien 1989, Fowler 1990, Pratchett et al. 2008b). It is currently unknown if these juveniles move between adjacent colonies or whether their entire feeding effort over a period of weeks is directed towards this single colony. If juveniles are confined to this one colony they have the potential to represent a relatively large stressor to these corals, especially when multiple individuals recruit to the same colony. Under these conditions, the total loss of coral tissue may actually be larger on the level of an individual colony than that removed by adults which forage over a much larger area and disperse their feeding efforts across multiple colonies. Although it has never been tested I expect that chronic predation by polyp-feeding corallivores will result in an energy trade-off, whereby energy spent in tissue regeneration will not be available for other life-history processes such as growth and reproduction.

1.2 Aims and thesis outline:

Considering the important ecosystem functions that corals perform (Pratchett et al. 2008), and the high number of small-bodied corallivores (e.g. butterflyfishes) that feed directly from them, it is surprising that the potential effects of their predation have been ignored by coral reef ecologists (reviewed by Rotjan and Lewis 2008, see also chapter 2). While considerable research has been conducted on the feeding behaviour of a handful of coral-feeding fishes, few of these studies have considered the effect of this predation on coral populations and the broad implications of corallivory on coral reef systems remain largely unknown, and even basic information on the full range of species and families that consume corals still needs to be compiled. Progress in evaluating the ecological significance of coral consumption by polyp-feeding fishes has been hampered by the limited number of experimental studies which have demonstrated the impacts of corallivory. The overall goal of this thesis is to quantify the energetic cost of chronic fish predation by polyp-feeding corallivores on common reef corals and to explore whether this predation has the potential to exacerbate changes to coral reef dynamics resulting from global environmental change. To answer this question I first assessed the full range and relative abundances of reef fishes which feed on live corals to gain an idea of which species are likely to be most important in terms of the total amount of coral tissue removed from a reef system. I then conducted a series of related observational and experimental studies which assessed i) how the feeding effort of polyp-feeding corallivores is dispersed amongst different reef corals, ii) how much coral tissue these fishes actually remove from the reef, and what proportion of available coral biomass and productivity this represents and iii) whether coral predation from both adult and juvenile polyp-feeders has any meaningful effects upon the growth and condition of common reef-building corals.

The different components of the study are addressed in a series of six data chapters which correspond to the publications arising from this thesis (see appendix for other papers published during my candidature). Chapter 2 synthesizes the findings of the existing literature on the coral-corallivore interaction and collates the full range of reef fishes which are currently known to feed on live corals. This chapter highlights the limited number of experimental studies which have tried to assess the functional role that coral predation has on reef corals. Chapter 3 presents an observational study which assesses how the feeding activity of polyp-feeding corallivores is distributed within and among different species of reef-building corals. This field-based study also investigates the relationship between colony size and the amount of predation received by different colonies within a species. Chapter 4 uses aquarium based feeding trials to quantify the amount of coral tissue removed per bite by corallivorous fishes. These values were then combined with data on the feeding rates and abundances of corallivorous butterflyfishes to estimate coral consumption rates at the population level. Chapter 5 assesses the energetic cost to a coral colony which is used as settlement habitat by juvenile corallivorous butterflyfish. To assess the question of whether juveniles impact their host corals a controlled experiment was conducted in which coral tissue biomass per unit area and total lipid content was measured before and after juvenile butterflyfishes were artificially settled onto colonies of *Acropora spathulata*. Chapter 6 extends the findings from chapter 4 and relates the population level coral consumption rates of coral-feeding butterflyfishes to the available biomass of tabular acroporid corals on exposed reef crests at Lizard Island, Great Barrier Reef. This chapter provides an estimate of the proportion of standing biomass and potential productivity of tabular acroporid corals which are consumed by corallivorous butterflyfishes. Chapter 7 evaluates the energetic cost that chronic predation has on prey corals. This chapter uses a long term corallivore removal experiment, where the density of corallivorous fishes was significantly reduced and the coral growth rates, condition and reproductive output were monitored for three species of reef-building corals over a 19 month period. Finally, Chapter 8 is a general discussion that assesses the functional role that polyp-feeding corallivores have on coral reef ecosystems and whether the effect of coral predation will be exacerbated by global climate change. In addition to discussing the implications of this research I also highlight areas of future research on the link between corals and corallivorous fishes. Although the chapters in this thesis have deliberately been created as stand-alone papers suitable for publication, they have also been designed to complement each other and present a clear narrative that has a common underlying theme: investigating the effect that chronic coral consumption by polyp-feeding fishes has on reef-building corals.

Chapter 2: Diversity and functional importance of coral-feeding fishes on tropical coral reefs[1]

2.1 Abstract

Fishes that feed from live corals (corallivores) are a conspicuous component of healthy coral reef environments. However, knowledge of the occurrence and ecological significance of this feeding mode is fragmentary. Historically, very few fish were considered capable of feeding from live coral, and those few that did were considered ecologically insignificant. More recently, the role of corallivores has been re-evaluated; published records document 128 corallivorous fish species from 11 different families, with 69 of these belonging to the family Chaetodontidae. Other families, including the Labridae, Tetraodontidae, Balistidae, Monacanthidae, Pomacentridae and Scaridae, all have between seven and ten coral-feeding species. One third of coral-feeding fishes feed almost exclusively on corals, with more than 80% of their diet based on coral. Corallivorous fishes show distinct prey preferences and consume only a small subset of available corals, usually the genera *Acropora*, *Pocillopora* and *Porites*. This selective predation by corallivores can limit abundance and distribution of preferred corals. Chronic predation by corallivores may also exacerbate effects of coral disturbance (e.g. climate-induced coral bleaching), impeding reef recovery and causing further coral loss. Conversely, the cover of preferred corals can be a primary determinant of corallivore abundance and physiological condition. Due to this close association, obligate corallivores invariably decline in response to loss of coral cover. Increased knowledge of the number of corallivores and their diets suggest that this feeding mode is more important to coral reef food webs than traditionally thought.

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[1] This chapter appears in the journal *Fish and Fisheries*: Cole, A.J., Pratchett, M.S., Jones, G.P. (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries*, 9: 286-307.

2.2 Introduction

Corals are the foundation species of coral reef ecosystems, forming the predominant structural habitat and are the foremost contributors to reef development and growth (Jones et al. 1994, Reaka-Kudla 1997). Corals are fundamental in providing essential habitat and resources for numerous sedentary and mobile organisms. Chief amongst these are coral reef fishes, an extraordinarily diverse group of species, characterized by their close association with coral reefs (Choat and Bellwood 1991, Robertson 1998, Bellwood and Hughes 2001). Key aspects of reef habitats that influence the structure of resident fish communities are live coral cover and topographic complexity (Jennings et al. 1996, Öhman et al. 1998a, Syms and Jones 2000, Garpe and Öhman 2003). However, fishes themselves also exert an influence on coral reef habitats. Corallivorous fishes are foremost in their association with coral habitats, as they have an obvious dependence on corals for food in addition to shelter and living space. Historically, research suggested that corals were largely inaccessible as a viable prey source, and that there were very few fishes capable of feeding directly on corals (Connell 1973, Goldman and Talbot 1976, Huston 1985). Furthermore, few trophic studies of coral reef fish communities have recognised corallivores as a distinct functional group or ascribed them any significant role in coral reef ecosystems (e.g. Yonge 1968, Stoddart 1969, Robertson 1970, Hixon 1997). However, Randall (1974) considered corallivory to be one of the most specialised feeding guilds, encompassing some of the most evolutionarily advanced fishes on coral reefs.

Most of the research on corallivory has been directed towards invertebrate corallivores, especially those with the potential to cause massive, but acute devastation, such as the crown-of-thorns starfish (*Acanthaster planci*) (Glynn 1974, Glynn and Krupp 1986, Williams 1986, Glynn 1994, Reyes-Bonilla and Calderon-Aguilera 1999) and *Drupella* spp. (Boucher 1986, Turner 1994, McClanahan 1997). In contrast, corallivorous fishes impose more permanent and chronic pressures on scleractinian corals and are thus assumed to have limited overall impact on prey corals (Hourigan et al. 1988, Gochfeld 2004). Corallivorous fishes are generally assumed to have very minimal influence on distribution, abundance or community structure of potential prey corals (e.g. Hiatt and Strasburg 1960, Yonge 1968, Stoddart 1969, Robertson 1970, Harmelin-Vivien and Bouchon-Navaro 1983). However, there is increasing evidence that the continual removal of coral tissue represents a substantial energetic cost to corals and that chronic predation by some corallivorous fishes may be important in regulating distribution, abundance and fitness of certain prey corals (Neudecker 1979, Wellington 1982, Cox 1986, Kosaki 1989, Littler et al. 1989, Grottoli-Everett and Wellington 1997, Miller and Hay 1998, Rotjan and Lewis 2005, Rotjan et al. 2006). Cox (1986), for example, demonstrated that selective predation by *Chaetodon unimaculatus* had a significant influence on the growth, competitive ability and zonation of *Montipora verrucosa* in Kaneohe Bay, Hawaii.

Interactions between corals and coral-feeding fishes are particularly important in the context of the increasing threats to coral reef biodiversity, including climate-induced coral bleaching, increasing incidence of coral disease, and direct anthropogenic stresses such as sedimentation, eutrophication and overfishing (Hughes 1994, Sebens 1994, Chadwick-Furman 1996, Hughes et al. 2003). Notably, corallivores are particularly sensitive to the declining abundance of certain prey corals, and are typically among the first and worst affected fishes during extensive coral loss (Wilson et al. 2006, Pratchett et al. 2007). Conversely, chronic predation by corallivores may contribute to the ultimate demise of corals that are already stressed by the synergistic effects of other disturbances (Glynn 1996, Bellwood et al. 2006), and possibly even limit recovery of scleractinian corals (Glynn 1985, Knowlton et al. 1988, Guzman and Robertson 1989, McClanahan 2005, Rotjan et al. 2006).

Progress in the evaluation of ecological significance of corallivory has been hampered by limited information on the range of fish species that consume corals, and the species of coral that are consumed (Jones et al. 1991). The review by Jones et al. (1991) also drew attention to the limited number of experimental studies demonstrating an impact of corallivory. Since then, the number of studies on corallivores has steadily accumulated, although there has been no recent synthesis of the major findings. The aim of this review is to provide the first comprehensive assessment of the extent and importance of corallivory among fishes on coral reefs, from the perspective of both the corallivores and the corals. This review covers all fishes which ingest live tissue, whether they feed on coral mucous (e.g. *Chaetodon ornatissimus*), coral polyps (e.g. *Chaetodon trifascialis*) or coral skeleton (e.g. *Arothron* *meleagris*). We do not, however, include species which feed on dead coral skeletons (e.g. scraping scarids) as they do not ingest any coral tissue. We begin by assessing the taxonomic breadth of corallivory, which appears to be more widespread than once thought. Secondly, we consider the specific diets of corallivores, how dependent they are on coral, regional variation in diets and patterns of coral preferences. This is followed by an assessment of the impact corallivorous fishes have on the scleractinian coral community, and conversely, the influence the coral community has on regulating the abundance of corallivores. Finally, we discuss the importance of the role played by corallivorous fishes in the transfer of energy on coral reefs.

2.3 How widespread is corallivory?

Corallivory is usually considered synonymous with just a single family of coral reef fishes, the butterflyfishes (family Chaetodontidae), where it is unusually prevalent and well-known (Reese 1977, Harmelin-Vivien and Bouchon-Navaro 1983, Roberts and Ormond 1992, Cox 1994). However, the incidence of corallivory is taxonomically widespread, and has been documented in at least 128[2] species and 11 reef-fish families (Table 2.1). While the butterflyfishes account for just over half of known corallivores (69 species), this feeding mode is also noteworthy in other families such as the Labridae, Tetraodontidae, Monacanthidae, Pomacentridae, Scaridae and Balistidae, which all have between seven and ten corallivorous species (Figure 2.1). In terms of species representation, corallivory can be considered a minor feeding mode in these families with less than 5% of species known to consume coral. It is only in the Chaetodontidae family where corallivory is a major feeding mode, as just over 50% of species feed at least in part on coral.

Understandably, the literature on corallivory is heavily biased towards butterflyfishes, which account for approximately 75% of the publications. There is considerable information available on their feeding behaviour (e.g. Hiatt and Strasburg 1960, Reese 1977, 1981, Tricas 1985, 1989a, Harmelin-Vivien and Bouchon-Navaro 1983, Harmelin-Vivien 1989, Irons 1989,

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[2] Since publication two further species have been identified as feeding on live coral, the pufferfish *Arothron diadematus* and the wrasse *Psuedocheilinus hexataenia* (Berumen and Rotjan 2010).

Sano 1989, Wylie and Paul 1989, Alwany et al. 2003, Pratchett 2005, 2007, Graham 2007) and on their social organization (e.g. Pitts 1991, Wrathal et al. 1992, Roberts and Ormond 1992, Cox 1994, Zekeria et al. 2002, 2005, Brokovich and Baranes 2005, Pratchett 2005). Apart from a few detailed studies (Glynn 1985, Guzman and Robertson 1989, Guzman and Lopez 1991, McIlwain and Jones 1997) the majority of information regarding non-chaetodontid corallivores comes from reef-wide gut analyses with low sample sizes and little standardisation (e.g. Hiatt and Strasburg 1960, Randall 1967, Hobson 1974, Sano et al. 1984). These studies, while important for their identification of corallivorous species, seldom provide detailed information on the range of coral species consumed.

2.4 What corals do corallivores eat?

2.4.1 Facultative and obligate corallivory

Corallivorous fishes can be broadly divided into obligate or facultative corallivores, which has important ramifications for both dependence on coral resources and also potential impacts of species on coral communities. If we define corallivores as obligate when more than 80% of their diet is centred on coral, approximately one third of known corallivorous fishes fall into this category. Corallivores that have diets containing more than 80% coral show a disproportionate decline following coral loss, which indicates that these species are highly dependent upon coral for survival (Pratchett et al. 2008b). Most obligate corallivores belong to the family Chaetodontidae (Figure 2.1); although the Labridae (wrasses) are of special note as the only family to have more obligate than facultative species.

Coral-feeders primarily target scleractinian (hard) corals, although several species (e.g. *Chaetodon melannotus*) feed extensively on alcyonarian (soft) corals (Sano 1989, Alino et al. 1992, Pratchett 2005). Still, there are no obligate soft coral-feeders and in general, soft coral makes up a minor component of corallivores’ diets. Butterflyfishes are the only corallivores found to consume soft coral; all other corallivorous families have only been observed to feed on scleractinian coral, although this may reflect the lack of detailed diet studies for many of these species (Table 2.1). Further, reliance on soft coral is often subject to regional variation; for example, *C. unimaculatus*, has been found to consume large amounts of soft coral on the

Great Barrier Reef (Pratchett 2005), while in Hawaii it is a specialist hard coral-feeder (Cox 1986, 1994, Hourigan et al. 1988).

Most corallivores feed only partly on live coral tissue and supplement their diet with motile invertebrates, sedentary polychaetes, sponges and algae, among others (Birkeland and Neudecker 1981, Harmelin-Vivien and Bouchon-Navaro 1983, Sano 1989). Facultative species span the full spectrum of coral dependence, from species which have the majority of their diet focused on coral to those for which coral is only a minor component. Additionally, the level of reliance on coral shown by facultative species varies greatly between individuals and between locations, making it difficult to assess the level of coral dependence for many facultative species. Furthermore, several species exhibit marked ontogenetic diet shifts, meaning coral is only an important food source for a part of their lives. For example, the tubelip wrasse group (genus *Labropsis*, *Larabicus*, *Diproctacanthus*) typically clean ectoparasites from other fish as juveniles, before becoming obligate corallivores as adults (Cole 2010).

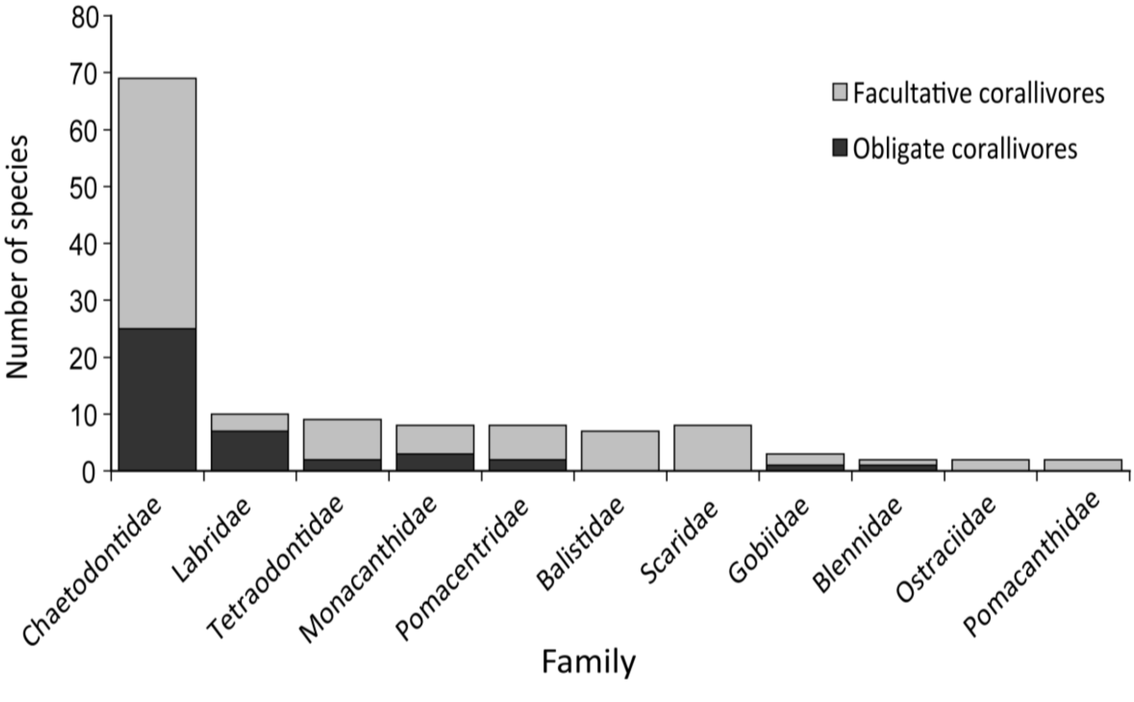

Figure 2.1: Number of obligate and facultative corallivores within each family. Each species was classified based on descriptions in identification books and, where applicable, peer-reviewed journals. When there was doubt about the extent to which coral-feeding occurred, species were classified as facultative.

Table 2.1: List of documented corallivores, species listed by family, their dependence on coral, geographical distribution and the type of evidence used to classify each species. Diet: O- obligate corallivore, F- facultative corallivore, *- ingests skeletal material, †- includes soft coral in diet. Evidence: Obs- Observations only, Gut- Observations and Gut analysis, Anec- anecdotal evidence, including species descriptions from identification books and fishbase.

Species	Diet	Distribution	Evidence	Reference
Balistidae				
*Balistapus undulatus**	F	Red Sea, Indo-Pacific	Gut	Hiatt Strasburg (1960), Lieske and Myers (2001), McClanahan et al. (2005)
*Balistoides viridescens**	F	Red Sea, Indo-Pacific	Anec	Lieske and Myers (2001)
*Rhinecanthus aculeatus**	F	Indo-Pacific	Gut	Hiatt and Strasburg (1960)
*Melichthys niger**	F	All regions	Gut	Hobson (1974)
*Pseudobalistes flavimarginatus**	F	Red Sea, Indo-Pacific	Anec	Lieske and Myers (2001)
P. naufragium	F	East Pacific	Anec	Glynn (2004)
*Sufflamen fraenatum**	F	Indo-Pacific	Gut	Kulbicki et al. (2005)
Blennidae				
Ecsenius bicolor	F	Indo-Pacific	Obs	Randall (1974), Carlson (1992)
*Exallias brevis**	O	Indo-Pacific	Gut	Hobson (1974), Sano et al. (1984)
Chaetodontidae				
C. adiergastos	F	West Pacific	Anec	Michael (2004), Froese and Pauly (2007)
C. andamanensis	O	East Indian	Anec	Michael (2004), Froese and Pauly (2007)
C. argentatus †	F	West Pacific	Gut	Sano (1989)
C. aureofasciatus †	O	Indo-Pacific	Obs	Pratchett (2005), Michael (2004)
C. auriga †	F	Red Sea, Indo-Pacific	Gut	Sano et al. (1984), Bouchon-Navaro (1986), Harmelin-Vivien (1989), Pratchett (2005)
C. auripes	F	West Pacific	Gut	Sano et al. (1984)
C. austriacus	O	Red Sea	Gut	Bouchon-Navaro (1986), Wrathal et al. (1992), Righton et al. (1998), Alwany et al. (2002)
C. baronessa	O	East Pacific	Gut	Anderson et al. (1981), Sano (1989), Pratchett (2005), Berumen et al. (2005)
C. bennetti	O	Indo-Pacific	Gut	Harmelin-Vivien and Bouchon-Navaro (1983), Sano et al. (1984), Sano (1989)
C. blackburnii †	F	Indian	Anec	Harmelin-Vivien (1989), Michael (2004)
C. capistratus	F	Carribean	Gut	Birkeland and Neudecker (1981), Gore (1984), Lasker (1985), Pitts (1991)
C. citrinellus †	F	Indo-Pacific	Gut	Bouchon-Navaro (1986), Harmelin-Vivien (1989), Sano (1989), Pratchett (2005)
C. collare	F	Red Sea, Indian Ocean	Anec	Allen et al. (1998), Michael (2004), Kuiter (2002)
C. daedalma	F	NW Pacific	Gut	Sano (1989), Michael (2004)
C. decussatus	F	Indian	Anec	Allen et al. (1998), Michael (2004)
C. ephippium †	F	Indo-Pacific	Gut	Sano et al. (1984), Harmelin-Vivien and Bouchon-Navaro (1983), Pratchett (2005)
C. falcula	F	Indian	Obs	McClanahan et al. (2005)
C. fasciatus †	F	Red Sea	Gut	Harmelin-Vivien and Bouchon-Navaro (1982)
C. flavirostris	F	Pacific	Anec	Allen et al. (1998), Kuiter (2002)
C. fremblii	F	Hawaii	Anec	Lieske and Myers (2001), Michael (2004)
C. guttatissimus	F	Indian	Anec	Allen et al. (1998), Lieske and Myers (2001)

Table 2.1 continued:

Species	Diet	Distribution	Evidence	Reference
*C. interruptus** †	F	Indian	Anec	Allen et al. (1998)
C. kleinii †	F	Indo-Pacific	Gut	Sano (1989), Pratchett (2005)
C. larvatus	O	Red Sea	Gut	Zekeria et al. (2002)
C. leucopleura	F	West Indian	Anec	Michael (2004)
C. lineolatus	F	Indo-Pacific	Anec	Lieske and Myers (2001), Froese and Pauly (2007)
C. lunula	F	Indo-Pacific	Gut	Harmelin-Vivien and Bouchon-Navaro (1983), Harmelin-Vivien (1989), Pratchett (2005)
C. lunulatus	O	Indo-Pacific	Gut	Sano (1989), Cox (1994), Pratchett et al. (2004), Berumen et al. (2005), Pratchett (2005)
C. melannotus †	O	Red Sea, Indo-Pacific	Gut	Bouchon-Navaro (1986), Alino et al. (1988), (1992), Sano (1989), Pratchett (2005)
C. melapterus †	O	Red Sea	Gut	Zekeria et al. (2002)
C. mertensii	F	Indo-Pacific	Gut	Harmelin-Vivien (1989)
C. mesoleucos	F	Red Sea	Gut	Zekeria et al. (2002)
C. meyeri	O	Indo-Pacific	Gut	Sano et al. (1984), Sano (1989)
C. multicinctus	O	Hawaii	Gut	Tricas (1985), (1989a, b), Cox (1994), Aedy (2002), Gochfeld (2004)
C. nigropunctatus	F	Red Sea	Anec	Allen et al. (1998), Michael (2004)
C. nippon †	F	Pacific	Gut	Sano (1989)
C. ocellatus	F	Caribbean	Anec	Pitts (1991), Michael (2004)
C. ocellicaudus †	O	West Pacific	Anec	Allen et al. (1998), Froese and Pauly (2007)
C. octofasciatus	O	Indo-Pacific	Anec	Allen et al. (1998), Michael (2004)
C. ornatissimus	O	Indo-Pacific	Gut	Reese (1977), Harmelin-Vivien and Bouchon-Navaro (1983), Sano (1989), Cox (1994)
C. oxycephalus	F	Indo-Pacific	Anec	Allen et al. (1998), Lieske and Myers (2001)
C. paucifasciatus †	F	Red Sea	Gut	Harmelin-Vivien and Bouchon-Navaro (1982)
C. pelewensis †	F	Indo-Pacific	Gut	Harmelin-Vivien and Bouchon-Navaro (1983)
C. plebeius	O	Indo-Pacific	Gut	Sano et al. (1984), Sano (1989), Pratchett (2005)
C. punctatofasciatus †	O	Indo-Pacific	Gut	Sano (1989)
C. quadrimaculatus †	F	Indo-Pacific	Gut	Harmelin-Vivien and Bouchon-Navaro (1983), Hourigan et al. (1988)
C. rafflesi †	F	Indo-Pacific	Gut	Sano et al. (1984), Sano (1989), Pratchett (2005)
C. rainfordi †	O	West Pacific	Obs	Pratchett (2005, 2007)
C. reticulatus	O	Pacific	Gut	Harmelin-Vivien and Bouchon-Navaro (1983), Michael (2004)
C. semilarvatus	O	Red Sea	Gut	Zekeria et al. (2002)
C. speculum	F	Indo-Pacific	Gut	Sano et al. (1984), Sano (1989), Pratchett (2005)
C. triangulum	O	Indian	Anec	Allen et al. (1998), Michael (2004)
C. tricinctus	F	Lord Howe	Obs	Kuiter (1996)
C. trichrous	F	Society Is.	Obs	Randall (2005)
C. trifascialis	O	Red Sea, Indo-Pacific	Gut	Reese (1981), Harmelin-Vivien (1989), Irons (1989), Sano (1989), Alwany et al. (2003), Pratchett (2005), Samways (2005)
C. trifasciatus	O	Indian	Gut	Harmelin-Vivien (1989)
C. ulietensis †	F	Indo-Pacific	Gut	Sano et al. (1984), Bouchon-Navaro (1986), Sano (1989), Pitts (1991), Pratchett (2005)

Table 2.1 continued:

Species	Diet [1]	Distribution	Evidence [2]	Reference
*C. unimaculatus** †	O	Indo-Pacific	Gut	Harmelin-Vivien and Bouchon-Navaro (1983), Cox (1986, 1994) Wylie and Paul (1989), Sano (1989), Pratchett (2005, 2007)
C. vagabundus †	F	Red Sea, Indo-Pacific	Gut	Harmelin-Vivien and Bouchon-Navaro (1983), Sano et al. (1984), Harmelin-Vivien (1989)
C. xanthocephalus	F	Indian	Gut	Harmelin-Vivien (1989), Michael (2004)
C. xanthurus	F	Pacific	Anec	Michael (2004)
C. zanzibariensis	O	West Indian	Obs	Samways (2005), Froese and Pauly (2007)
Forcipiger flavissimus	F	Red Sea, Indo-Pacific	Gut	Bouchon-Navaro (1986)
Heniochus acuminatus	F	Indo-Pacific	Anec	Michael (2004)
H. chrysostomus †	F	Indo-Pacific	Gut	Bouchon-Navaro (1986), Sano (1989)
H. intermedius	F	Red Sea	Gut	Bouchon-Navaro (1986), Zekeria et al. (2002)
H. singularius	O	Indo-Pacific	Gut	Sano (1989)
Heniochus varius	F	Pacific	Gut	Allen et al. (1998), Sano (1989)
Gobiidae				
Gobiodon citrinus	O	Red Sea, Indo-Pacific	Gut	Sano et al. (1984)
G. okinawae	F	West Pacific	Gut	P.L. Munday *personal communication*
Paragobidon echinocephalus	F	Indo-Pacific	Anec	Pattern (1974)
Labridae				
*Choerodon graphicus**	F	SW Pacific	Gut	Kulbicki et al. (2005)
Diproctacanthus xanthurus	O	West Pacific	Obs	Randall 1974, Cole et al. (2010)
Labrichthys unilineatus	O	Indo-Pacific	Gut	Sano et al. (1984), McIlwain and Jones (1997)
Labropsis alleni	O	West Pacific	Obs	Randall 1974, Cole e
L. australis	O	West Pacific	Anec	Randall (2005), Froese and Pauly (2007)
L. manabei	O	Indo-pacific	Anec	Randall (1981)
L. micronesica	F	West Pacific	Anec	Parenti and Randall (2000)
L. polynesica	F	East Pacific	Anec	Parenti and Randall (2000)
L. xanthonota	O	Indo-Pacific	Anec	Lieske and Myers (2001), Froese and Pauly (2007)
Larabicus quadrilineatus	O	Red Sea	Obs	Randall (1974, 1986)
Monacanthidae				
Aluterus scriptus	F	All regions	Gut	Randall (1967), Randall (2005)
*Cantherhines dumerilii**	O	Indo-Pacific	Gut	Hiatt and Strasburg (1960), Randall (1974), Jayewardene and Birkeland (2006)
C. macrocerus				
C. pullus	F	Caribbean	Gut	Randall (1967)
C. sandwichiensis	F	East Pacific	Anec	Lieske and Myers (2001), Froese and Pauly (2007)
Oxymonacanthus halli	O	Red Sea	Anec	Lieske and Myers (2001), Froese and Pauly (2007)
O. longirostris	O	Indo-Pacific	Gut	Hiatt and Strasburg (1960), Kokita and Nakazono (1999, 2001), Lieske and Myers (2001)
Pervagor spilosoma	F	Hawaii	Gut	Randall (1967), Hobson (1974)
Ostraciidae				
*Ostracion cubicus**	F	Red Sea, Indo-Pacific	Gut	Moyer and Sano (1987)

Table 2.1 continued:

Species	**Diet** [1]	**Distribution**	**Evidence** [2]	**Reference**
*Lactoria diaphana**	F	Indo-Pacific	Gut	Moyer and Sano (1987)
Pomacanthidae				
Centropyge multispinus	F	Indo-Pacific	Anec	Garpe et al. (2006), Froese and Pauly (2007)
Pomacanthus arcuatus	F	Caribbean	Anec	Allen et al. (1998), Froese and Pauly (2007)
Pomacentridae				
Cheiloprion labiatus	O	Indo-Pacific	Gut	Randall (1974), Sano et al. (1984)
Neoglyphidodon melas	F	Red Sea, Indo-Pacific	Gut	Sano et al. (1984), Lieske and Myers (2001)
Microspathodon chrysurus	F	Caribbean	Gut	Randall (1967), Lieske and Myers (2001), Froese and Pauly (2007)
Plectroglyphidodon dickii	F	Indo-Pacific	Gut	Randall (1974), Sano et al. (1984)
P. johnstonianus	O	Indo-Pacific	Gut	Sano et al. (1984), Macdonald (1981)
Stegastes acapulcoensis	F	East Pacific	Anec	Wellington (1982), Glynn (2004)
S. leucostictus	F	Caribbean	Gut	Randall (1967)
S. variabilis	F	Caribbean	Gut	Randall (1967)
Scaridae				
*Bolbometopon muricatum**	F	Red Sea, Indo-Pacific	Obs	Bellwood and Choat (1990), Bellwood et al. (2003), Lieske and Myers (2001)
*Cetoscarus bicolour**	F	Indo-Pacific	Obs	Bellwood and Choat (1990)
*Chlorurus microrhinos**	F	Indo-Pacific	Obs	Bellwood and Choat (1990)
*C. strongylocephalus**	F	Indian	Obs	McClanahan et al. (2005)
*Sparisoma aurofrenatum**	F	Caribbean	Anec	Miller and Hay (1998), Rotjan and Lewis (2005)
*S. viride**	F	Caribbean	Obs	Brugeman et al. (1994), Miller and Hay (1998), Rotjan and Lewis (2005)
*Scarus coelestinus**	F	Caribbean	Gut	Randall (1967, 1974)
S. guacamaia	F	Caribean	Obs	Glynn (1973)
Tetraodontidae				
*Arothron hispidus**	F	Red Sea, Indo-Pacific	Gut	Hiatt and Strasburg (1960), Randall (1974)
*A. meleagris**	O	Indo-Pacific	Gut	Randall (1974), Glynn (1972), Guzman and Robertson (1989), Guzman and Lopez (1991)
*A. nigropunctatus**	O	Indo-Pacific	Gut	Hiatt and Strasburg (1960), Randall (1974), Sano et al. (1984)
*A. reticularis**	F	Indo-Pacific	Anec	Froese and Pauly (2007)
*A. stellatus**	F	Red Sea, Indo-Pacific	Anec	Lieske and Myers (2001)
*Canthigaster amboinensis**	F	Indo-Pacific	Gut	Allen and Randall (1977)
*C. margaritata**	F	Red Sea, Indo-Pacific	Anec	Lieske and Myers (2001)
*C. solandri**	F	Indo-Pacific	Gut	Hiatt and Strasburg (1960), Allen and Randall (1977), Froese and Pauly (2007)
*C. valentine**	F	Red Sea, Indo-Pacific	Obs	McClanahan et al. (2005), Froese and Pauly (2007)

2.4.2 Diet and feeding preferences

Historically, feeding studies on corallivores have considered hard coral as a single prey category (Harmelin-Vivien and Bouchon-Navaro 1981, 1983, Bouchon-Navaro 1986, Sano

1989, Zekeria et al. 2002). This can be misleading as it implies an extremely high resource overlap between coral-feeding fishes. Recent studies on dietary composition have assessed coral consumption at finer taxonomic scales and have shown that corallivores can be exceptionally specialised, often consuming only a small range of available coral species (Cox 1986, 1994, Irons 1989, McIlwain and Jones 1997, Berumen et al. 2005, Pratchett 2005, 2007).

Most studies which have examined the species-specific diets of corallivores have shown that the majority exhibit prey preferences and consume only a small suite of available prey items (Table 2.2) (Reese 1981, Irons 1989, Cox 1994, McIlwain and Jones 1997, Pratchett 2005, Berumen et al. 2005, Graham 2007). Despite these prey preferences, when preferred prey is not readily available many species do show an ability to include other, less preferred, corals in their diet, although this ability decreases as dietary specialisation increases. Butterflyfishes exhibit particularly high levels of dietary specialisation (Reese 1977, Cox 1994, Tricas 1989a, Hourigan et al. 1988, Alwany et al. 2003 Berumen et al. 2005, Pratchett 2005, 2007). For example, the chevron butterflyfish is the most specialised and feeds almost exclusively on tabular *Acropora* colonies throughout its geographical range (Reese 1981, Harmelin-Vivien 1989, Irons 1989, Alwany et al. 2003, Berumen and Pratchett 2006b). At Johnston Atoll this species fed exclusively from *Acropora cytherea* when *A. cytherea* was in high abundance (91.9%). When *A. cytherea* comprised only 0.32% of the coral cover, the chevron butterflyfish still took 82.7% of its bites from these colonies (Irons 1989). Obligate corallivores tend to have a more specialised predator-prey relationship, which is considered evidence of the close co-evolution between the coral community and obligate corallivores (Reese 1977). Even the most generalist coral-feeding butterflyfish, *Chaetodon lunulatus*, eats <30% of available coral species (Pratchett et al. 2004). These more flexible species are capable of changing their diets based on local environmental conditions such as coral cover (Neudecker 1985, Berumen et al. 2005) or the presence of superior competitors (Cox 1994, Berumen et al. 2005).

There is very high concordance among coral-feeding butterflyfishes in feeding preferences, with most species preferentially consuming corals of the genus *Acropora* and *Pocillopora* (Table 2.2). In one multi-species study, Pratchett (2007) examined 14 corallivorous chaetodontids at Lizard Island and noted all species exhibited significant dietary selectivity, consuming preferred prey disproportionately to their abundance. This has considerable ramifications for potential effects of corallivores on community structure of corals: if the preferred prey is scarce, selective feeding may lead to the local extirpation of this prey coral. Alternatively, if the preferred prey is a spatially dominant species, then selective feeding could increase the diversity of the coral assemblage.

Many different coral-feeding organisms (including butterflyfishes, crown-of-thorns starfish and *Drupella* spp.) exhibit strong and consistent patterns of feeding selectivity, but the underlying basis of these preferences is unclear (Hourigan et al. 1988, Pratchett 2007). For example, Tricas (1989a) examined the calorific content of different coral species in Hawaii and found only a minor correlation between prey preferences of butterflyfishes and the relative food quality (Carbon: Nitrogen) of different coral species. Additionally, nutritional quality will vary greatly between colonies, depending on many environmental factors (i.e. light intensity, water movement, etc.), making a clear causal relationship between prey preferences and nutritional quality difficult to establish.

Apart from nutritional quality, patterns of prey preferences exhibited by coral-feeding butterflyfishes may be structured by: 1) differences in the morphology of corals, where certain corals are easier to feed upon (Reese 1977, Tricas 1989a); 2) variation in the physical defences of corals, such as the size and density of nematocysts (Tricas 1989a, Gochfeld 2004); 3) the presence of secondary metabolites, mainly in soft corals, that act as feeding deterrents (Alino et al. 1988, 1992, Wylie and Paul 1989); 4) susceptibility of coral to physical damage and subsequent mucous production (McIlwain and Jones 1997, Morton et al. 2001); 5) variation in reproductive condition, where colonies containing ripe eggs may be more nutritious (Lasker 1985, Miller and Hay 1998); or 6) differences in the density of macroborers, which may provide increased nutritional benefit from the associated invertebrates (Rotjan and Lewis 2005). However, it is difficult to ascribe any one of these factors to particular feeding preferences and it is quite likely that many factors interact to determine patterns of prey use.

Table 2.2: Comparison of dietary preferences and prey use by corallivorous fishes. To differentiate between varying degrees of prey use, the following symbols were used: (+++) major dietary item, (++) moderate dietary item, (+) minor dietary item, (±) will consume if in high abundance or if preferred prey is scarce and (--) avoids. Blank spaces indicate no mention of this genus. For comparison species are ordered by family and only studies that included a breakdown of the coral genera consumed were used for this table.

Species	**Coral dependence** [1]	**Coral genus consumed**							**Reference**
		Acropora	***Pocillopora***	***Montipora***	***Porites***	***Montastrea***	***Other HC***	***Soft coral***	
Blennidae									
xallias brevis	O	+++	+	+	+++		+		Sano et al. (1984), Carlson (1992)
Chaetodontidae									
Chaetodon aureofasciatus	O	+++	++	++	+++		+	±	Pratchett (2005, 2007)
C. austriacus	O	+++	++	+	++		+		Wrathal et al. (1992), Alwany et al. (2003)
C. auriga	F	++	++		--		++		Pratchett (2005), Graham (2007)
C. baronessa	O	+++	++	--	--	±	+	--	Berumen et al. (2005), Pratchett (2005, 2007)
C. capistratus	F				+	+	++		Gore (1984), Neudecker (1985)
C. citrinellus	F	+++	++	+	±		±	--	Pratchett (2005, 2007)
C. kleinii	F	+++	+++	+	±		±	++	Pratchett (2005, 2007)
C. lunula	F	++	±	+	±		+	--	Pratchett (2005, 2007)
C. lunulatus	O	+++	+++	++	+	±	++	--	Cox (1994), Pratchett et al. (2004), Berumen et al. (2005), Pratchett (2005, 2007)
C. melannotus	O	++	--	+++	--		--	+++	Sano (1989), Pratchett (2005, 2007),
C. multicinctus	O		+++	--	++				Tricas (1989a), Cox (1994)
C. ornatissimus	O	++	++	++	+		++		Reese (1977), Cox (1994)
C. plebeius	O	+++	+++	++	+		+	--	Pratchett (2005, 2007)
C. quadrimaculatus	F		++	+					Hourigan et al. (1988), Cox (1994)

Table 2.2 continued:

Species	Coral dependence [1]	Coral genus consumed							Reference
		Acropora	*Pocillopora*	*Montipora*	*Porites*	*Montastrea*	*Other HC*	*Soft coral*	
C. rafflesi	F	+++	±	±	±		±	±	Pratchett (2005, 2007)
C. rainfordi	O	++	++	±	+		++	+	Pratchett (2005, 2007)
C. speculum	F	+	--	++			++	--	Pratchett (2005, 2007)
C. trifascialis	O	+++	+	±					Reese (1981), Irons (1989), Alwany et al. (2003), Pratchett (2005, 2007), Samways (2005)
C. trifasciatus	O	+++	+++		++		+		Graham (2007)
C. ulietensis	F	++	--	+++	--			+++	Pratchett (2005, 2007)
C. unimaculatus	O	++	--	+++	+		+	+++	Cox (1986, 1994), Sano (1989), Wylie and Paul (1989), Pratchett (2005,2007)
C. zanzibariensis	O				+++		+		Samways (2005)
Gobidae									
Gobidon citrinus	O	+++							Sano et al. (1984)
Labridae									
Diproctacanthus xanthurus	O	+++	+++	+	+		+	--	Cole et al. 2010
Labropsis alleni	O	+	+	+++	+		++	--	Cole et al. 2010
Labrichthys unilineatus	O	+++	+++	++	++		+	--	McIlwain and Jones (1997), Cole et al. 2010
Monacanthidae									
Cantherhines dumerilli	O	+++	++	+	++		+		Randall (1974), Jayewardene and Birkeland (2006)
Oxymonacanthus longirostris	O	+++							Sano et al. (1984), Kokita and Nakazono (2001)

Table 2.2 continued:

Species	Coral dependence [1]	Coral genus consumed							Reference
		Acropora	*Pocillopora*	*Montipora*	*Porites*	*Montastrea*	*Other HC*	*Soft coral*	
Pomacentridae									
Plectroglyphidodon johnstonianus	O	+++	++	+++	++				Randall (1974), Sano et al. (1984), Macdonald (1981)
Cheiloprion labiatus	O	+++		+++					Randall (1974), Sano et al. (1984)
Scaridae									
Bolbometopon muricatum	F	++	++	--	+		++		Bellwood et al. (2003), Hoey and Bellwood (2008)
Sparisoma aurofrenatum	F				++	+++	±		Miller and Hay (1998)
S. viride	F				++	+++	±		Littler and Littler (1989), Miller and Hay (1998), Rotjan and Lewis (2005)
Tetraodontidae									
Arothron meleagris	F	++	+++	++	+++		+		Wellington (1982), Guzman and Lopez (1991
A. nigropunctatus	F	+++	+++	++			+		Randall (1974), Sano et al. (1984)

[1] Coral dependence O- obligate, F- facultative.

Coral colony morphology was first suggested by Reese (1977) to be a co-evolved response by coral colonies to reduce predation rates. Corallivores can likely feed more easily on morphologies where the polyps are raised above the surface of the coral on "knob-like" projections, as opposed to corallites which are depressed in the colony's surface. Likewise, Tricas (1989a) found the preferred prey of *Chaetodon multicinctus* was *Pocillopora meandrina,* whose polyps have a clustered distribution around raised verrucae. *Chaetodon multicinctus* also showed a clear preference for *Porites lobata* over *Porites compressa*, although nutritional quality was almost identical. Despite this preference, when whole colony morphology was masked during controlled experiments the multiband butterflyfish fed equally from both species. This was interpreted as a morphological influence on feeding behaviour. *Porites compressa* has a branching growth form, and as such, more time is required by fish to locate suitable polyps. In contrast, *P. lobata* is a massive species with a relatively flat, two-dimensional feeding surface. *Porites compressa* has larger polyp sizes and is expected to be fed from more readily, but the branched morphology decreases the rate at which fish can harvest polyps. When microstructural differences are relatively equal (nematocysts densities, polyp sizes, etc.), gross colony morphology can greatly influence foraging behaviour.

While gross colony morphology and higher handling times explained the preference between *Porites* spp., it did not explain the higher feeding rates upon *P. meandrina* (a low-abundance coral which is preferentially consumed by several corallivores), which was fed from significantly more than *P. lobata* in both whole colony and masked morphology feeding trials (Tricas 1989a). This preference was explained through smaller nematocysts, exposed fat bodies and the clustered distribution of polyps. When feeding from *P. meandrina,* foraging efficiency is increased, as a greater volume of polyp tissue is removed per bite compared to *Porites* spp*.* (Tricas 1989a). Hourigan et al. (1988) estimated that 32% more calories were ingested per bite when feeding upon *P. meandrina* compared to *P. lobata.* Further, *P. meandrina* has an imperforate corallite skeleton, where all tissue and fat bodies are located on the surface and are accessible to polyp-feeding corallivores (Tricas 1989a). In contrast, *Porites* spp. have a perforate skeleton where most of the living tissue and fat bodies are located under the corallite skeleton (Stimson 1987). Gross morphology appears to be largely irrelevant when substantial microstructural differences exist, such as the clustered distribution of polyps, small nematocysts and exposed fat bodies. As these examples show, the physical attributes of coral colonies can strongly influence the dietary preferences of corallivores.

Colony condition can also have a great influence on feeding behaviour; several species are highly selective towards damaged coral (McIlwain and Jones 1997, Pratchett 2005). This has been most clearly illustrated for the coral-mucous-feeder, *Labrichthys unilineatus*, where naturally damaged coral account for half of all bites taken in the field. Under experimental conditions, mechanically damaged coral colonies became the focus of intense feeding activity (McIlwain and Jones 1997). This phenomenon has also been seen in the butterflyfish, *Chaetodon auriga*; at Lizard Island, coral is only a minor component of its diet, with less than 10% of individuals observed feeding on coral. Despite the low reliance on coral, three individuals fed exclusively on recently damaged *Lobophyllia hemprichii* colonies for up to 90 minutes (Pratchett 2005). Corals respond to physical damage by increasing mucous production, and thus increased olfactory attractants were proposed to explain this increased feeding behaviour, although this has not been well studied (McIlwain and Jones 1997).

2.5 Spatial variation in dietary composition

The dietary composition of individual corallivore species can vary among geographic locations and between habitats, in response to changes in availability of different corals (Berumen et al. 2005) or inter-specific competition (Cox 1994, Pratchett 2005). This is most apparent when comparing the diet of the facultative corallivore, *C. auriga* across its geographical range: coral polyps make up notable proportions of this species' diet in several regions (Moorea, French Polynesia: Harmelin-Vivien 1989; Marshall Islands: Hiatt andStrasburg 1960; Red Sea: Harmelin-Vivien and Bouchon-Navaro 1983; Indian Ocean: Harmelin-Vivien 1989; Japan: Sano et al. 1984; Seychelles: Graham 2007), however in Hawaii (Hobson 1974) and the Great Barrier Reef (Andersen 1981) *C. auriga* has been classified as a non-coralline invertebrate-feeder, with coral polyps making up less than 4% of its diet (Pratchett 2005). Even among obligate corallivores, which feed almost exclusively on coral throughout their range, the exact coral species consumed may vary. For example, at Lizard Island on the Great Barrier

Reef, both *Chaetodon baronessa* and *C. lunulatus* display considerable differences in the coral species consumed between front and back reef locations (Berumen et al. 2005).

The differences shown by species between geographical regions are even more extreme. The adaptation to feed on coral is largely confined to the Indo-Pacific and the Red Sea. No obligate coral-feeding fishes are found in the Caribbean; however, several facultative species are present (Table 2.1). *Chaetodon capistratus* is the only Caribbean species which consumes coral in any large proportion, with up to 75% of its diet derived from coral (Birkeland and Neudecker 1981, Gore 1984, Pitts 1991). Most Caribbean species include coral in only very small proportions and this functional group is poorly developed in this region.

Another major difference between regions is the number and type of skleletal-feeding corallivores. In the Indo-Pacific, skeletal-feeders are represented in several reef fish families. However, in this region, corallivorous scarids are generally poorly developed, with only a few large excavating species, principally the humphead parrotfish (*Bolbometopon muricatum*) (Bellwood and Choat 1990, Belwood et al. 2003). In contrast, Caribbean skeletal-feeding corallivores are limited to only a few grazing scarids. Coral is generally a minor component of their diet and accounts for less than 5% of their bites (Brugeman et al. 1994, Rotjan and Lewis 2005) but due to their dietary selectivity and ability to cause significant damage to corals they are capable of having a disproportionately large impact on the structure of Caribbean reefs (Littler et al. 1989, Grottoli-Everett and Wellington 1997, Bruckner and Bruckner 1998, Miller and Hay 1998, Bruckner et al. 2000, Rotjan et al. 2006, Rotjan and Lewis 2005, 2006).

In addition to differences in the make-up of the corallivore community, patterns of prey use also vary greatly between regions. In the Indo-Pacific, *Acropora* and *Pocillopora* are the preferred prey of most species (Randall 1974, Hourigan et al. 1988, Pratchett 2007) while in the Caribbean, *Montastrea* and *Porites* species are major prey corals (Birkeland and Neudecker 1981, Littler et al. 1989, Rotjan and Lewis 2006). These differences can likely be explained by differences in availability; *Pocillopora* and *Acropora* species are poorly represented in the Caribbean, while *Montastrea* spp. are major reef-builders in this region (Rotjan and Lewis 2006).

2.6 Impact of corallivores on the coral communities

The majority of corallivorous fishes can be classed as polyp-feeders, removing coral tissue without harming the underlying corallite (Hourigan et al. 1988). The impact of such species on coral communities is presumed to be fairly limited (e.g. Harmelin-Vivien and Bouchon-Navaro 1983, Hixon 1997). However, many polyp-grazing corallivores confine foraging activities to small territories (Roberts and Ormond 1992) and concentrate feeding on only a subset of coral species (Pratchett 2005). Within these territories feeding rates can be considerable, often estimated between 400 and 700 bites per hour (Tricas 1985, Gochfeld 2004, Zekeria et al. 2002, Alwany et al. 2003). To maintain coral colonies as an ongoing food source, a balance must be met between feeding intensity and coral regeneration (Gochfeld 2004).

Other corallivores (mainly tetradontids, balistids and scarids) ingest large portions of skeletal material, often biting off growing tips (Hiatt and Strasburg 1960, Sano et al. 1984). Such species have a much greater potential impact on the physical structure of reef habitats, as well as modifying the distribution and abundance of prey corals. Of skleletal-feeders, the large humphead parrotfish has the most profound impact on coral communities, with an estimated 12.7-15kg m^{-2} of live coral skeleton removed annually from outer shelf reefs of the Great Barrier Reef (Bellwood et al. 2003, Hoey and Bellwood 2008). *Bolbometopon muricatum* selectively removes the upper portions of fast growing Acroporid and Pocilloporid corals but avoids feeding from flat or concave surfaces. Skleletal-feeding species such as *B. muricatum* provide a dual role on reefs; in addition to being a coral predator they are also important in reef consolidation through bio-erosion (Bellwood et al. 2003).

Even small skeletal-feeders have a much greater impact on coral communities than polyp-feeders. For example, *A. meleagris* has been observed to remove coral branches up to 31mm long and 5mm wide (Randall 1974). A number of robust jawed butterflyfishes, such as *C. unimaculatus*, can also remove large portions of skeletal material when feeding (Reese 1977, Sano 1989, Motta 1988, Cox 1986). In one study, full regeneration of injured skeletal tissue, caused by *Cantherhines dumerilli* and *A. meleagris*, took 42 days (Jayewardene and Birkeland

2006). In contrast, small single-polyp wounds caused during feeding by *C. multicintus* on *P. compressa* required only 7-10 days for complete regeneration (Gochfeld 2004). Due to these relatively fast regeneration times the incidence and potential importance of coral predation, although frequent, is often overlooked (Jayewardene and Birkeland 2006).

Very few studies have quantified the amount of material removed by polyp-feeding corallivores in the field (Jones et al. 1991). However, a few studies have estimated the amount of material removed by corallivores who ingest skeletal material (Glynn et al. 1972, Glynn 1985, Cox 1986, Reyes-Bonilla and Calderon-Aguilera 1999, Bellwood et al. 2003, Hoey and Bellwood 2008). For example, *A. meleagris* ingests 15-20g of live coral per day yet due to low reef-wide populations, only 20-30g/m^2 of coral is removed annually (Glynn et al. 1972, Reyes-Bonilla and Calderon-Aguiera 1999). Despite this low reef-wide impact, community effects of skleletal-feeders can be quite pronounced. On the Pacific coast of Panama, selective predation by the guineafowl puffer restricts the growth of branching *Pocillopora* colonies to shallow refuges within damselfish territories. In deeper water where pufferfish grazing is not restricted, coral cover is fairly uniform and is limited to the grazing resistant massive, *Pavona gigantea* (Wellington 1982).

In contrast to skeletal-feeders which leave visible damage, quantifying coral tissue removed by polyp-feeders proves more difficult. Only one method has been attempted thus far. Harmelin-Vivien and Bouchon-Navaro (1982, 1983) attempted to quantify gross material removed by polyp-feeding chaetodontids from two regions: Aqaba, Red Sea and Moorea, French Polynesia. They used an equation linking the known mean weight of coral tissue found inside stomachs, along with estimates of fish biomass for nine sections of the reef. This equation provided a reef-wide estimation of 27.6 (± 21.0) g.1000m^{-2}.day^{-2}; although a peak of 62.5g was estimated for the outer reef slope of Moorea at 10m. These estimates prompted the authors to conclude that chaetodontids had only minor impact on coral growth. Their equation assumed that stomachs would be filled only twice daily; however this is likely to be a major underestimation as corallivores feed continuously throughout the day (Tricas 1989b) and stomachs have the potential to be filled multiple times. Cox (1986) experimentally determined that coral material (a mix of tissue and skeleton) could pass through the gut of *C. unimaculatus* within 1.5-2 hours, which means that the gut could be filled at least six times per day. This butterflyfish was also found to have a profound impact on the coral community with a single 100g fish potentially removing 4kg of coral tissue per year. In another attempt to quantify removal rates, Lasker (1985) estimated that *C. capistratus*, consumed 34% of a gorgonian's polyps over the course of the year. To attain this number, Lasker was required to extrapolate and assume some unknowns; despite this, his results raise the possibility that even facultative corallivores are capable of consuming a large biomass of preferred coral prey.

Given the extent of specific prey preferences of corallivorous fishes (Hourigan et al. 1988, Pratchett 2007), a differential effect may be expected for certain coral species. Jayewardene and Birkeland (2006) argue that chronic predation by corallivorous fishes is likely to have a larger influence on particular coral species than previously thought. While 'grazing' corallivores rarely cause whole-colony mortality, the continual removal of tissue by predators must represent a substantial energetic cost to the coral (Meester et al. 1994). Further, energy invested in colony defence increases following intense grazing (Gochfeld 2004). Regenerated tissue was found to have significantly higher densities of nematocysts; however, these morphological changes were only induced in the laboratory, where grazing levels were considerably higher than occurs under field conditions (Gochfeld 2004). Although few studies have investigated causal relationships, chronic predation is likely to severely limit coral growth, reproduction and the capacity for corals to cope with additional stress.

The influence that corallivory has on the competitive interactions between coral species, although possibly substantial, is often overlooked. Only one study to date has experimentally investigated these indirect effects of corallivory. Cox (1986) concluded that predation by the teardrop butterflyfish upon its preferred prey, *Montipora verrucosa*, decreased the ability of *M. verrucosa* to compete for space. In laboratory tests of competitive ability *M. verrucosa* consistently killed and overgrew *P. compressa*. These results were consistent both inside predator exclusion cages and on patch reefs where the teardrop butterflyfish was absent; however, when the teardrop butterflyfish was present this competitive hierarchy was reversed. The teardrop butterflyfish forages primarily around the fringes of patch reefs, and in these areas *M. verrucosa* showed an 86% decrease in vertical growth between caged and uncaged colonies. Predation by the teardrop butterflyfish appears to restrict the distribution of *M. verrucosa* away from reef margins and reverses the outcome of competitive interactions between *M. verrucosa* and *P. compressa* colonies.

Jones et al. (1991) argued that inferences about the impact of corallivores have been limited due to the lack of experimental studies. Since that review, despite the much improved database on diets and feeding selectivity, little has changed. Corallivores appear capable of having profound direct effects upon the distribution, abundance and growth of preferred corals (Neudecker 1977, 1979, Wellington 1982, Cox 1986, Kosaki 1989, Littler et al. 1989, Grottoli-Everett and Wellington 1997, Miller and Hay 1998), but experimental support is limited. Neudecker (1979) transplanted *Pocillopora damicornis* colonies from the reef flat to depths of 15m and 30m, and found that within one week corallivorous fishes had removed almost one quarter of the colony wet weight. In another study, however, he found that *P. damicornis* colonies in fish-exclusion cages survived and grew well at depth (Neudecker 1977). The author concluded from this that corallivores are important in restricting the growth, local zonation and general distribution of preferred species.

The impact of corallivory may be more pronounced under conditions where coral has been depleted due to other disturbances (Glynn 1985, 1988, Knowlton et al. 1988, Guzman and Robertson 1989, Rotjan et al. 2006). Rotjan et al. (2006) found that parrotfish grazing reduced the density of zooxanthellae and increased the severity of a bleaching event in Belize. Grazed *Montastrea* spp. had consistently lower zooxanthellae densities and exhibited slower recovery rates compared to ungrazed colonies. The stress induced by long recovery times has direct implications for colony fitness and fecundity (Ward et al. 2000, Baird and Marshall 2002). Corals which do not recover quickly enough will not complete gametogenesis and will be unable to reproduce until the following year (Szmant and Gassman 1990). The impacts of corallivorous grazing and coral bleaching appear to interact and exacerbate one another.

To maintain corals as a renewable food resource corallivore density and feeding intensity must be balanced with coral regeneration. Following a disturbance event which results in coral mortality available food will decrease relative to corallivore populations. Hence, a higher consumer to resource ratio will result in increased feeding effort directed towards the remaining colonies (Glynn 1990, 1996, Cros and McClanahan 2003, Bellwood et al. 2006), resulting in a rapid depletion of food resources. Coral mortality following the 1998 mass bleaching event was greatly exacerbated by extensive predation by *L. unilineatus,* with up to eight individuals feeding simultaneously upon remnant *Acropora* colonies (Bellwood et al. 2006). The same mass bleaching event saw reef composition completely altered following recovery in the Indian Ocean. McClanahan et al. (2005) found that Kenyan reefs with high densities of skleletal-feeding corallivores experienced a shift from branching *Acropora* and *Porites* to grazing-resistant *Echinopora* and *Galaxea* colonies. The exact role which skleletal-feeders played in this shift is not concrete, although the authors did document a significant link between coral predator biomass and survival of transplanted colonies. Although corallivory may appear to have minimal impacts on a healthy reef, when combined with other stressors corallivores can greatly influence the extent of coral mortality and the structure of recovering coral communities.

2.7 Influence of corals on corallivore abundance and condition

Coral reef fishes are all dependent upon coral reef habitats to some degree, although some fishes (e.g. corallivores) are more reliant than others (Jones 1991, Robertson 1998, Jones and Syms 1998, Wilson et al. 2006). If the distribution and abundance of corallivores is limited by prey availability, one would predict a substantial effect of coral distribution and abundance on their numbers. On a local scale, corallivore territory sizes and levels of aggression are often determined by coral cover (Tricas 1989b, Crosby and Reese 1996, Righton 1998, Samways 2005). However, on larger scales, the effects of coral cover on patterns of abundance are less clear.

Several studies have examined the relationship between coral cover and the abundance of corallivores, primarily chaetodontids (Bell and Galzin 1984, Bell et al. 1985, Bouchon-Navaro and Bouchon 1989, Harmelin-Vivien 1989, Zekeria and Videler 2000, Bozec 2005). The strength of the correlation varies, but positive relationships appear to be strongest when coral cover is low (Bell et al. 1985). One of the strongest fish-coral relationships was shown by McIlwain and Jones (1997), who found that coral cover, explained up to 75% of the variance in the abundance of the obligate coral-feeding tubelip wrasse. The strength of this correlation decreased with increasing spatial scales. Other studies have found little or no effect of substrate on corallivore abundance (Findley and Findley 1985, Roberts and Ormond 1987, Fowler 1990, Cox 1994, Khalaf and Crosby 2005).

The make-up of the coral community can have surprising influences on the physiological condition of coral-feeding fishes, if not actual abundance (Pratchett et al. 2004, Berumen et al. 2005). Berumen et al. (2005) utilised liver lipid concentrations (the preferred energy store of fishes) to assess the effects of diet choice and reef location on the physiological condition of *C. baronessa* and *C. lunulatus*. Individuals feeding in front reef areas with high cover of preferred prey (e.g. *A. hyacinthus*) had significantly higher lipid concentrations than fish feeding in the back reef zones. Similar abundances and bite rates were observed at all sites, despite the twofold difference in coral cover between sites. In this study, densities of corallivores did not appear to be regulated by the availability of coral prey. However, reduced physiological condition as a result of coral composition may have important ramifications on fecundity and subsequent recruitment. Likewise, the corals from which juvenile butterflyfishes feed can also greatly influence their growth and condition (Berumen and Pratchett 2008). Juvenile's of *C. trifascialis* and *C. plebeius* maintained for 26 days on a diet of *Porites cyclindrica* became emaciated with noticeable contraction along the lateral line and ultimately resulted in negative growth. Conversely, juveniles maintained on their preferred coral prey, either *A. hyacinthus* or *P. damicornis,* grew well (Berumen and Pratchett 2008).

Corallivores are often strongly affected by temporal changes in coral abundance (Wilson et al. 2006, Munday et al. 2007, Pratchett et al. 2007). Many studies have shown a decline in corallivore abundance following natural disturbances that result in coral mortality, including coral bleaching (Kokita and Nakazona 2001, Booth and Beretta 2002, Jones et al. 2004, Sano 2004, Garpe et al. 2006, Graham et al. 2006, Wilson et al. 2006) and crown-of-thorns outbreaks (Bouchon-Navaro et al. 1985, Williams 1986, Sano et al. 1987). The abundance of corallivorous species also recovers quickly with subsequent increases in coral cover (Sano 2000, Halford et al. 2004), but recovery is strongly dependent upon both increases in coral cover and re-establishment of initial coral communities (Berumen and Pratchett 2006b).

Coral bleaching represents an environmental challenge for the survival and future of corallivores. In mild bleaching events, colonies will recover quickly with little direct impact upon the fishes' energetic needs. Direct observations of corallivores during bleaching events are scarce. Kokita and Nakazono (2001) found the obligate polyp-feeder *Oxymonacanthus longirostris* significantly increased its feeding rate during a severe bleaching event. Despite an increase in feeding rate, growth and reproduction were severely impaired. The end result of this bleaching event was the eventual disappearance of the local *O. longirostris* population. Bleached coral was unable to sustain this species, despite it increasing its overall coral consumption, indicating that the nutritional quality of bleached coral is lacking in some key nutritional elements.

The difference in nutritional quality of bleached versus healthy colonies has not yet been investigated. In the short-term (few days) nutritional differences should be negligible and restricted to the loss of zooxanthellae which are not digested by corallivores (Harmelin-Vivien and Bouchon-Navaro 1983, Parker 1984). Over time, bleached corals will become less nutritious as they use up their energy reserves (Grottoli 2004, Bachok et al. 2006), mainly lipids, which are the primary source of nutrition for corallivores (Tricas 1989a). However, some species (e.g. *Montipora capitata*) can increase heterotrophic feeding during bleaching events to maintain energy reserves (Grottoli et al. 2006, Rodrigues and Grottoli 2007). Whether coral-feeding fish can change their diets and survive on these heterotrophic corals during severe bleaching events remains to be seen.

Pratchett et al. (2004) investigated the sublethal effects of coral bleaching on the obligate corallivore *C. lunulatus*. In this bleaching event, coral cover declined by 55%, though no decline was observed in the abundance *C. lunulatus*. However, there was a marked shift in diet composition, with an increase in the proportion of bites taken from previously non-preferred corals. The main effect of this bleaching event was on the physiological condition of *C. lunulatus*; liver lipid levels significantly declined over a two-year period. This suggests that less preferred corals are not as nutritious or as easily assimilated but are capable of sustaining corallivore populations over the short term (similar to Berumen et al. 2005). A follow up study three years after the bleaching event found a further reduction in coral cover (90% decline from pre-bleached levels) and coral diversity (55% decline in genera), with significant declines in the abundance of all obligate hard coral-feeders; facultative species were relatively unaffected (Pratchett et al. 2006). The initial stability of butterflyfish abundances after a severe coral bleaching event suggests that on healthy reefs, corallivore populations are not limited by food resources; however, once coral cover drops below a critical point, populations are no longer sustainable (Cox 1994, Pratchett et al. 2006).

2.8 Role of corallivory in coral reef ecosystems

Estimates of coral consumption by corallivores are fundamental to understanding their role in coral reef dynamics. Given the substantial number of fish species that feed on corals it is likely that the coral-corallivore link in the coral reef food web may be significantly more important than traditionally thought. A review by Hatcher (1988) on coral reef primary productivity dismissed corallivory as a major pathway by which coral production enters the food web. This conclusion was based on the idea that a substantial proportion of coral primary production is consumed within the organism itself and that little coral tissue is consumed directly by predators (either invertebrate or vertebrate). Additionally, Hatcher (1988) assumed that excess photosynthetic production was released into the water column in the form of high-energy compounds such as mucous, wax esters and dissolved organic carbon which was not considered to enter the food chain directly.

The amount of photosynthetically fixed carbon released by corals daily is considerable, for example, Wild et al. (2004) estimated that *Acropora* colonies release $4.8 L/m^2$ of mucous daily. Bensen and Muscatine (1974) investigated wax esters in coral mucous and provided anecdotal evidence that many species of reef fish ingest this energy-rich component of coral primary production. These wax esters (particularly cetyl palmitate) and triglycerides make coral mucous a relatively rich energy source for those species capable of digesting them (Bensen and Muscatine 1974). Corallivorous fishes have some of the longest intestines of all fishes (Elliot and Bellwood 2003), which facilitates high gut retention times and may allow the digestion of these complex wax esters. Coral mucous may contain a large protein-nitrogen component which results in a carbon to nitrogen ratio comparable to coral tissue (Brown and Bythell 2005). However, the actual energy content, digestibility and assimilation of coral mucous remains unknown, but at least one corallivore, *C. ornatissimus*, has been shown to consume large quantities of coral mucous when feeding (Coles and Strathman 1973, Reese 1977, Hobson 1974, Sano et al. 1984, Sano 1989).

Glynn (2004) found corallivores to be an important link in the food web on Eastern Pacific reefs with 287+ links between coral prey, invertebrate and fish corallivores, and top level carnivores. The study sites were typical Eastern Pacific reefs with low diversity of scleractinian coral. As a consequence of this low diversity, the corallivore link was mostly focused on five species (three invertebrates and two pufferfish, *A. meleagris* and *A. hispidus*); logically, on higher diversity reefs the depth of corallivore interactions with the coral community will likely increase, thus increasing the net transport of energy up the food web. One problem with this idea, however, is that mortality associated with predation is often cited as being very low, at least for coral-feeding butterflyfish (Neudecker 1989, Roberts and Ormond 1992). Individuals of several coral-feeding butterflyfish species have been observed occupying the same home ranges over several years (Reese 1981, Tricas 1985, Hourigan et al. 1988). Furthermore, coral-feeding butterflyfishes are relatively long-lived, commonly exceeding more than ten years in age (e.g. Berumen 2005 Zekeria et al. 2006). However, quantifying accurate mortality rates on coral reef fish still remains relatively difficult, making the extent to which energy is transferred up to top level carnivores uncertain; though simply by ingesting material, corallivorous species will be adding to the detrital food web.

2.9 Conclusions

This review has shown that corallivorous fishes are taxonomically and ecologically more diverse than once appreciated. While corallivory is the predominant feeding mode in butterflyfishes, it is widespread across many teleost families, where it has received little attention. Research in the last 10-15 years has documented the variety of feeding modes, including the range of coral dependence shown by species and the high level of specialization on particular coral taxa. While this has important implications for the impact of corallivory on coral communities, their ecological role has not been fully demonstrated. Chronic coral predation by fishes can play a significant role in reducing the abundance of preferred coral species and may limit recovery following extrinsic disturbances. The potential impacts of corallivorous fishes on coral communities have been largely unappreciated, partly due to limited information on the amount of coral tissue that is removed by corallivorous fishes. It may also be due in part to the difficulties with isolating individual cause and effect relationships over extended temporal scales. In the future, controlled experiments are needed in addition to descriptive diet studies to quantify the sub-lethal effects on corals subjected to long-term predation. Factors such as coral growth, reproductive capacity and physiological condition may be hindered by corallivory, so concrete data is necessary to predict how these natural stresses will interact with increased climatic pressures.

Similarly, there is still a need for further research on the converse link: how corallivorous fishes are influenced by the availability of suitable coral prey. There is undoubtedly a major influence of coral distribution and abundance on the condition and density of corallivorous fishes. Dietary plasticity of coral-feeding fishes is much lower than previously thought and not all coral species can provide adequate nutrition. More studies are needed which investigate the flow-on effects to coral-feeding fishes following sudden changes to the coral community. Corallivores are highly responsive to the wide range of natural and human-induced disturbances that have reduced the cover and abundance of preferred corals. Obligate corallivores may be threatened with extinction, given the present state and predicted impacts of climate change on coral reefs.

Chapter 3: Inter-specific variation in susceptibility to grazing among common reef corals[3]

3.1 Abstract

Many species of reef fishes, such as butterflyfishes and wrasses, feed almost continuously and at very high rates upon reef-building corals. This study quantified grazing rates on four common reef corals (*Acropora hyacinthus*, *Acropora millepora*, *Pocillopora damicornis*, and massive *Porites*) to assess the variation in susceptibility to coral predation. We also assessed the variation in predation intensity within *A. hyacinthus* and *A. millepora* by standardising grazing rates by colony surface. Rates of grazing on individual colonies were lowest (0.95 (± 0.33 SE) bites.20 minutes^{-1}) for massive *Porites* and highest (16.75 (± 0.30 SE) bites.20 minutes^{-1}) for *A. hyacinthus*. Within coral species, grazing rates showed a linear increase with increasing size of the colony, however the intensity of predation showed a negative relationship with increasing colony size. Predation intensity was highest for small to medium sized colonies with a peak intensity of 1.13 (± 0.17) bites 100cm^{-2}.20minutes^{-1}.colony^{-1} for *A. hyacinthus* colonies and 0.56 (± 0.09) bites 100cm^{-2}.20 minutes^{-1}.colony^{-1} for *A. millepora* colonies (200-600cm^{2}). In contrast, predation intensity was lowest for both very small and very large colonies, with very small colonies (<200cm^{2}) rarely being consumed by corallivorous fishes.

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3.2 Introduction

Predation is a key ecological process, affecting individual fitness, as well the structure and dynamics of both populations and communities (Peckarsky 1980, Sih et al. 1985, Holbrook and Schmitt 2002, Schmitz 2007, Post et al. 2008). In most cases (e.g. among unitary organisms), predation is a discrete event and results in the direct consumption and elimination of prey organisms from the community (Taylor 1984). In this case, differential susceptibility to predation among prey organisms affects their distribution and behaviour (Abramsky et al. 2002, Holmes and McCormick 2006), and exerts a major influence on the local population and community structure (Anderson 2001, Webster 2003). In contrast, in systems where predation is non-discrete, resulting in only partial consumption or partial mortality (reviewed by Henry and Hart 2005) such as in many soft bodied invertebrates and modular organisms such as plants or scleractinian reef corals, these grazing predators can exert a major influence on the fitness of prey organisms, but rarely cause direct mortality (Cox 1986, Skilleter and Peterson 1994, Irlandi and Mehlich 1996). For example, partial predation on the siphons of juvenile scallops reduces shell growth by 25% when exposed to predation. This predation reduces shell growth through the combination of increased regeneration costs and reduced foraging times (Irlandi and Mehlich 1996).

Coral reef fishes from 11 families totalling 130 species feed directly upon live corals (Cole et al. 2008, Rotjan and Lewis 2008, Berumen and Rotjan 2010). The effects of these predators vary greatly, ranging from those which physically damage the carbonate skeleton of corals (e.g. Scaridae, Tetradontidae) to those which only pick at the surface tissues and/or exposed tentacles of individual coral polyps (Hourigan et al. 1988, Tricas 1989a), and generally consume only a small part of a coral colony with each bite. These polyp-feeders (e.g. Chaetodontidae, Labridae) are the dominant coral-feeders on reefs throughout the Indo-Pacific (Cole et al. 2008). Average recorded densities of these coral-feeders range between 12 to 25 individuals per 200m^2 (Fowler 1990, Berumen and Pratchett 2006b, Cole et al. 2010) with most individuals feeding almost continuously and at very high rates (Tricas 1985, 1989a, Gregson et al. 2008); yet, the potential effects on prey corals are often regarded as negligible

(Robertson 1970, Harmelin-Vivien and Bouchon-Navaro 1983, Hixon 1997, but see Cox 1986). Most polyp-feeders spread their feeding effort across many different colonies distributed throughout relatively large territories and do not leave any visible signs of damage on prey corals (Hourigan et al. 1988, but see Cole et al. 2009a). However, the amount of coral tissue removed by polyp-feeders can be as high as 2 to 3g wet weight of coral tissue per day, which implies a significant energetic cost to prey corals (Cole et al. 2011, chapter 4).

Chronic predation by coral-feeding fishes is expected to have significant effects on the structure and dynamics of coral assemblages, especially if there is disproportionate feeding on certain coral species (e.g. Wellington 1982, Cox 1986). Studies that have examined dietary patterns of corallivorous fishes have consistently documented that only a small suite of available coral species are consumed, with most coral-feeders in the Indo-Pacific preferentially selecting *Acropora hyacinthus* and *Pocillopora damicornis* above all others (Berumen et al. 2005, Pratchett 2005, 2007, Cole et al. 2008). It is expected that these preferred prey corals will be visited more frequently and will have more bites taken, resulting in these corals experiencing a greater net loss of coral tissue. This concentration of feeding effort has the potential to influence the structure of coral communities; corals that escape predation will have a significant competitive advantage over corals that are frequently consumed. In Hawaii predation by the corallivorous butterflyfish *Chaetodon unimaculatus* upon its preferred prey *Montipora verrucosa* reduces the growth rate and restricts its distribution away from reef margins (Cox 1986). This selective predation also gives adjacent corals a competitive advantage and reverses the outcome of colony interactions, allowing the competitively inferior *Porites compressa* to overgrow *M. verrucosa* in the presence of predation.

Even within coral species several factors may lead to differential rates of predation among colonies. Colony size is an especially important characteristic for clonal modular organisms as growth, reproduction and the risk of partial verses total mortality are all strongly related to a coral colony’s size (Meesters et al. 2001). It is currently unknown how predation is dispersed between coral colonies of the same species. Optimal foraging theory predicts that larger colonies will receive the highest rates of predation: feeding from these colonies will maximise energy intake as the chance of finding extended polyps will increase (Hughes 1980, Pyke 1984). It is expected that larger colonies will receive a greater rate of predation; however the consequences of predation in terms of the energetic cost of regeneration may be higher for smaller colonies. When standardized to size, each bite upon a small colony will relate to a higher proportion of the tissue biomass being consumed compared to larger colonies. As regeneration is a function of the surrounding coral tissue (Meesters et al. 1997 Oren et al. 1997, Lirman 2000), these smaller colonies will, potentially, have only limited energy reserves to draw upon leading to a higher net cost of regeneration (Oren et al. 2001, but see Jayewardene 2010).

The ability of modular organisms to regenerate and recover from grazing injuries is of considerable importance to the health and continued growth of coral reef communities. Although the energy required by corals to regenerate these removed polyps has not been quantified, it has been estimated that a coral colony takes an average of 7-10 days to successfully regenerate a coral polyp (Gochfeld 2004) and up to 42 days if the coral skeleton is damaged (Jayewardene 2010). Chronic grazing by polyp-feeding fishes is not expected to cause the death of prey corals directly, but rather will act as a sub-lethal stress. The result is a net drain on the energy reserves of coral colonies as energy spent in regenerating grazed tissue increases instead of being stored as energy reserves or invested in other life-history processes such as growth and reproduction (Henry and Hart 2005). Although coral-feeders are unlikely to be the direct cause of coral death the continual loss of coral tissue may interact with other anthropogenic stress to increase the rate of overall coral mortality (Bellwood et al. 2006, Cole et al. 2009b).

A key determinant of a coral's ability to survive and recover from a bleaching event is the magnitude of its stored energy reserves (Grottoli et al. 2006, Rodrigues and Grottoli 2007, Anthony et al. 2009). The two most preferred prey corals, *A. hyacinthus* and *P. damicornis*, are also two of the most susceptible corals to climate-induced mass bleaching (Marshall and Baird 2000, McClanahan et al. 2004). As such, factors like chronic predation which have the potential to reduce a colony's energy stores are likely to have significant consequences on the ability of these frequently eaten corals to survive future bleaching events (Rotjan et al. 2006).

The purpose of this study is to quantify variation in the frequency and intensity of predation by polyp-feeding fishes, within and among common coral species. Specifically we addressed the following questions: (1) does the frequency of predation vary between four common species of reef coral, and (2) is there a relationship between predation rate and intensity and the size of a coral colony? These questions were addressed over a spatial scale of three reefs, to account for differential feeding in accordance with local abundance and composition of both the coral community and the population of coral-feeding fishes. The study is focused entirely upon polyp-feeding corallivores from the families Labridae and Chaetodontidae which are the numerically dominant corallivores on most reefs in the Indo-Pacific.

3.3 Methods

3.3.1 Study site

This study was conducted between August and September 2008 on three platform reefs on the western side of Kimbe Bay (5° 25'S, 150° 05'E), a large sheltered bay on the northern coast of New Britain Island, Papua New Guinea. The three study reefs (Lady Di, Luba Luba and No Name) are all isolated platform reefs with steep slopes and shallow reef tops, located <1 km from the mainland island of New Britain.

3.3.2 Fish and coral abundances

To assess variation in abundance and composition of coral grazing fishes on each of the three reefs, five replicate 50 x 4m belt transects were used at each reef. On each transect all coral-feeding fish observed (>60mm) were recorded to species level, and classed as obligate or facultative coral-feeders based on the classification in Cole et al. (2008). On each of these transects, coral community composition was assessed using point-intercept transects, with the substrate directly under the tape recorded to species level at 50cm intervals, providing 100 sample points per transect.

To ensure our observations were comparable among the three reefs we used separate one-way analysis of variance (ANOVA) to test for differences in both the abundance of corallivorous fishes and the total cover of live scleractinian corals. Variation in the structure of the coral community was examined using a multivariate analysis of variance (MANOVA) using seven resource categories (*A. hyacinthus, A. millepora,* other *Acropora* spp., *P. damicornis*, massive *Porites* spp., *Montipora* spp. and other hard corals). Pillai's trace statistic was used to determine the significance of the MANOVA result. Tukey's Honestly Significant Difference (HSD) *post hoc* test was then used to identify which means contributed to any significant differences detected. Residual plots were used to examine univariate and multivariate assumptions of homogeneity and normality.

3.3.3 Frequency of coral predation

Predation frequency was determined using focal animal sampling (Lehner 1996) for four common coral species: *A. hyacinthus, A. millepora, P. damicornis* and massive *Porites* colonies. From each species forty haphazardly chosen colonies (>25cm diameter) were observed for 20 minutes each. During an observation each coral was watched from a distance of 5m, and all bites taken by corallivorous fish were recorded to species level. Following each observation, the length, width and height were measured for each colony. A two-way ANOVA was used to test for differences in predation rates between species and between reefs. ANOVA assumptions were checked using residual plots. Tukeys HSD *post hoc* test was used to identify where differences in group means occurred.

3.3.4 Intensity of coral predation

To quantify variation in predation rates among colonies of different sizes, a total of 163 colonies of *A. hyacinthus* and 153 colonies of *A. millepora* were observed for 20 minutes and the total number of bites taken by each corallivore species was recorded. To quantify the size of coral colonies, the 2-dimensional horizontal surface area (S) was calculated using the equation of an ellipse, $S = \pi(d_1 d_2)/4$, where d_1 and d_2 are the minor and major axis, respectively, and assuming all colonies were approximately circular, following Hall and Hughes (1996). Predation intensity was determined for each colony by dividing the number of bites taken during a 20 minute observation by the planar S of the colony to give the predation intensity per square cm of coral. This allowed the predation intensity to be compared among differently sized coral colonies within and between species.

As predation intensity did not show a linear relationship with colony size, we used polynomial regression which identified a significant relationship between colony size and predation intensity. As the data deviated from a normal distribution all analyses were run on the natural log of colony area and predation intensity. To identify which colony sizes were driving this non-linear relationship we assigned each feeding observation into one of 4 size classes: very small (<200cm^2), small (200-600cm^2), medium (600-1200cm^2) and large (1200-2400cm^2). As *A. hyacinthus* has a larger size range than *A. millepora* a further very large size class (>2400cm^2) was used for this species. Between 21 and 64 colonies were observed within each size class for each species. Two separate one-way ANOVAs were used to test for differences in predation intensity between size classes for each coral species. Type II sums of squares were used to account for the unequal sample sizes between coral size classes following Langsrud (2003). Tukey's multiple comparison tests were then used to compare the means of treatment groups and identify where differences occurred.

3.4 Results

3.4.1 Abundance of scleractinian coral and coral-feeding fishes

No significant differences were detected in either the total cover of scleractinian corals (ANOVA, $F_{2,12}$=0.27, p>0.05) or the densities of corallivorous fishes (ANOVA, $F_{2,12}$=0.6, p>0.05) between the three reefs . Overall coral cover ranged from 41.2% (± 5.6) to 47.6% (± 5.0). Coral composition did differ slightly between the three reefs with Luba Luba having a significantly (Tukey's HSD, p<0.05) higher cover of *P. damicornis* (10.6% ± 0.8) compared to No Name (3.6% ± 1.3) and Lady Di (5% ± 0.6). No Name reef had the lowest cover of *A. hyacinthus* and *A. millepora* (4.2% ± 0.9 and 2.4% ± 0.75 respectively), compared to Luba Luba (8.4% ± 2.1 and 2.8% ± 1.1) and Lady Di (12% ± 3.9 and 4.0% ± 1.1), although these differences were not found to be significant (Tukey's HSD, p>0.05). Five species of obligate coral-feeders (*Chaetodon baronessa*, *C. lunulatus*, *C. trifascialis*, *Diproctacanthus xanthurus* and *Labrichthys unilineatus*) and 4 facultative species (*Chaetodon citrinellus, C. kleinii, C. rafflesi* and *C. vagabundus*) were recorded on the study reefs. Mean abundances of obligate coral-feeding fish ranged from 26.8 (± 3.4) to 28.6 (± 3.2) individuals per $200m^2$, while facultative coral-feeders had a mean density between 2.6 (± 1.3) and 5.8 (± 1.5) fish per transect. *Chaetodon baronessa* and *L. unilineatus* were the two most abundant coral-feeders on the three reefs and accounted for 82.5% of all coral-feeders observed. This abundance corresponded to the relative contribution to observed bites, with these two species accounting for 86.8% (3051/3513) of the total number of bites taken by all corallivores in this study.

3.4.2 Inter-specific differences in the frequency of predation

The frequency of predation differed significantly between the four species of coral, although no difference was detected within a species between the three reefs (Table 3.1, Figure 3.1). Likewise, no major differences were detected in the species composition of corallivores that fed on each of the coral species, with *C. baronessa* and *L. unilineatus* accounting for between 82-90% of all bites on each of the four corals. *Acropora hyacinthus* received the highest rate of predation with an average ranging from 14.9 (± 2.7) to 16.7 (± 2.3) bites.20 minute $\text{observation}^{-1}.\text{colony}^{-1}$. This was significantly (Tukey's HSD, $p<0.001$) higher than the predation rate upon any other species and was 37% higher than the rate felt by the second most frequently eaten coral, *P. damicornis*, which received an average bite rate ranging from 8.4 (± 1.7) to 10.5 (± 2.7) bites.20 $\text{minute}^{-1}.\text{colony}^{-1}$ across the three reefs. *Acropora millepora* and massive *Porites* colonies received significantly (Tukey's HSD, $p>0.05$) less predation than either *A. hyacinthus* or *P. damicornis*. *Acropora millepora* received an average rate ranging from 2.1 (± 0.6) and 3.8 (± 0.9) bites.20 $\text{minutes}^{-1}.\text{colony}^{-1}$ while massive *Porites* colonies rates ranged from 0.95 (± 0.3) to 1.3 (± 0.6) bites per observation. *Acropora hyacinthus* and *P. damicornis* also had the highest consistency in predation frequency with 96% (116/120) and 92.5% (111/120) of *A. hyacinthus* and *P. damicornis* colonies observed receiving predation during an observation, compared to only 65% (78/120) and 41.6% (50/120) of *A. millepora* and massive *Porites* colonies.

Table 3.1: Two-way ANOVA results comparing the frequency of predation among the 4 coral species (*A. hyacinthus*, *A. millepora*, *P. damicornis* and massive *Porites* spp.) across 3 reefs. Values in bold are significant

Source of Variation	d.f	MS	F	P
Coral species	3	5373.36	79.84	**<0.0001**
Reef	2	35.29	0.52	0.59
Coral x reef	6	29.83	0.44	0.85
Error	468	67.30		

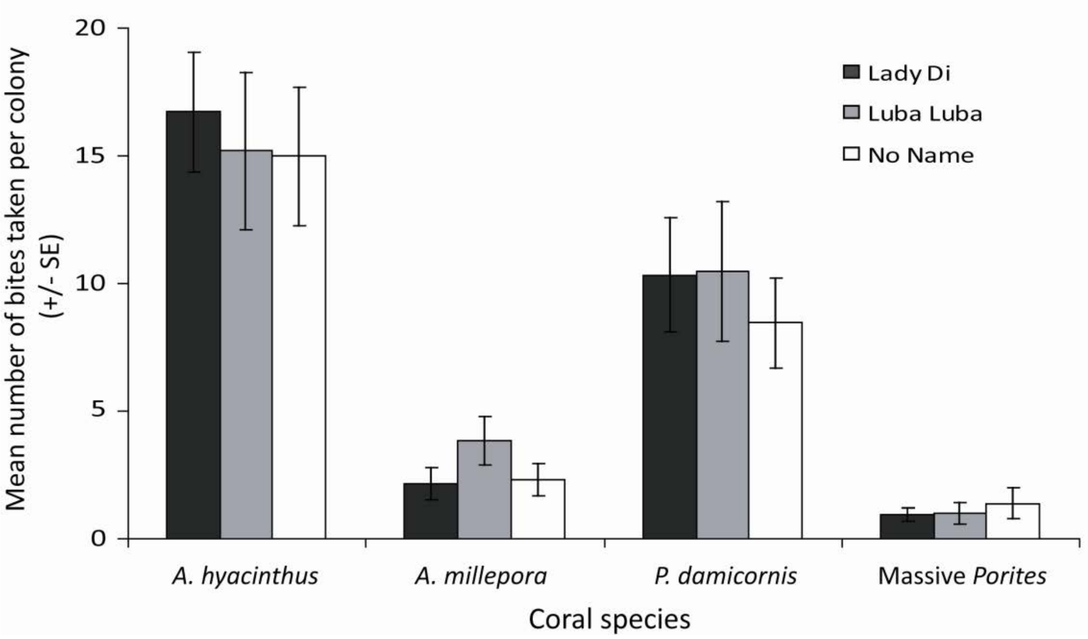

Figure 3.1: Differences in the frequency of predation by coral-feeding fish on four common scleractinian corals. Values are the means and standard errors of the number of bites taken during a 20 minute observations (n=40 colonies) at each of three reefs.

3.4.3 Size-specific differences in predation intensity

Colony size explained 65.7% and 33.4% of the variation in the number of bites received by colonies of both *A. hyacinthus* and *A. millepora* (Figure 3.2). This relationship was largely caused by the absence of predation on very small colonies, with only 21.4% (6/28) of *A. hyacinthus* colonies and 17.2% (5/29) of colonies of *A. millepora* with a surface area less than

200 cm^2 (<15cm diameter longest side) being preyed upon during an observation compared to 95.6% (129/135) of *A. hyacinthus* and 72.6% (90/124) of *A. millepora* colonies with a surface area larger than 200 cm^2. Further, only 18.6% (2/11) of these very small colonies that were preyed upon received more than one bite during an observation, compared to 97.7% (126/129) and 82.2% (74/90) of larger colonies of *A. hyacinthus* and *A. millepora* respectively. Although the frequency of predation shows a general increase with increasing size the actual intensity of predation when standardized to colony surface area declines for larger size classes (Figure 3.3).

Coral colony size was found to be a significant factor that influenced the intensity of predation received for both *A. hyacinthus* (ANOVA, $F_{4,158}$=12.23, p<0.0001) and *A. millepora* (ANOVA, $F_{3,149}$=4.71, p =0.0036). Very small colonies (<200cm^2) of both *A. hyacinthus* and *A. millepora* received the lowest intensity of predation of any size class with an average rate of 0.23 (± 0.1) and 0.15 (± 0.08) bites 100cm^{-2}.20 $minutes^{-1}$.$colony^{-1}$ respectively (Figure 3.3). This rate was significantly (Tukey's HSD, p<0.0001) lower than all other size classes for *A. hyacinthus* and significantly (Tukey's HSD, p<0.01) lower than all but the largest size class for *A. millepora*. Predation intensity then increased 5-fold to a peak of 1.13 (± 0.17) bites 100cm^{-2}.20 $minutes^{-1}$.$colony^{-1}$ for small colonies (200-600cm^2) of *A. hyacinthus*, while predation intensity upon *A. millepora* increases 3-fold and peaks at 0.56 (± 0.09) bites 100cm^{-2}.20 $minutes^{-1}$.$colony^{-1}$ for small sized colonies (200-600cm^2). Predation intensity then gradually declines with further increases in colony size, with the largest size class of *A. hyacinthus* (>2500cm^2) and *A. millepora* (1200-2400cm^2) receiving an average predation intensity of 0.71 (± 0.08) and 0.35 (± 0.07) bites 100cm^{-2}.20 $minutes^{-1}$.$colony^{-1}$, a 40% decline from the peak intensity received by small colonies (200-600cm^2).

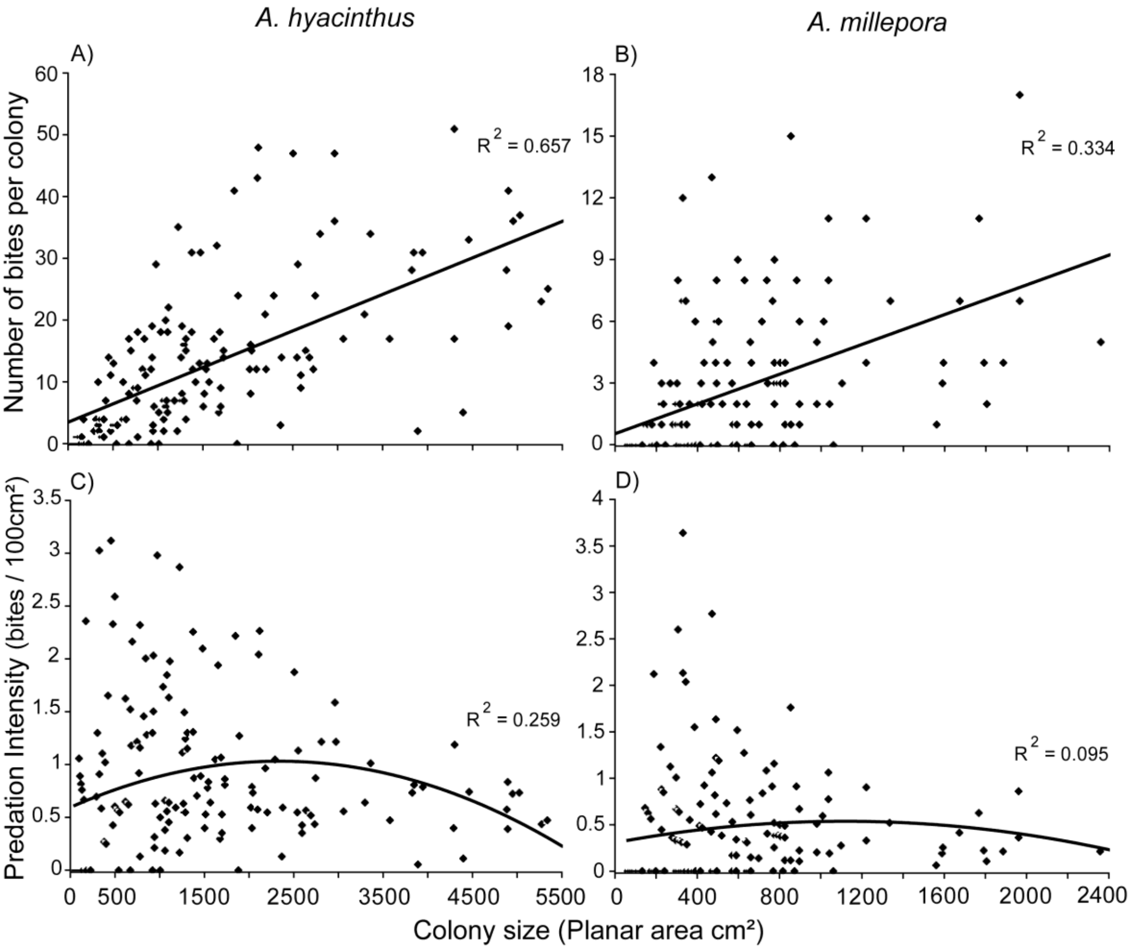

Figure 3.2: Changes in the number of bites taken by coral-feeding fishes during 20 minute observations for A) *A. hyacinthus* and B) *A. millepora* and changes in predation intensity when the number of bites taken is standardised to colony size for C) *A. hyacinthus* and D) *A. millepora*.

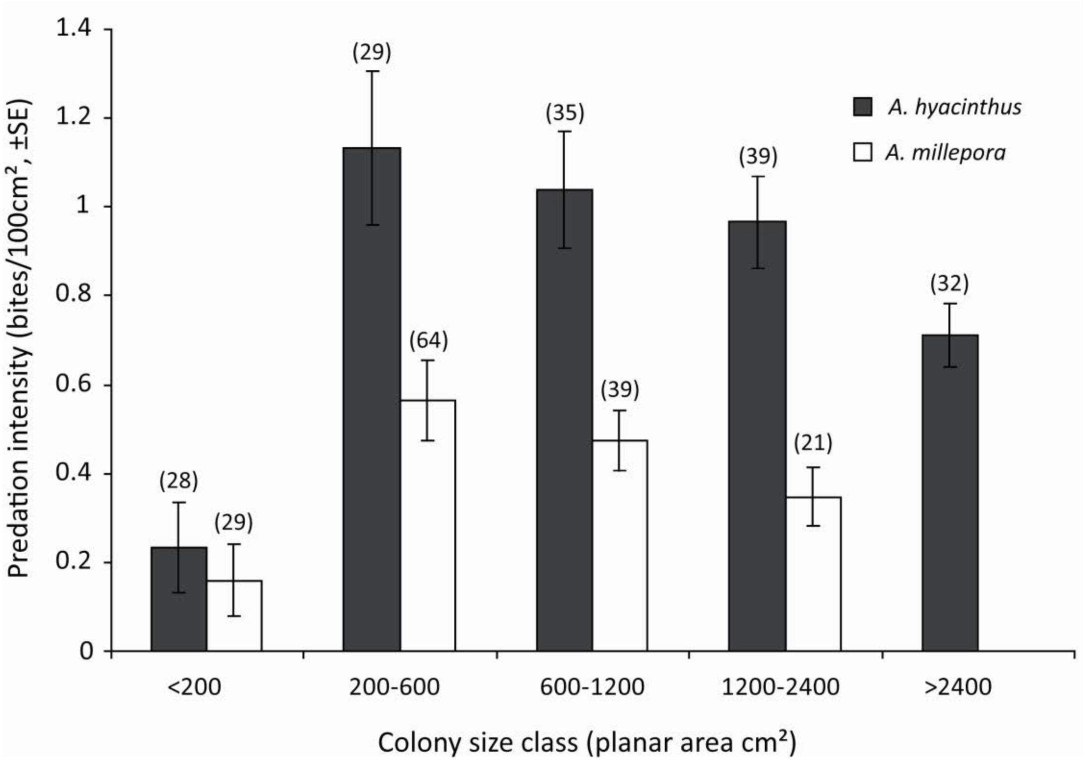

Figure 3.3: Differences in the intensity of predation received by coral colonies within five size classes for *Acropora hyacinthus* and *A. millepora*. Values: mean (± SE) of the number of bites taken during 20 minute observations standardised to colony size. Numbers in parenthesis above bars represent the number of observations for each size class.

3.5 Discussion

Previous studies which have tried to assess the effects of chronic fish predation on coral communities have quantified the amount of coral tissue removed across an entire reef system (Harmelin-Vivien and Bouchon-Navaro 1982, 1983), implicitly assuming that predation will be distributed evenly across a reef and the subsequent effect of this predation will be uniform across all coral species and colonies. In contrast, our study demonstrates that the frequency and intensity of predation by polyp-feeders differs greatly both within and among coral species. In this study, the highest feeding rates were reported for *A. hyacinthus* and *P. damicornis* which received 3-16 times more bites than *A. millepora* and massive *Porites* species. This finding is consistent with reported feeding preferences of corallivorous fishes which have regularly found that *A. hyacinthus* and *P. damicornis* are consumed in greater proportions than expected based on their availability (Alwany et al. 2003, Pratchett 2007, Cole et al. 2010), with highly selective corallivores like *Chaetodon baronessa* and *Chaetodon trifascialis* often taking more than 80% of their bites from these two corals (Berumen et al. 2005, Pratchett 2005). In the present study, a corresponding result was found with 86.7% (3046/3513) of the total observed bites directed towards *A. hyacinthus* and *P. damicornis* colonies.

Interestingly, the frequency of predation upon a coral species showed little variability between the three study reefs despite a relatively large variation in the composition of the coral community. It was expected that the frequency of predation upon a colony would correspond to the consumer to resource ratio present on each reef. As the abundance of coral consumers was very similar amongst the three reefs, we hypothesised that as the relative cover of a preferred coral prey species decreased the rate of predation received by a colony would increase as selective feeding would cause a concentration of feeding effort. This relationship was not observed for the two most frequently consumed corals *A. hyacinthus* and *P. damicornis*, but the inverse relationship was weakly observed for *A. millepora* and massive *Porites* colonies. Predation upon these species was highest on the reefs that had the highest availability, which is consistent with the predictions of optimal foraging theory. However, the size of this effect was relatively low compared to the differences in coral availability: for example only a 1.5 fold increase in the rate of predation (0.95 ± 0.29 vs 1.38 ± 0.61 bites per colony) was observed for a 5.6 fold (2.4 ± 0.5% vs 13.4 ± 3.5%) increase in the availability of massive *Porites* colonies between the reefs. No relationship was found between coral availability and predation pressure for either of the two most frequently eaten prey corals. The average rate of predation on a colony of *A. hyacinthus* differed by only 1.75 bites per colony between reefs even though there was an 8% difference (range 4-12%) in relative cover of this coral species. A similar relationship was observed for *P. damicornis* where the average bite rate on Lady Di and Luba Luba differed by only 0.15 bites per colony (10.32 ± 2.3 vs 10.47 ± 2.7) while the relative cover of *P. damicornis* doubled (5.0 ± 0.6 vs 10.6 ± 0.8) on Luba Luba compared to Lady Di. The lack of a clear relationship between predation pressure and relative coral cover indicates that under healthy reef conditions grazing pressure is largely independent to coral availability and corals are unlikely to be overgrazed.

The high stability in predation rates between the three study reefs suggests that chronic predation by polyp-feeding fishes does not appear to be a major force in structuring coral communities, at least in Kimbe Bay. On reefs subjected to frequent or unusual disturbance events the effect of chronic predation by polyp-feeders may become much more pronounced (e.g. Bellwood et al. 2006, Cole et al. 2009b). Reefs in Guam and Moorea have had a long history of disturbance events, from outbreaks of *Acanthaster planci* to climate-induced mass bleaching events (Done et al. 1991, Burdick et al. 2008, Pratchett et al. 2011b). These disturbances have led to major changes in the community structure of coral assemblages (Gochfeld 2010, Pratchett et al. 2011b). Gochfeld's (2010) observations indicate that *Acropora* and *Pocillopora* colonies have become extremely rare on some reefs with the distribution of these colonies restricted to spatial refuges inside territories of herbivorous damselfishes. When colonies of *P. damicornis* were experimentally transplanted away from these territories rapid and intense predation occurred and resulted in these colonies being overgrazed, with up to 85% of accessible tissue removed within 88 hours (Gochfeld 2010). Undoubtedly, some of the predator response is a result of mechanical disturbance, which has been shown to be a feeding attractant to many corallivores (McIlwain and Jones 1997, Cole et al. 2009b). Additionally, Gochfeld's study was restricted to only one site at each location, which may not be representative of reefs within the broader region. However, her study does provide strong evidence that coral-feeding butterflyfish can limit the recovery of preferred coral prey on disturbed reefs. Selective predation by coral-feeders did not initially cause the decline in abundance of these corals, but has restricted the recovery of *P. damicornis* and *Acropora* spp. to refuges free of predation. A similar result was modelled in Hawaii, USA, where the skeletal-feeding corallivore *Arothron meleagris* will potentially prevent the recovery of *P. compressa* colonies when the relative cover of this species drops below 5% (Jayewardene et al. 2009)

An unexpected finding of our study is the absence of predation upon very small colonies (<200cm^2). This size refuge implies that predation from polyp-feeding fishes is unlikely to influence coral growth and mortality of these very small juvenile corals. This finding is in contrast to Penin et al. (2010), who tracked the percentage mortality of juvenile corals around Moorea and found a weak (R=0.46) but significant correlation between the abundance of chaetodontids at a site and the percentage mortality of juvenile colonies (1-5 cm diameter). They suggested that spatial variation in predation from chaetodontids plays a significant role in the distribution of adult coral populations. This idea seems unlikely considering the findings of Niedermüller et al. (2009) and our observations, in which only 11/57 very small colonies of *A. hyacinthus* and *A. millepora* were ever fed upon during an observation. These small colonies received <1% (17/2391) of the observed bites. Further the intensity of predation on these very small colonies was the lowest of all size classes, which suggests predation-induced mortality by polyp-feeders on juvenile corals is only likely to occur when these small colonies are the only remaining corals left on a reef (e.g. Samways 2005, Gochfeld 2010). Likewise, very large corals are also expected to experience a lower net effect from chronic predation as the impact of tissue loss is dispersed over a larger surface area, with larger colonies having a greater capacity for regeneration (Oren et al. 2001). In contrast, medium-sized colonies within a size range of 200-1200cm^2 of both *A. hyacinthus* and *A. millepora* receive the highest intensity of predation. Any negative effects of chronic fish predation are likely to be felt first and foremost by these intermediate-sized colonies with a lessening effect for very small and very large colonies. These potential negative effects include reduced growth rate, larger size at first reproduction and reduced lipid stores as more energy is allocated to regeneration of lost tissue.

Colony size was also found to be an important factor influencing coral consumption in the Red Sea for the polyp-feeding butterflyfish *Chaetodon austriacus*. This species avoided feeding upon *Acropora* colonies smaller than 400cm^2 with these colonies consumed in proportions significantly lower than expected given their availability, while it positively selected for all colonies larger 400cm^2 (Niedermüller et al. 2009). The factors structuring this avoidance of small colonies are unclear, but are likely to be related to optimal foraging theory. This theory predicts that an organism will try to maximize its energy intake per unit of time (Pyke 1984, Stephens and Krebs 1986, Tricas 1989a, Bergman et al. 2001). Following predation or other local disturbance corals retract their polyps in the area surrounding the disturbance (e.g. fish bite) (Tricas 1989a, Gochfeld 2004, Cole et al. 2010). Repeated feeding in the same location must be delayed long enough for polyps to once again become fully extended (Gochfeld 2004). In our study, on the few occasions when a corallivore did feed upon very small colonies (<200 cm^2) it was rare for more than 1 bite to be taken. In contrast, coral-feeders took multiple bites upon larger colonies and spent more time inspecting the coral after each bite. The size and arrangement of potential prey corals will therefore affect the differential feeding on small versus large corals, so as to maximise access to extended polyps.

The regenerative capacity of corals and other modular organisms has been well documented (reviewed by Henry and Hart 2005). However, quantifying the energetic cost of predation has been predominantly confined to relatively large (>1cm^2) man-made injuries (Lirman 2000, Oren et al. 2001, Edmunds and Lenihan 2010, Lenihan and Edmunds 2010). Many of these studies have found an energy tradeoff, with regenerating corals showing declines in growth and fecundity (Van Veghel and Bak 1994, Ward 1995, Hall 2001, Oren et al. 2001, Edmunds and Lenihan 2010, Jayewardene 2010). Only one study has looked at how regeneration of lost tissue and coral growth are related to an actual fish predation injury. The skleletal-feeding corallivore, *A. meleagris*, bites off the growing tips of *P. compressa*, reducing branch growth rates relative to controls; although no difference in colony growth rates were observed (Jayewardene 2010). Unlike these acute man-made injuries or bites from skeletal-feeders, polyp-feeding corallivores cause numerous small discrete injuries dispersed across the surface of the colony. It takes between 7-10 days to regenerate a grazed polyp (Gochfeld 2004), although the energetic cost of this constant regeneration is unknown. Manipulative experiments are needed to quantify how the chronic stress of polyp-feeding corallivores influences the condition and overall fitness of different coral species and whether this predation reduces their capacity to survive additional stressors such as climate-induced bleaching events.

Coral-feeding fishes have traditionally been viewed as a minor component of coral reef dynamics (e.g. Hixon 1997). However the present study and other recent findings (e.g. Pratchett 2007, Gochfeld 2010, Cole et al. 2011) have all demonstrated that polyp-feeding corallivores are a highly selective functional group that consume considerably more coral tissue than previously suspected. They are capable of having significant effects upon the structure of the coral community, especially after major disturbance events (Bellwood et al. 2006, Gochfeld 2010). The energetic cost imposed by coral-feeders upon coral colonies still needs to be quantified and incorporated into coral reef resilience models, as it is likely that this chronic stress will interact with and be potentially compounded by future anthropogenic stresses. The small but frequent injuries to corals imposed by chronic fish predation are likely to result in a significant energetic drain on a coral colony's energy reserves and may even be the proximate cause of death for corals that are already stressed by the combination of direct anthropogenic distrubances and climate change.

Chapter 4: Chronic coral consumption by butterflyfishes[4]

4.1 Abstract

Interactions between predators and prey organisms are of fundamental importance to ecological communities. While the ecological impacts that grazing predators can have in terrestrial and temperate marine systems are well established, the importance of coral grazers on tropical reefs has rarely been considered. In this study we estimate the biomass of coral tissue consumed by four prominent species of corallivorous butterflyfishes. Sub-adult butterflyfishes (60-70mm, 6-11g) remove between 0.6 and 0.9g of live coral tissue per day, while larger adults (>110mm, ~40-50g) remove between 1.5 and 3g of coral tissue each day. These individual consumption rates correspond to the population of coral-feeding butterflyfishes at three exposed reef crest habitats at Lizard Island, Great Barrier Reef consuming between 14.6g (± 2.0) and 19.6g (± 3.9).$200m^{-2}.day^{-1}$ of coral tissue. When standardised to the biomass of butterflyfishes present, a combined reef wide removal rate of 4.2g (± 1.2) of coral tissue is consumed per $200m^{-2}.kg^{-1}$ of coral-feeding butterflyfishes. The quantity of coral tissue removed by these predators is considerably larger than previously expected and indicates that coral-grazers are likely to play an important role in the transfer of energy fixed by corals to higher consumers. Chronic coral consumption by butterflyfishes is expected to exact a large energetic cost upon prey corals and contribute to an increased rate of coral loss on reefs already threatened by anthropogenic pressure and ongoing climate change.

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[4] This chapter appears in the journal *Coral Reefs*: Cole A.J., Lawton, R.J., Pratchett, M.S., Wilson S.K. (2011) Chronic coral consumption by butterflyfishes. *Coral Reefs*, 30: 85-93.

4.2 Introduction

Interactions between predators and prey species are a primary focus of community ecology (Carpenter et al. 1985, Schmitz et al. 1997, Ives et al. 2005, Schmitz 2007, Mutshinda et al. 2009). The abundance of consumers generally correllates with negative effects on biomass, growth and survival of prey assemblages (Belsky 1986, Crawley 1997, Bigger and Marvier 1998, Preisser et al. 2005). In most predator-prey interactions, predators influence prey communities either directly, by eliminating prey individuals from the community, or through indirect effects, whereby the presence of a predator induces behavioural changes in prey assemablages which creates a risk/reward trade-off for prey species (Pitcher et al. 1988, Scrimgeour and Culp 1994, Abramsky et al. 2002). In systems where predation results in only partial consumption or partial mortality of the prey individual (grazing), potential negative effects include: reduced growth rates (e.g. Midoko-Iponga et al. 2005, Maron and Crone 2006), impaired photosynthetic rates (e.g. Meyer 1998, Zangerl et al. 2002), lowered reproductive output (e.g. Leavitt and Robertson 2006, Hladun and Adler 2009), increased energy allocation to repair and regeneration following tissue loss (e.g. defoliation) (Belsky et al. 1993, Verges et al. 2008) and an overall reduction in fitness (e.g. Wisdom et al. 1989, Avila-Sakar et al. 2003, Rudgers and Whitney 2006). Grazing can also have positive effects under some circumstances. By removing senescent material, grazers can maintain an organism in a highly productive fast growing state and limit the transition to a slower growing plant or algal community (Klumpp and Polunin 1990, Russ 2003).

The biomass removed by grazing organisms can be considerable. The leaf-cutter ant *Atta* spp. removes 13-17% of the foliar biomass produced annually by woody plants in the Neotropical Savanna habitat of Brazil (Costa et al. 2008). Similarly, grasshoppers in the Swiss Alps remove 19-30% of the aboveground phenerogram biomass (Blumer and Diemer 1996). In the Serengeti, 31 species of ungulate grazing herbivores collectively consume 60% of the green grass biomass produced over the course of the year (McNaughton 1985). Likewise, marine herbivores also consume a large component of the daily algal primary productivity on coral reefs (Horn 1989, Russ 2003). In the Northern Red Sea a population of the surgeonfish

Acanthurus nigrofuscus was estimated to remove 16.9kg.m^2.yr^{-1} of algal growth (Montgomery et al. 1989). One of the clearest examples of the effect grazing organisms can have on prey communities is the interaction between sea urchins and kelp forests. Across several locations, declines in keystone predators (e.g. sea otters, cod, lobsters, etc.) have led to unchecked grazing by sea urchins, resulting in the collapse of kelp forest ecosystems (Steneck et al. 2002).

Grazing is typically implicated in the consumption of plants by herbivores, but there are many similarities between plant-herbivore interactions and those seen on tropical coral reefs between corals and coral-feeding fishes. Whereas in plant-herbivore interactions the plants act as the primary habitat builder, in coral reef ecosystems the scleractinian corals fulfil this role of ecosystem engineer (Jones et al. 1994). The corals themselves support numerous sedentary and mobile organisms that depend either directly or indirectly on them for critical resources such as food, shelter or living space (Bruno et al. 2003, Idjadi and Edmunds 2006). While the ecological impact that grazing organisms can have in terrestrial and temperate marine systems are well established (Ritchie et al. 1998, Maron and Crone 2006, Korpinen et al. 2007), the importance of coral grazers on tropical reefs has focused on impacts from acute outbreaks of coral-feeding invertebrates (e.g. crown-of-thorns starfish, *Drupella* spp.) (Sano et al. 1987, Pratchett et al. 2009). The relevance of chronic grazing by fishes has rarely been investigated, even though corallivores are a prominent component of fish assemblages on coral reefs (Cole et al. 2008, Rotjan and Lewis 2008). On the few occasions where they have been considered, coral-feeding fishes have been dismissed as only of minor importance (Robertson 1970, Harmelin-Vivien and Bouchon-Navaro 1982, 1983, Hatcher 1988, Hixon 1997, but see Neudecker 1979, Wellington 1982, Cox 1986).

Coral-feeding butterflyfishes are the numerically dominant coral-predators on most reef systems (Cole et al. 2008), removing individual coral polyps without harming the underlying coral skeleton (Hourigan et al. 1998). This partial predation leaves minimal, if any, visible evidence of damage to the coral colony itself, which has led to the assumption that coral-feeding butterflyfishes have a negligible impact on the structure of coral communities (Harmelin-Vivien and Bouchon-Navaro 1983, Hixon 1997). Only one previous study has tried to quantify the amount of coral tissue removed by coral-feeding fishes: Harmelin-Vivien and

Bouchon-Navaro (1983) estimated that coral-feeding butterflyfishes consume a maximum of 62.5g coral per $1000\text{m}^{-2}.\text{day}^{-1}$ from the barrier reef in Moorea, French Polynesia. However, this estimate was based on mean weight of coral tissue found inside fish stomachs and the assumption that stomachs would be filled only twice daily. Coral-feeding butterflyfishes spend more than 90% of their time feeding and regularly take between 400-700 bites per hour (Tricas 1985, Gregson et al. 2008, Cole et al. 2008). Moreover, Cox (1986) demonstrated that the coral-feeding butterflyfish *Chaetodon unimaculatus* could fill its stomach every 1.5-2hrs, which suggests that butterflyfish stomachs can be filled 5-7 times daily. Thus, it is possible that the amount of coral tissue removed by coral-feeding butterflyfish will be 2-5 times higher than that previously estimated by Harmelin-Vivien and Bouchon-Navaro (1983).

Chronic grazing by butterflyfishes is not expected to be the primary cause of coral death, though it may be a contributing factor in coral mortality when corals are subjected to other stresses. Anthropogenic disturbances and global climate change have had significant effects upon the health of coral reefs around the world (Hughes et al. 2003, Pandolfi et al. 2003). In particular, increasing sea surface temperatures (Veron et al. 2009), ocean acidification (Hoegh-Guldberg et al. 2007, Anthony et al. 2008) and increasing intensity of tropical cyclones (Emanuel 2005) have all negatively impacted corals. However, the effects of chronic biotic stresses, like coral grazing butterflyfishes, have rarely been explored. The amount of coral tissue consumed by these coral predators will be an important factor in determining the functional role of coral predators and their long term effect on the structure and condition of coral communities. Coral colonies frequently eaten by corallivorous fishes will have to invest a higher proportion of their energy into the regeneration of grazed tissue, which will result in lower energy reserves with implications for energy trade-offs between regeneration, growth and reproduction. Additionally, sufficient energy reserves are integral for autotrophic corals to survive climate-induced coral bleaching events (Rodrigues and Grottoli 2007).

In order to fully understand the functional role of coral-feeding butterflyfishes on coral reef dynamics, the amount of coral biomass removed by this functional group must be accurately quantified. The objective of this study is to quantify the amount of coral tissue consumed per bite by four species of widely abundant obligate coral-feeding butterflyfish. This amount is coupled with the densities and feeding rates of coral-feeders to calculate the daily removal of coral tissue on exposed reef crests, the habitat where densities of corallivorous butterflyfishes are highest (Pratchett and Berumen 2008).

4.3 Methods

4.3.1 Coral consumption per bite

Aquarium-feeding trials were used to quantify the amount of coral tissue removed per bite by coral-feeding butterflyfishes. Twenty individuals from each of four common butterflyfishes: *Chaetodon baronessa, C. lunulatus, C. plebeius* and *C. aureofasciatus* were collected from reefs around Lizard Island and maintained in the flow-through aquarium system at the Lizard Island Research Station. These four species were chosen based on their range of dietary specialisation, their high abundances around Lizard Island, and their wide geographical distribution throughout the western Pacific region.

Once acclimated, the live corals used to provide an introduction to the tank environment were removed from the aquarium in the afternoon (by 3pm) and fish were starved overnight (~15-20hrs). Pilot studies indicated that this was sufficient time to ensure that stomachs and upper intestines were empty for the following morning's feeding trial. In these trials approximately 15-20 fragments (≈20-40cm^2) of either *Acropora hyacinthus* or *Pocillopora damicornis* were provided, enough to cover approximately half the surface area of the tank. These two coral species were chosen for experiments as feeding observations have revealed these species to be a prominent component of the diets of most chaetodontids (Berumen et al. 2005, Pratchett 2005). In each tank, the number of bites was recorded for each individual fish. Fish were allowed to feed uninterupted for a maximum of 75 minutes or until they took 600 bites; the trial was aborted if the fish did not take at least 400 bites in this timeframe. After each trial fish were euthanized, weighed, measured and dissected. The stomach and upper intestines were visually checked to ensure that no food had passed into the upper intestines. The stomach was then blotted dry and its contents squeezed onto a dry petrie dish and weighed to 4 decimal places, providing an estimate of the total amount of coral tissue removed for a given number of bites.

These estimates of coral material removed per bite will be slightly inflated as they also include the weight of any digestive enzymes and acids already present in the stomachs of these fish. To account for this, 5 individuals from each species were used in empty stomach control trials. These fish were treated in the same manner as previous trials, however a caged piece of live coral was placed in the control tanks. The caged coral provided visual and olfactory feeding cues which is expected to stimulate the production of digestive enzymes while preventing any feeding. The weight of gastric juices inside empty stomachs was then determined through weighing the stomach contents. There was no significant difference in the weight of digestive juices between the four chaetodon species (ANCOVA, $F_{3,15}=2.14$, $p>0.1$). However, there was a significant increase in the weight of digestive juices with increasing size across all species (ANCOVA, $F_{1,15}=115.58$, $p<0.001$), with size explaining 87.6% of the variation in weight of digestive products. The regression equation of $y = 0.0006x - 0.026$, where x is the total length of the fish in mm, was then used to determine the weight of gastric juices (y) for each fish used in the previous feeding trials. This amount was then subtracted from the total amount of coral tissue ingested by each fish to obtain an adjusted estimate of coral tissue removed per bite.

4.3.2 Daily consumption rates

To determine the amount of coral tissue an individual fish consumes per day for each of the four chaetodon species we multiplied the adjusted amount of coral tissue removed per bite with the average number of bites taken per day. The average feeding rates of the four chaetodon species were taken from Gregson et al. (2008), which includes diurnal changes in feeding rate. As most coral-feeding chaetodontids feed continuously throughout all daylight hours (Tricas 1985, Hourigan 1989, Pratchett 2005, Gregson et al. 2008), the daily feeding period used in this study has been conservatively based on a 10 hour feeding period.

To compare the amount of coral tissue removed per bite and per day by the four species of butterflyfish a two factor analysis of covariance (ANCOVA) was performed using the amount of coral tissue removed as the dependant variable, the coral species fed from as a fixed factor with two levels (*A. hyacinthus* and *P. damicornis*) and fish size treated as a continuous predictor (covariate). The assumption of homogeneity of variance as well as equality of variance (for the covariate) was tested and satisfied for both the categorical predictors and the covariates including the interactions.

4.3.3 Reef wide rates of coral consumption

To determine the amount of coral tissue removed from reefs the abundance and total lengths of all obligate coral-feeding butterflyfishes were estimated using five 50x4m belt transects run haphazardly at each of 3 sites along a 1.5km stretch of exposed reef crest on the southeastern face of Lizard Island, Great Barrier Reef. Size estimations were validated by catching a subset of fish and comparing estimated versus actual length, all cases were found to be accurate within 5mm. Abundances of fishes were combined with the estimates of coral consumption for each species for a given size of fish, providing an estimate of the total coral removed per day from the reef crest habitat at each site. Two species (*C. rainfordi, C. trifascialis*), for which actual bite size was not known, were also found on the transects. In these cases the bite size of the closest related species was used (*C. aureofasciatus* and *C. baronessa* respectively). A length-weight relationship ($y=0.0747x-42.228$) based on the fishes used in the aquarium feeding trials was used to convert the length of each fish observed on the reef crest to provide a biomass estimate for each of these sites.

4.4 Results

4.4.1 Coral consumption per bite

Bite size was directly related to body size (total length) for all four chaetodon species (ANCOVA, $F_{1,71}=287.8$, $p=0.00001$) with size accounting for 70-89% of the variation in the amount of coral tissue removed per bite (Figure 4.1). The size of bites taken by each individual within a species did not vary when feeding on either *P. damicornis* or *A. hyacinthus* (ANCOVA, $F_{1,71}=0.39$, $p=0.53$), however the amount of coral tissue removed per bite varied significantly between the 4 fish species (ANCOVA, $F_{3,71}=20.56$, $p=0.00001$). The interaction between the species of fish and coral was not significant (ANCOVA, $F_{3,71}$=2.14, p=0.1). *Chaetodon aureofasciatus* had a significantly (Tukey's HSD p<0.05) larger bite size and removed approximately 12, 28 and 29% more coral per bite than *C. plebeius, C. lunulatus* and *C. baronessa* respectively. A large adult of *C. aureofasciatus* (117mm) removed 0.56mg per bite compared to 0.51mg for *C. plebeius*, 0.41mg for *C. lunulatus* and 0.37mg for *C. baronessa* of the same size. Likewise a subadult of *C. aureofasciatus* (70mm) removes 0.22mg per bite compared to 0.14mg for *C. plebeius*, 0.15mg for *C. lunulatus* and 0.16mg for *C. baronessa* (Figure 4.1).

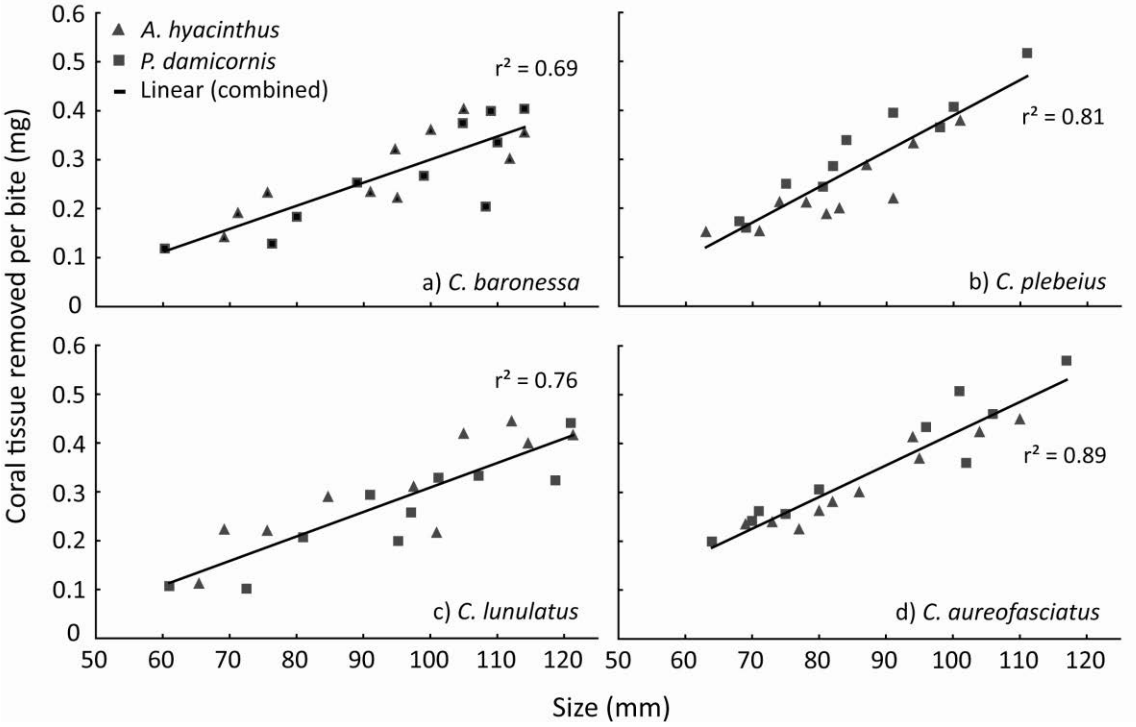

Figure 4.1: Amount of coral tissue (mg) removed per bite by four species of butterflyfish of varying sizes a) *Chaetodon baronessa*, b) *Chaetodon plebeius*, c) *Chaetodon lunulatus* and d) *Chaetodon aureofasciatus*.

4.4.2 Coral consumed per day

Daily coral consumption rates ranged from 0.6-0.85g for a subadult (60-70mm TL, 6-11g wet weight) and up to 1.5-3g for larger adults (>100mm, 40-50g) (Figure 4.2). As a consequence of the differences in bite size and feeding rates, the amount of coral tissue consumed per day differed significantly between the 4 chaetodon species (ANCOVA,

$F_{3,71}$=13.85, *p*=0.00001). *Chaetodon baronessa* had the highest feeding rate (12.2 bites per minute) and subsequently consumed significantly (Tukey's HSD, *p*<0.001) more coral tissue per day than *C. lunulatus, C. plebeius* or *C. aureofasciatus*. *Chaetodon baronessa* removed approximately 30% more coral per day than a similar sized *C. plebeius. Chaetodon plebeius* had the lowest feeding rate (6.8 bites/minute) and removed significantly (Tukey's HSD *p*<0.001) less coral per day than any other species of butterflyfish. The remaining two species, *C. lunulatus* and *C. aureofasciatus,* formed an intermediate group and consumed ~12% less tissue than *C. baronessa* and ~20% more tissue than *C. plebeius* (Figure 4.2). These values relate to each fish consuming between 4-12% of its body weight in coral tissue each day, with the magnitude of this relationship generally decreasing with increasing body mass.

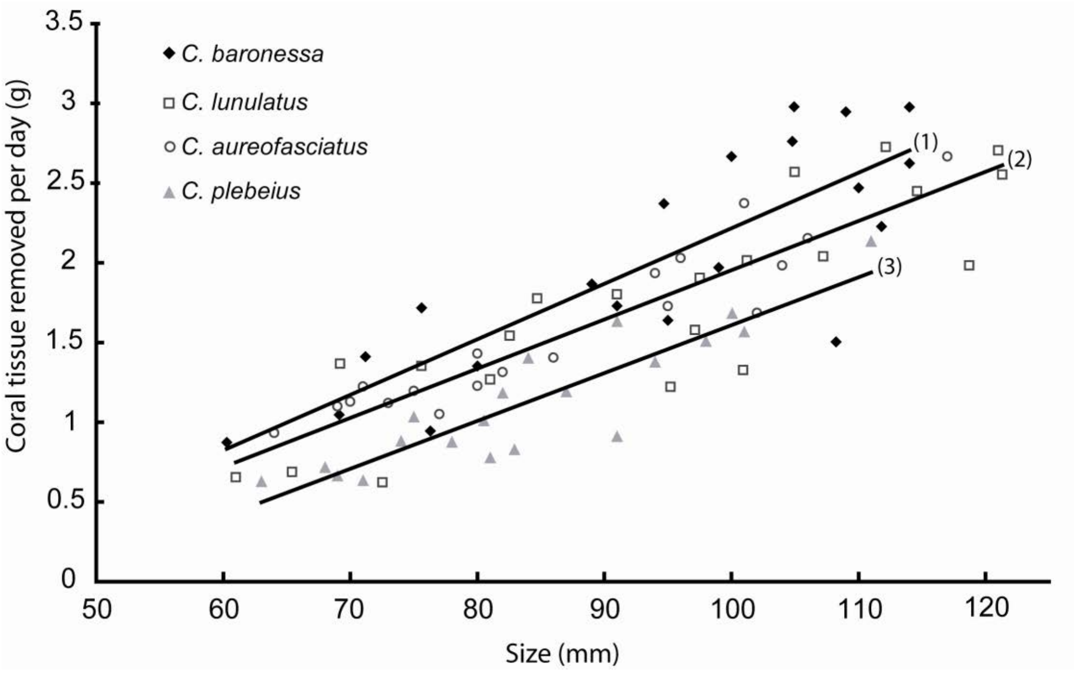

Figure 4.2: Amount of coral tissue removed per day (g) for four species of chaetodon butterflyfish of varying sizes (total length in mm). Trendlines denote homogenous groups identified using Tukey's HSD test following significant ANCOVA result, (1) *Chaetodon baronessa*, (2) *Chaetodon lunulatus* and *Chaetodon auerofasciatus* and (3) *Chaetodon plebeius.*

4.4.3 Reef wide coral consumption

Six species (*C. baronessa, C. lunulatus, C. plebeius, C. aureofasciatus, C. rainfordi* and *Chaetodon trifascialis*) of obligate corallivorous chaetodontids were recorded at the 3 exposed reef crest sites surveyed. The density of these coral-feeders did not differ significantly (ANOVA, $F_{2,12}$= 0.51, *p=0.61*) between sites, with a mean density ranging from 8.2 (± 1.3) to 10.4 (± 2.0) (mean ± SE) butterflyfish per 200m^2 at South Bay and Bird Islet respectively. However, the amount of coral tissue removed per day at each site did differ significantly (ANOVA, $F_{2,135}$=4.55, *P*=0.012) and ranged from a low of 14.6g (± 1.9) per 200m^2 at South Bay to a high of 18.9 (± 2.3) at South Island and 19.6g (± 3.8) per 200m^2 at Bird Islet (mean ± SE). This difference was largely caused by differences in the size frequency distribution of coral-feeders between sites (Figure 4.3). The two sites (Bird Islet and South Island) which had the highest consumption of coral tissue had a size frequency distribution skewed towards the largest size classes, with 73% (33/45) and 59% (31/52) of all fishes observed at Bird Islet and South Island being larger than 100mm compared to only 46% (19/41) at South Bay. When these daily consumption rates are standardised to the biomass of butterflyfishes a combined removal rate of 4.2g (± 1.2) of coral tissue is removed from these 3 sites per 200m^{-2}.day^{-1}.kg^{-1} of coral-feeding butterflyfish.

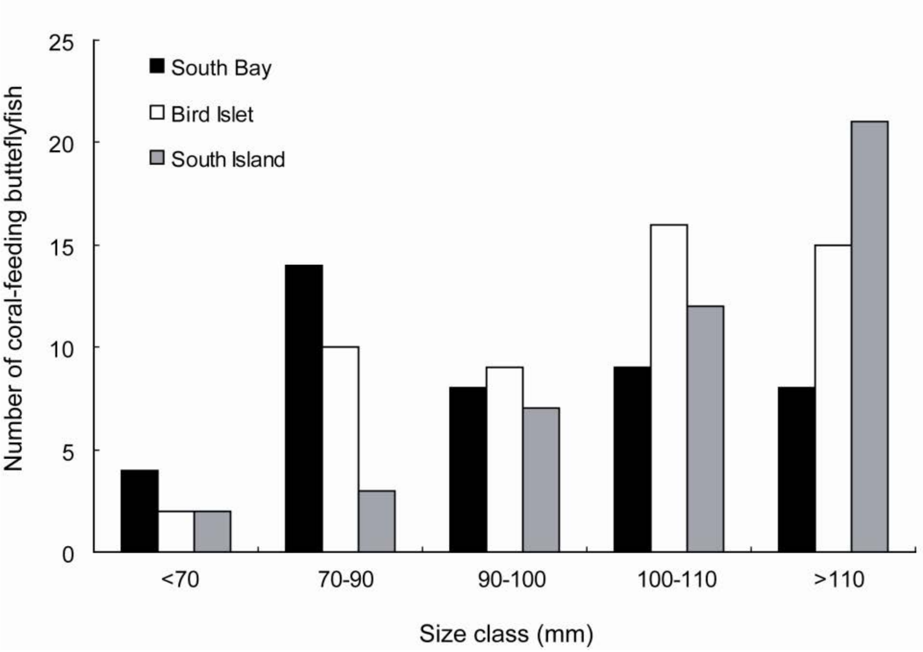

Figure 4.3: Size frequency distribution of obligate coral-feeding butterflyfish on the exposed reef crest at three sites around Lizard Island, Great Barrier Reef.

4.5 Discussion

Although rarely quantified, the amount of coral tissue removed by coral-feeding butterflyfishes has traditionally been considered to be negligible (Harmelin-Vivien and Bouchon-Navaro 1982, 1983). As a result, the functional role that polyp-feeding corallivores play on coral reefs has been dismissed as minor and unimportant (e.g. Harmelin-Vivien and Bouchon-Navaro 1982, 1983, Hatcher 1988, Hixon 1997). In contrast, this study demonstrates that the amount of coral tissue consumed by obligate coral-feeding butterflyfishes is considerable. Depending on size, each individual obligate coral-feeding adult butterflyfish on the reef removes between 1.5-3g of live coral tissue each day. The constant removal of up to 3g of coral tissue per fish per day must represent a net drain on a coral colony's energy reserves. Corals and coral-feeding fishes have co-evolved (Reese 1977) and on healthy reef systems the impact of this predation will most likely take the form of sublethal effects, such as reduced growth and energy reserves, lowered fecundity and overall condition, rather than direct overgrazing and eventual death of a coral colony. The magnitude of these sublethal effects will depend upon the intensity of predation upon individual colonies, and the expense incurred by a coral from regenerating grazed tissue.

The constant removal of tissue indicates that polyp-feeding corallivores, as a guild, are likely to be an important trophic link in the transfer of energy between corals and higher consumers. As such, the coral-corallivore interaction represents an important but relatively unexplored component of coral reef dynamics. Our estimates of the reefwide removal rates averaged across the three sites are 300% higher (17.8g vs 5.5g per 200m2.day-1) than the previous estimates of coral tissue removed across an entire reef in Moorea and 50% higher (17.8g vs 12.0g per 200 m^2) than the maximum amount removed from any one zone on this reef, the outer slope at 10m (Harmelin-Vivien and Bouchon-Navaro 1983). The magnitude of this difference is smaller than expected, and is likely a consequence of our study being confined to obligate corallivores whereas the estimates from Moorea included both obligate (5 spp.) and facultative (11 spp.) corallivores which ingest material other than coral tissue (Harmelin-Vivien and Bouchon-Navaro 1983). Additionally, the corallivore guild on most reef systems within the Indo-Pacific also includes several species of obligate coral-feeders from the labrid and pomacentrid families (Cole et al. 2008). Thus, our estimates of daily coral consumption rates and the size of the coral-corallivore trophic link are conservative estimates and are likely to be considerably larger if the entire guild of polyp-feeding corallivores is considered.

Corallivorous fishes have been the focus of ecological research for over 30 years (e.g. Reese 1977, Glynn 1985, Tricas 1989a, Berumen et al. 2005, Pratchett 2005, 2007, etc.) but we still have little idea what effect these coral predators have on the structure and condition of the scleractinian coral community. Few studies have successfully demonstrated that selective predation by butterflyfishes has any influence on the structure of the coral community. Cox (1986) demonstrated that selective predation by the skeletal-feeding butterflyfish *C. unimaculatus* upon its preferred prey *Montipora verrucosa* reduced this coral's growth rates, restricted its distribution and allowed overgrowth by inferior competitors. Similarly, selective predation by polyp-feeding butterflyfishes in Moorea and Guam have made *P. damicornis* colonies rare on these reefs, except inside damselfish territories (Gochfeld 2010). Within these territories, damselfish aggressively deny access to coral predators and provide *P. damicornis* a refuge from predation (Wellington 1982, Gochfeld 2010). However, when colonies are transplanted away from these refuges, rapid and intense predation resulted with these colonies losing more than 85% of their exposed tissue within 88 hours (Gochfeld 2010).

Coral-feeding butterflyfishes live within relatively large overlapping territories or home ranges (Roberts and Ormond 1992), meaning the biomass of coral tissue removed is dispersed over a number of coral colonies. However these polyp-feeders do not feed indiscriminately upon the coral community (Cox 1994, Pratchett 2005, 2007, Berumen et al. 2005, Cole and Pratchett 2011: chapter 3). Rather, most species of butterflyfish show distinct patterns of prey use. Around Lizard Island all 14 species of coral-feeding butterflyfish studied exhibit significant selectivity in their patterns of prey use (Pratchett 2007), with the majority consuming either *A. hyacinthus* and/or *P. damicornis* in proportions significantly greater than expected given their availability. This feeding selectivity has important consequences for both the coral species affected by predation and the magnitude of any effect upon a colony. For example, at Lizard

Island, the highly selective *C. baronessa* takes up to 87.5% of bites from *A. hyacinthus* in exposed front reef habitats and up to 44% of its bites on *P. damicornis* in back reef habitats (Berumen et al. 2005). As such, the total coral material removed by *C. baronessa* will not be evenly dispersed across an area of reef but will be directed towards *A. hyacinthus* and, to a lesser extent, *P. damicornis*.

The intensity of predation felt by an individual coral colony will be largely dependent upon the relationship between the abundance of coral-feeders and coral colonies. For example, following a disturbance event which results in a reduction in coral cover, coral predation will be focussed on fewer coral colonies and significant effects on the health of these remaining colonies is expected (e.g. Glynn 1996, Bellwood et al. 2006, Cole et al. 2009). This scenario was observed when, following a mass bleaching event, predation by the coral-feeding wrasse *Labrichthys unilineatus* intensified on healthy colonies, exacerbating the loss of coral (Bellwood et al. 2006). Likewise, experimental bleaching of coral colonies under field conditions resulted in a 50% increase in the average number of bites taken by coral-feeders upon remaining healthy colonies (Cole et al. 2009). This resource-to-consumer ratio effect may be further pronounced when the abundance of preferred coral prey species declines even though other corals are relatively unaffected. This may occur when some coral species or growth forms are more susceptible to a particular type of disturbance, as has been observed following bleaching, storms, crown-of-thorns starfish and coral disease outbreaks (Lirman and Fong 1997, Marshall and Baird 2000, Page and Willis 2006, Thompson and Dolman 2010).

The rate of energy intake and subsequent cost of regenerating grazed tissue will also influence the effect that predation has on a coral colony's fitness. In healthy corals, excess energy produced during photosynthesis is stored in the tissue as lipid reserves. If the energy acquired during photosynthesis is a limiting factor in terms of coral growth and condition the regeneration of grazed tissue is likely to be an expensive component of coral colony upkeep. Subsequently, the energy needed to regenerate grazed tissue would have to be diverted from other life-history processes such as growth or reproduction. Quantifying the energetic cost of injury regeneration in corals has been predominantly confined to relatively large (≥1cm^2) man-made injuries (Lirman 2000, Oren et al. 2001, Hall 2001, Titlyanov et al. 2005). These studies have often found an energy trade-off, with regenerating colonies showing declines in growth and fecundity (Van Veghel and Bak 1994, Ward 1995, Oren et al. 2001). Only one study has looked at how regeneration of lost tissue and coral growth are related following fish predation injury. The corallivorous pufferfish, *Arothron meleagris* bites off the growing tips of *Porites compressa*, reducing branch growth rates relative to controls (Jayewardene 2010). Unlike predation from this pufferfish which causes a direct injury to the coral skeleton through a single large bite wound, polyp-feeding butterflyfishes cause multiple small injuries dispersed across a colony. The effect that this type of chronic grazing has on the allocation of energy to regeneration versus other life-histroy processes remains unclear and manipulative experiments are needed to quantify the energetic costs that this type of predation has on a coral colony's energy reserves and overall fitness.

Coral colonies on future reefs are expected to be under significantly higher levels of stress than on today's reefs. Climate change, especially increases in temperature and ocean acidification, will increase stress, reducing calcification and growth and increasing mortality of scleractinian coral populations (Hoegh-Guldberg et al. 2007, Lesser 2007, Carpenter et al. 2008). On healthy coral reefs the influence of predation on the scleractinian coral community is difficult to discern due to the multitude of biotic and abiotic factors which interact to create coral communities at the reef scale. However, the impact on reefs from future anthropogenic pressures is likely to compound and expose the more subtle effects of chronic predation. Currently the coral species most at threat from climate change (Marshall and Baird 2000) are also the most commonly consumed prey by coral-feeding butterflyfishes (Pratchett 2005). As such, it is important to understand the natural stressors which already act upon these colonies to gain a better understanding of whether reef-building corals are capable of accommodating the predicted increase in stress caused by anthropogenic factors.

Chapter 5: Effects of juvenile coral-feeding butterflyfishes on host corals[5]

5.1 Abstract

Corals provide critical settlement habitat for a wide range of coral reef fishes, particularly corallivorous butterflyfishes which not only settle directly into live corals but also use this coral as an exclusive food source. This study examines the consequences of chronic predation by juvenile coral-feeding butterflyfishes on their specific host corals. Juvenile butterflyfishes had high levels of site fidelity for host corals with 88% (38/43) of small (<30mm) juveniles of *Chaetodon plebeius* feeding exclusively from a single host colony. This highly concentrated predation had negative effects on the condition of these colonies, with tissue biomass declining with increasing predation intensity. Declines were consistent across both field observations and a controlled experiment. Coral tissue biomass declined by 26.7%, 44.5% and 53.4% in low, medium and high predation intensity treatments. Similarly, a 41.7% difference in coral tissue biomass was observed between colonies that were naturally inhabited by juvenile butterflyfish compared to uninhabited control colonies. Total lipid content of host corals declined by 29-38% across all treatments including controls and was not related to predation intensity; rather, this decline coincided with the mass spawning of corals and the loss of lipid-rich eggs. Although the speed at which lost coral tissue is regenerated, and the long-term consequences for growth and reproduction remain unknown, our findings indicate that predation by juvenile butterflyfishes represents a chronic stress to these coral colonies and will have negative energetic consequences for the corals used as settlement habitat.

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[5] This chapter appears as is in the Journal *Coral Reefs*: Cole A.J., Pratchett, M.S. (2011) Effects of juvenile coral-feeding butterflyfishes on host corals. *Coral Reefs*, 30:1-8.

5.2 Introduction

Scleractinian corals are the foundation species of tropical reef ecosystems (Jones et al. 1994), providing the structural habitat that facilitates the colonisation and continued survival of reef fish populations (Graham et al. 2006, Munday et al. 2008, Pratchett et al. 2008b). Reef fishes benefit from the complex branching structure of many scleractinian corals in three main ways: corals provide critical settlement cues (Danilowicz 1996, Öhman et al. 1998b, Feary et al. 2007), living space (Harmelin-Vivien 1989, Pratchett et al. 2008b, Wilson et al. 2010) and increased survivorship by reducing predator-induced mortality (Beukers and Jones 1997, Holbrook and Schmitt 2002, Coker et al. 2009). The close association of many reef fishes with live corals is largely a mutualistic relationship (Liberman et al. 1995). While reef fishes benefit from increased survival, the corals which provide this habitat also benefit from increased growth rates, tissue condition and enhanced reproductive output (Meyer and Schultz 1985a, Liberman et al. 1995, Holbrook et al. 2008).

Corals live in an oligotrophic environment, with dissolved nutrients rapidly dispersed by water motion (Holbrook et al. 2008). Coral-dwelling fishes represent an important source of ammonium, nitrogen and phosphorous for host colonies (Meyer and Schultz 1985b), with levels of ammonium significantly elevated in the interior spaces of *Pocillopora eydouxi* colonies occupied by damselfishes compared to colonies without inhabitants (Holbrook et al. 2008). This local enhancement of nutrients has measurable benefits for corals, with nubbins of *P. eydouxi* growing at a 50% faster rate when coral-dwelling damselfish were present (Holbrook et al. 2008). Likewise, colonies of *Stylophora pistillata*, which were used as habitat by the damselfish *Dascyllus marginatus*, grew significantly faster, had higher skeletal weight and subsequently had a higher reproductive output over a 13 month period compared to adjacent colonies which did not host damselfish (Liberman et al. 1995).

The benefits of fishes to corals have been well established (Meyer and Schultz 1985a, Liberman et al. 1995, Holbrook and Schmitt 2005, Holbrook et al. 2008), however it is unknown if the beneficial aspects of this relationship extends to corallivorous fishes. Corallivorous fishes use the coral directly as a source of food (reviewed by Cole et al. 2008) and are highly dependent on coral resources for survival, being the first and most affected group of fishes following disturbances which result in major declines in coral abundance (Wilson et al. 2006, Pratchett et al. 2006, 2008a). Butterflyfishes (F: Chaetodontidae) account for just over half of all coral-feeding fishes (Cole et al. 2008) and typically feed by removing individual coral polyps or tissues without harming the underlying corallite (Tricas 1989a, Cole et al. 2010). Adult butterflyfishes forage over relatively wide home ranges taking multiple bites from a single colony before moving on to the next one, a pattern that is repeated continuously throughout the day (Tricas 1989a). Adult butterflyfishes can remove up to 3g of coral tissue each day and the majority of this predation is directed towards *Acropora* and *Pocillopora* corals (Pratchett 2005, Cole et al. 2011). This constant predation is expected to act as a chronic drain on a coral colony's energy reserves and is likely to outweigh the benefits provided by other fishes which live within the colony but do not feed upon the coral.

During the summer recruitment season juvenile butterflyfishes are a common feature of coral reefs throughout the Indo-Pacific, with finely branched corals providing important settlement habitat for these fishes (Harmelin-Vivien 1989, Fowler et al. 1992, Pratchett et al. 2008b, Wilson et al. 2010). These juveniles settle directly into live coral and begin feeding upon coral immediately following settlement (Harmelin-Vivien 1989). The potential effects that juvenile coral-feeders have on the corals they inhabit has yet to be quantified, and will depend to a large extent on the number of juveniles present and the duration that these juveniles reside within the one coral colony. It is possible that juvenile butterflyfishes spend only a limited amount of time (days) residing in any one colony, although any large distance movements during this early juvenile stage will expose them to a very high risk of predation (Doherty and Sale 1986, Heinlein et al. 2010). If juveniles are site attached they have the potential to consume a significant proportion of coral tissue and exert a large energetic cost upon the colonies used as settlement habitat. Alternatively this chronic consumption may be offset by the beneficial aspects of enhanced supply of nutrients (e.g. ammonium) (Meyer and Schultz 1985b, Holbrook et al. 2008), resulting in a neutral or positive outcome for the health and condition of the coral colony.

This study aims to quantify the effect that juvenile coral-feeding butterflyfish have on the condition of corals that are used as settlement habitat, by measuring changes in the condition of host corals (specifically, tissue biomass and total lipid content) following experimentally induced recruitment. The study species, *Chaetodon plebeius,* recruits in high numbers throughout the Austral spring and summer on mid-shelf reefs of the Great Barrier Reef (Fowler 1990, Pratchett et al. 2008a). At Lizard Island *C. plebeius* uses a wide range of settlement corals, but was most frequently observed recruiting to *Acropora spathulata*, a coral that is relatively common and is representative of the close branching, corymbose morphology that is used by the majority of coral-feeding fishes during settlement (Pratchett et al. 2008a, Cole 2010). This study also assessed fidelity of newly settled butterflyfishes to their host corals, allowing a quantitative evaluation of feeding impacts by juvenile fishes.

5.3 Methods

5.3.1 Site fidelity and foraging area of juvenile butterflyfish

This study was conducted between September and December 2009, at Lizard Island (14°40'S, 145°27'E), in the northern section of the Great Barrier Reef, Australia. To determine if the foraging area of juvenile *C. plebeius* changes with size we conducted five minute observations in which both the microhabitat used within the colony and the total area over which the juvenile foraged was recorded. Three broad categories were used to differentiate microhabitat use: inside the branch structure of the colony, among the upper third of branches and across the colony's tips with minimal use of the branching structure of the colony. The edges of the foraging area were marked with flagging tape during the observation and the area was calculated by dividing the foraging area into simple geometric shapes. Most of the smaller individuals (<30mm) did not leave the coral colony where they were first observed, in which case their foraging area was taken as the planar area of the coral colony, using the equation $S=\pi(d_1d_2)/4$, where d_1 and d_2 are the diameter of the two longest sides of the colony (following Hall and Hughes 1996). During the observations we also recorded the coral species inhabited, the total number of coral colonies visited and the distance from the last colony fed from. Observations were conducted at reefs in the lagoon and back-reef habitats of Lizard Island with observations pooled across all sites. As a consequence of the small size and fast movements of small juveniles within the coral colony it was not possible to accurately record the number of feeding bites taken during an observation, but it was evident that all juveniles fed at very high rates upon their host coral. Following each focal observation the juvenile was captured using clove oil (following Munday and Wilson 1997) and total length was measured to the nearest mm. Observations on juvenile butterflyfish spanned a size range of 12-50mm, divided into 5 size classes; <20mm, 20.1-30mm, 30.1-35mm, 35.1-40mm, 40.1-50mm. Between 16 and 23 observations were made for each size class. To confirm the accuracy of our observations on foraging area and to ensure that small juveniles were not limiting their movements due to a diver effect during observations, ten colonies that hosted small juveniles were tagged and checked daily for ten consecutive days to ensure that the same juveniles were present. On each of these occasions the same sized individuals and number of juveniles were present in each of the 10 colonies on each day.

Separate one way ANOVAs were used to test for differences in foraging area and the number of coral colonies fed from by different size classes of juveniles. Residual plots were used to ensure ANOVA assumptions were met. To improve normality our estimates of foraging area were $\log_{10}$ (x+1) transformed. Tukey's HSD post hoc test was then used to identify where differences among group means occurred.

5.3.2 Effect of predation by C. plebeius juveniles on colony condition

The effects of chronic predation by newly settled butterflyfishes on the condition of coral colonies were assessed based on comparisons between naturally inhabited and uninhabited corals, as well as an experiment which manipulated the densities of juvenile butterflyfishes on colonies of *A. spathulata*. In late October 2009 we compared the total lipid content and tissue biomass per unit area between 20 colonies of *A. spathulata* which had no juvenile butterflyfish, and 20 colonies with at least one late stage juvenile (>30 mm) and up to a total of five juvenile *C. plebeius* living within their branches. The mean density of juvenile *C. plebeius* in these colonies was 2.75 (± 0.25) fish.colony^{-1}. To limit confounding factors the only other residential fishes on these colonies were coral-dwelling gobies. To standardise the environmental conditions experienced by these colonies we chose control colonies of a comparable size, located within 10m of the experimental colony at the same depth. Four branches (length of 6-8cm) were removed from each of these colonies and fixed in 10% phosphate buffered formalin. Two of the branches were used to measure total lipid content and two were used to calculate tissue mass per unit area. Before fixing, the surface area of two branches was determined using the aluminium foil method (Marsh 1970); the weight of this foil (*x*) was converted to surface area (*y*) using the calibration relationship $y = 288.4 \times x - 0.295$. After fixation, all four branches were decalcified in 5% formic acid for 24 hours, followed by 10% formic acid until all skeletal material had been dissolved. Samples were dried overnight at 55°C and weighed to nearest milligram. Tissue mass per unit area was determined by dividing the dried weight of each branch by the surface area of each branch and then combining to obtain a colony mean (following Anthony and Fabricius 2000). The remaining two branches were submerged for 24 hours in a 2:1 chloroform/methanol solution to extract the lipids. These samples were then re-dried at 55°C and re-weighed. Total lipid content of each branch was then taken as the weight lost during the extraction, with total lipid content presented as a percentage of the original tissue biomass (following Ward 1995). Separate one-way ANOVAs were used to examine differences in tissue biomass per unit area and total lipid content between colonies hosting juvenile butterflyfish and those without juveniles. Total lipid content was arcsine transformed to meet ANOVA assumptions.

The density of juvenile coral-feeders was manipulated on 32 previously unoccupied colonies of *A. spathulata* at two back reef sites around Lizard Island: Osprey Inlet and Station Reef. The size of each of these colonies was measured along the two longest diameters at right angles to each other. These diameters were used to calculate the planar surface area of each colony. Colonies were assigned to one of four treatments (n=8): control, low, medium and high predation intensity. Coral colony size did not differ significantly between our 4 treatments (ANOVA, $F_{3,27}$=0.56, p>0.05). As juvenile coral-feeders rarely move between coral colonies when small, we used the density of *C. plebeius* as a proxy for predation intensity. Four density levels were used: control (no juveniles), low (less than one juvenile per 1200cm^2), medium (1 juvenile per 650-900cm^2) and high (1 fish per 250-500cm^2), these densities correspond to approximately 1-2, 2-3 and 3-5 fish.colony^{-1} for our low, medium and high treatments. This experiment was started on the 29th October and ended on the 8th December.

Juvenile *C. plebeius* between 12-21mm (total length) were caught using clove oil and hand nets and maintained under aquarium conditions for 24 hrs before being randomly allocated to one of the three density treatments. These corals were checked daily and if any fish were missing a new juvenile was added to maintain the treatment density. It was rare (<5% of juveniles) for a juvenile to go missing after the first 48 hours. To limit the impact of branch removal on a coral colony's energetics and integrity of the branching structure, only two branches were removed from each colony at the beginning of the experiment; one was used to estimate tissue biomass per unit area and the other to determine total lipid content. A further four branches were taken 41 days later to quantify any changes to tissue biomass (2 branches) and total lipid content (2 branches) using the same techniques as described in the natural comparison of colonies. A repeated measures ANOVA was used to examine whether any changes in tissue mass per unit area and total lipid content corresponded with predation intensity. Residual plots were examined to validate ANOVA assumptions of normality and homogeneity of variance. Tukey's multiple comparison tests were then used to identify where differences occurred.

5.3.3 Variation in tissue mass and lipid content within a colony

To determine if the within-colony variance in total lipid content and tissue thickness is larger than our among-colony variance we sampled 10 branches from each of four colonies of *A. spathulata*. Five branches were used to determine tissue mass per unit area and five were used to calculate total lipid content. Branch position within a colony was standardised by taking branches from the central section of the colony with a minimum distance of 5cm from the colony margins. Both the variance in tissue mass (ANOVA, $F_{3,12}$=88.81, $p<0.05$) and total lipid content (ANOVA, $F_{3,12}$=108.65, $p<0.0001$) was greater among colonies than the variation in tissue mass (ANOVA, $F_{4,12}$=0.123, p<0.05) and lipid content (ANOVA, $F_{4,12}$=2.139, $p<0.05$) among branches within a colony. There was a maximum of 11% variation between the 5 branches sampled, as such we felt confident that our experiment would not be confounded by removing only two branches at the beginning and four at the end of our experiment.

5.4 Results

5.4.1 Site fidelity and foraging area of juvenile butterflyfish

The foraging area of juvenile *C. plebeius* differed significantly between size classes (ANOVA, $F_{4,86}$=172.14, p<0.0001) and showed a general increase with increasing size of each fish (Figure 5.1). Likewise, as foraging area increased there was also a significant increase in the number of colonies preyed upon (ANOVA, $F_{4,86}$=48.62, p<0.0001). Smaller juveniles (<30mm) were extremely site attached with 88% (38/43) of these juveniles foraging within only one coral colony. Foraging area increased rapidly for larger juveniles with a five-fold increase (0.43 ± 0.11 vs 1.95 ± 0.19m^2) between medium and large juveniles, with a further four-fold increase to 7.5m^2 (± 0.91) for very large juveniles. Very large juveniles also fed from significantly more coral colonies (Tukey's HSD, p<0.0001) (Figure 5.1). Feeding upon multiple colonies was only observed in 9.3% (5/43) of observations upon smaller juveniles (<30mm TL) compared to 87.5% (42/48) of larger juveniles (>30mm). When smaller juveniles did feed from multiple colonies they travelled less than 10cm. Furthermore, the smallest juveniles (<20mm) were always observed down inside the branches of the host coral, typically inhabiting the lower two thirds of the branch, whereas larger juveniles (>30mm) tended to forage across the top of the colony itself and only used the top section of branches as shelter when threatened.

5.4.2 Effect of predation by C. plebeius juveniles on colony condition

Colonies of *A. spathulata* that were naturally occupied by *C. plebeius* had significantly (ANOVA, $F_{1,38}$=38.43, p<0.0001) lower tissue biomass per unit area compared to colonies that did not host juveniles. Occupied colonies had 41.7% lower tissue biomass compared to unoccupied colonies, however no difference (ANOVA, $F_{1,38}$=1.13, p>0.05) in total lipid content was detected between the two groups (Figure 5.2).

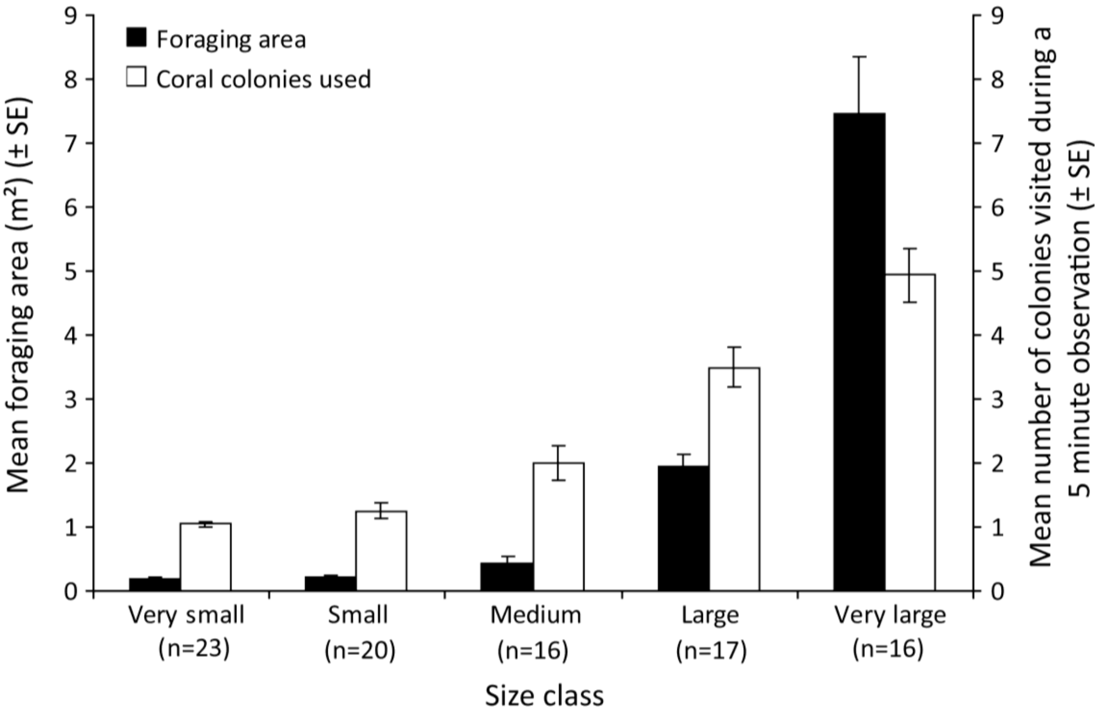

Figure 5.1: Foraging area size (m^2) and the number of coral colonies fed from during a 5 minute observation for five size classes of juvenile *Chaetodon plebeius*; very small (<20mm), small (20.1-30mm), medium (30.1-35mm), large (35.1-40) and very large (40.1-50mm).

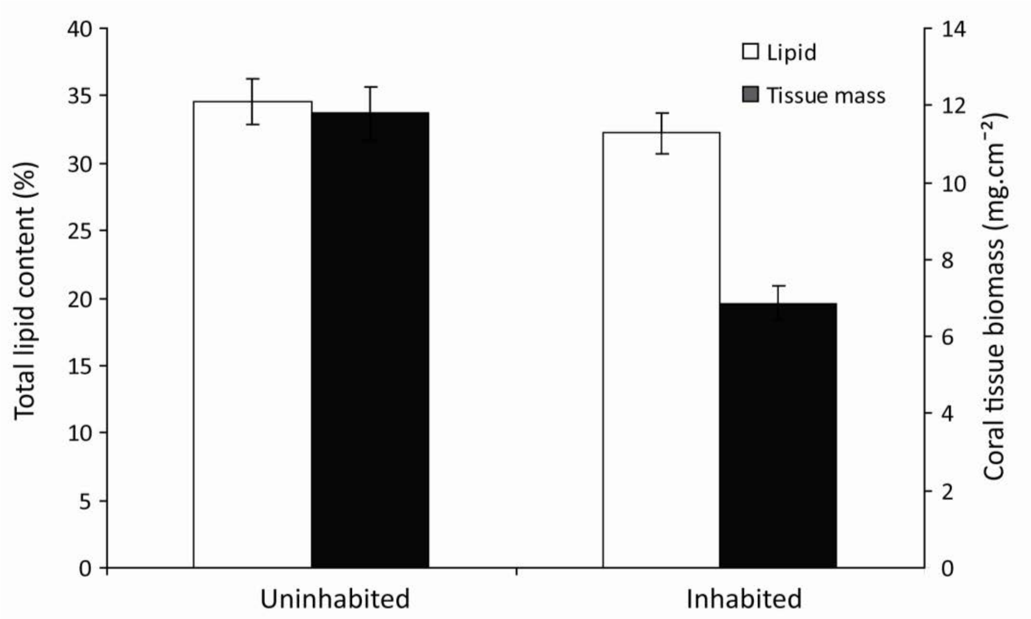

Figure 5.2: Total lipid content (%) and tissue biomass ($mg.cm^{-2}$) of *Acropora spathulata* colonies that were naturally inhabited by juvenile *Chaetodon plebeius* and those that were uninhabited.

Experimental manipulations, whereby juvenile *C. plebeius* were moved to previously unoccupied colonies, confirmed that declines in tissue biomass were attributable to feeding by resident fishes (Table 5.1). Increasing predator density caused a corresponding decline in tissue mass of 26.7%, 44.5% and 53.4% under low, medium and high predation intensities over the course of this experiment (Figure 5.3). In comparison, tissue mass in the control treatment declined by 16.1%. A significant (Table 5.1) decline in total lipid content of 29-38% occurred across all treatments at both reefs during this experiment (Figure 5.3). Declines in lipid content were independent of predation intensity and there was no significant interaction between time and predation intensity (Table 5.1).

Table 5.1: Repeated measures ANOVA comparing a) tissue mass and b) total lipid content of *Acropora spathulata* colonies exposed to 4 levels of predation intensity: control (no juveniles), low (less than one juvenile per 1200cm^2), medium (1 juvenile per 650-900cm^2) and high (1 fish per 250-500cm^2).

Source of variation	**d.f**	**F**	**P**
a) Tissue mass			
Intensity	3	38.379	**<0.0001**
Reef	2	0.338	NS
Time	1	319.057	**<0.0001**
Reef x intensity	6	1.967	NS
Time x reef	1	0.309	NS
Time x intensity	3	16.241	**<0.0001**
Time x reef x intensity	3	0.407	NS
Error	24		
b) Total lipid content			
Intensity	3	0.323	NS
Reef	2	1.652	NS
Time	1	85.89	**<0.0001**
Reef x intensity	6	2.631	NS
Time x reef	1	0.13	NS
Time x intensity	3	0.261	NS
Time x reef x intensity	3	0.124	NS
Error	24		

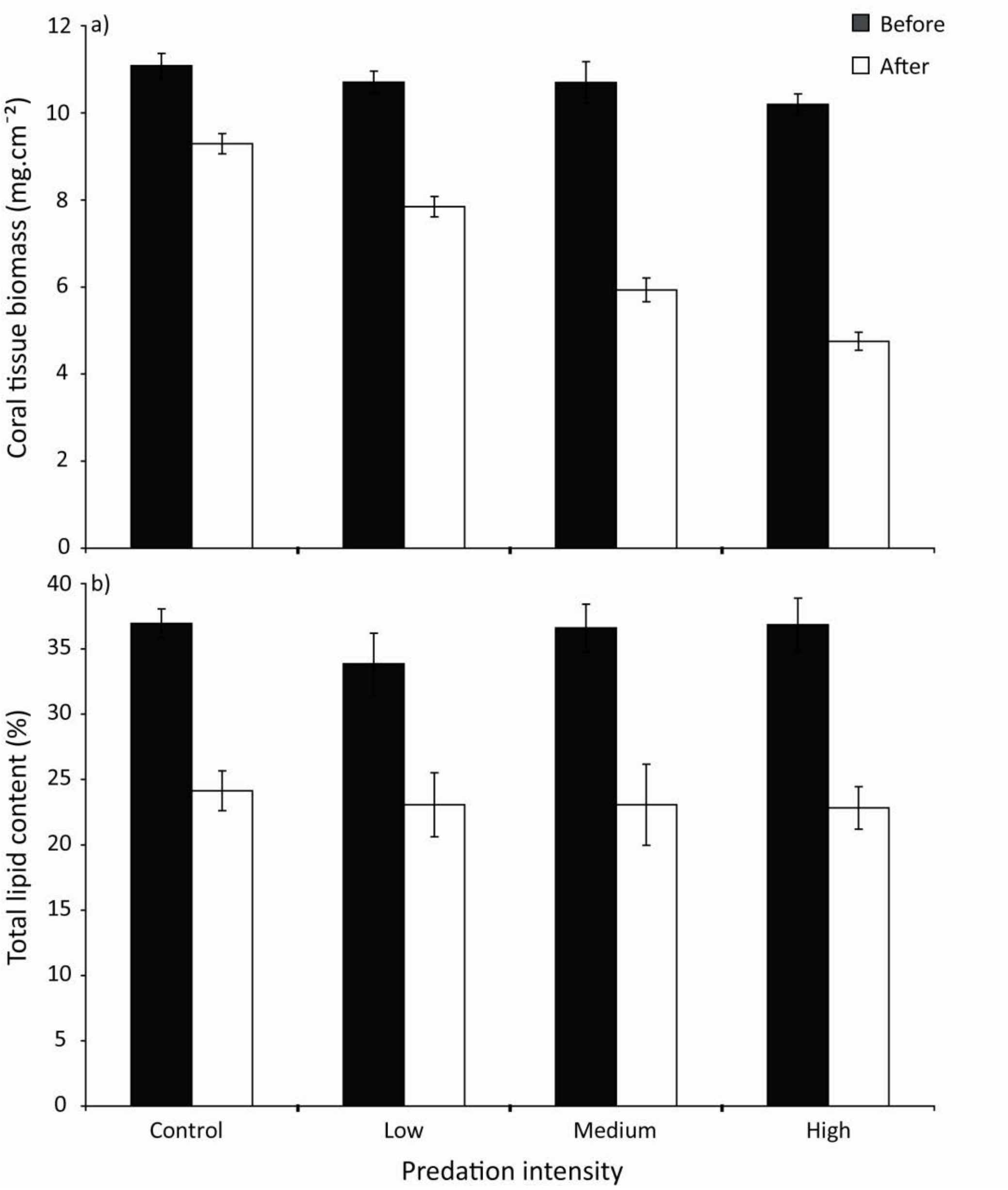

Figure 5.3: Mean tissue biomass (mg.cm^{-2}) and total lipid content (%) of *Acropora spathulata* colonies subjected to different predation intensities: control (no juveniles), low (less than one juvenile per 1200cm^2), medium (1 juvenile per 650-900cm^2) and high (1 fish per 250-500cm^2) by juvenile *Chaetodon plebeius*. Values are the means and standard errors of the two reefs: Osprey Inlet and Station reef combined.

5.5 Discussion

This study confirms that coral-feeding butterflyfishes show very high site fidelity to the coral colonies in which they initially settle (Fowler 1989, Pratchett et al. 2008a). Juvenile butterflyfishes direct their entire feeding effort towards their settlement coral and only begin to expand their foraging area when total length exceeds 30mm. Predation by juvenile butterflyfishes has negative consequences on tissue biomass but not total lipid content. Tissue biomass per unit area declined with increasing predation intensity in both our natural comparison and our experiment. Tissue biomass is an important measure of coral condition, with declines linked to a stressed state (Szmant and Gassman 1990, Barnes and Lough 1999, Fitt et al. 1993, 2000, Anthony and Fabricius 2000). Stress caused by experimentally shading colonies of *Porites cylindrica*, for example, resulted in an 80% reduction in tissue growth rates over a 2 month period, while the combination of high suspended particulate matter and shade resulted in negative tissue growth (Anthony and Fabricius 2000). Likewise, Barnes and Lough (1999) documented a linear decline in tissue thickness of massive *Porites* colonies across four sites of increasing levels of sedimentation.

In our study, total lipid content of all corals declined relatively evenly (29-38%) at both sites independently of predation intensity. This was most likely a consequence of the corals spawning midway through our experiment. At Lizard Island the mass spawning of corals occurs 2-7 days after the full moon in November (Baird et al. 2002). Coral propagules are composed of 50-70% lipids and represent a significant energetic investment by coral colonies (Richmond 1987, Arai et al. 1993, Leuzinger et al. 2003). Similar declines in lipid content of corals following spawning have been observed in previous studies (Ward 1992, 1995, Leuzinger et al. 2003, Anthony 2006, Harii et al. 2007). Total lipid content declined by 20-45% for *Acropora valida* following mass spawning on the central Great Barrier Reef in 2002 (Anthony 2006).

As a consequence of the mass spawning event and the loss of egg and sperm bundles the overall weight of coral tissue for a given area also declines. In our study all treatments experienced a decline in tissue biomass per unit area. However, our control colonies experienced a much lower decline in tissue biomass than the three predation treatments (Figure 5.3). A small component of this decline in tissue biomass can be explained by the loss of coral reproductive material, while the remaining decline is caused by the increase in predation intensity. The data from our natural comparison also supports this conclusion. In these colonies branch samples were taken prior to the mass spawning event, and no difference in total lipid content was detected between colonies inhabited by juveniles and those without juveniles. However, colonies that were occupied by juvenile butterflyfishes had a 41% lower tissue mass per unit are compared to unoccupied colonies (Figure 5.2). This congruency in the decline in tissue biomass between our experiment and natural comparison provides strong evidence that the decline in total lipid content is a consequence of coral reproduction and the loss of lipid-rich eggs, while the decline in tissue biomass is a consequence of chronic predation by juvenile butterflyfish. This implies that feeding by juveniles alters the quantity of coral tissue available, but not the nutritional quality of that tissue.

Predation by juvenile butterflyfishes is a significant energetic cost for the corals they inhabit, with no evidence of the positive benefits observed in other studies, such as where coral-dwelling damselfish increased the growth and condition of host colonies (Meyer and Schultz 1985a, Liberman et al. 1995, Holbrook et al. 2008). The mechanism that causes these benefits in other studies, nutrient enhancement through fish metabolism, should also be present in this study as juvenile butterflyfish live within the branch structure and produce ammonia and other nutrients similar to coral-dwelling damselfish (Meyer and Schultz 1985b, Holbrook et al. 2008). This suggests that the negative consequences of chronic tissue consumption outweigh the benefits of enhanced nutrient supply. Alternatively, the small size of juvenile butterflyfishes could mean that the amount of ammonia produced is minor compared to larger bodied damselfish (e.g. Holbrook et al. 2008). Further, to avoid confounding our experiments we used colonies that did not have resident damselfish living within their branches. On colonies that also host planktivorous damselfish, nutrient supply and overall colony growth rates will be higher and would be expected to mitigate some of the negative effects on tissue biomass that were observed in our study (e.g. Holbrook et al. 2011).

All of the feeding effort of small juveniles (<30mm) is concentrated entirely upon their host colony and when this is compounded daily over a 6-8 week period the loss of tissue from these colonies will be considerable. The actual amount of coral tissue consumed by juveniles remains unknown, although assuming that individual fishes consume approximately 12% of their body weight in coral tissue each day, we expect it to be in the range of 0.01-0.10g of coral tissue per day for juvenile butterflyfishes (12-30mm) (*sensu* Cole et al. 2011). Thus coral consumption by juveniles, especially in high densities, represents a large drain on an individual colony’s energy reserves. The decline in tissue biomass observed in this study with increasing predation intensity could result from a situation where the speed at which coral tissue is being consumed outweighs the regenerative capacity of the corals. Even a slight imbalance between consumption and regeneration would be compounded as these juveniles grow and consume more tissue each day. The reduction in tissue biomass observed in this study may be the proximal cue for juvenile coral-feeding butterflyfishes (30-35 mm) to begin to expand their foraging area.

Tissue biomass has also been shown to vary seasonally, peaking in spring before steadily declining during the summer as seawater temperatures increase (Fitt et al. 2000). Our study was performed in the Austral spring which corresponds to the period when coral tissue biomass is expected to be at its peak (Fitt et al. 2000). As such, the relatively rapid (42 day period) declines in tissue biomass observed in our study may have significant consequences for the energetics and survival of these colonies during the summer months. To regain tissue biomass these colonies will need to invest energy into the regeneration of lost tissue. The speed that tissue can be regenerated is currently unknown, but is not likely to occur until after the juvenile butterflyfishes have outgrown their host colony and begin to forage across a larger area. If lipid reserves are utilised in regeneration, these colonies will enter the potentially more stressful summer period with reduced energy reserves. As such, these colonies may have limited capacity to cope with additional stressors and potentially a higher susceptibility to mortality following a coral bleaching event (Anthony et al. 2009).

This study has identified clear negative effects for corals that act as settlement and growth habitat for juvenile butterflyfishes. Coral-feeding juveniles recruit in large numbers throughout the spring and summer months (Zekeria et al. 2006, Pratchett et al. 2008a) and it is not uncommon to observe 4-7 juvenile butterflyfishes co-habiting within the same colony. As such, coral-feeding juveniles are likely to represent a chronic, but seasonal, stress on coral colonies. The effects of coral-feeding butterflyfishes on individual colonies is also likely to interact with and compound other natural and anthropogenic disturbance events (e.g. mass bleaching events), which lead to increasing coral loss throughout the world (Nyström and Folke

2001, Hoegh-Guldberg et al. 2007, Pratchett et al. 2008b, Anthony et al. 2009). Moreover, declines in the abundance of suitable settlement colonies will likely cause increases in the densities of juvenile butterflyfishes settling within any one colony. The results will be further stress on these colonies, while any increase in energy used in regeneration will have implications for future growth, reproductive output and resilience to environmental change.

Chapter 6: Consumption of tabular acroporid corals by reef fishes: a comparison with plant-herbivore interactions[6]

6.1 Abstract

Interactions between primary producers and consumers (i.e., grazers) are of fundamental importance to the successful functioning of ecological communities. Plant-herbivore interactions have been extensively studied and herbivory has been accepted as an important process contributing to the structure of terrestrial and aquatic ecosystems. In contrast, the functional importance of the ecologically equivalent interaction between scleractinian reef corals and polyp-feeding fishes is largely untested, but has generally been dismissed as unimportant. This study quantified the amount of tabular acroporid coral tissue biomass consumed at the population level by corallivorous butterflyfishes and determined the proportion of both the standing biomass and productivity that is consumed annually at three exposed reef crest sites at Lizard Island, Great Barrier Reef, Australia. Total daily coral consumption ranged from 18.6 (± 1.6) to 27.4 (± 1.5) $g.200m^{-2}.day^{-1}$ with 61-68% of this consumption directed towards tabular acroporid corals. This selective feeding resulted in an annual consumption of between 8.9-13.5% of the total available tissue biomass and between 52-79% of the annual productivity of these tabular acroporid corals. The proportion of standing coral tissue biomass removed by corallivorous butterflyfishes is similar to that removed from terrestrial plants by herbivores. In terrestrial systems even relatively low levels of defoliation can have significant effects on plant growth rates, seed production and overall fitness. Considering the high proportion of productivity that is consumed by polyp-feeding fishes it would seem incongruous that these grazing fishes do not have similar effects on coral community structure and population dynamics. Our findings highlight the need to revisit previously held assumptions regarding the functional importance of corallivorous fishes to coral reef ecosystems.

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[6] This chapter is currently in review with the journal *Functional Ecology*.

6.2 Introduction

Predation is a common process structuring primary producers in all ecosystems. Trophic interactions between primary producers and consumers typically involve modular organisms in which predation results in only partial mortality, enabling the prey organism to regenerate lost tissue and maintain its place in the community (Henry and Hart 2005). One of the most extensively studied interactions between primary producers and consumers is that of herbivory (Crawley 1989, 1997, Huntly 1991, Bigger and Marvier 1998, Maron and Crone 2006). Herbivores exploit a food source that is fundamentally different from that of most other trophic levels. Plants represent a nutritionally poor but widely available, renewable food resource that is rarely consumed in its entirety by herbivores but rather only small proportions are consumed at any one time (Crawley 1983, Huntly 1991, Coley and Barone 1996). Understanding plant-herbivore interactions has been a major research focus of terrestrial ecologists and there is a general acceptance that grazing herbivores consume a significant proportion of the edible plant biomass within an ecosystem (Crawley 1997, Maron and Crone 2006, Engelkes et al. 2008*,* Ancheta and Heard 2011). For example, annual defoliation rates typically range between 3-30% of the total leaf biomass which equates to an average consumption of between 10-20% of the annual primary productivity of plant communities (Crawley 1989, 1997, Huntly 1991, Bigger and Marvier 1998).

On coral reefs, primary productivity by microscopic algae living within coral tissue provides much of the energy for corals and reef growth (Muscatine and Porter 1977). Although corals and their symbiotic algae are consumed by numerous reef fishes, the relationship between corallivorous fishes and scleractinian reef corals has received considerably less attention than interactions between plants and herbivores in either aquatic or terrestrial systems despite the broad similarities between these interactions (e.g. Carpenter 1986, Hay 1991, 1997, Bigger and Marvier 1998, Maron and Crone 2006). Furthermore, the majority of research investigating the role of corallivorous fishes on reefs has focused on predation from large bodied scarids and tetraodontids (e.g. *Bulbometapon muricatum, Arothron meleagris*), which can have strong direct effects on the coral community and limit the distribution and abundance of prey corals (e.g. Neudecker 1979, Wellington 1982, Littler et al. 1989, Miller and Hay 1998, Bellwood et al. 2003, Rotjan and Lewis 2008). These skeletal-feeding corallivores physically damage the coral skeleton when feeding and can remove a large biomass of coral material (Glynn et al. 1972, Reyes-Bonilla and Calderon-Aguilera 1999, Bonaldo and Bellwood 2011).

In contrast, small-bodied corallivores (e.g. butterflyfishes) consume live coral polyps and tissues but do not harm the underlying coral skeleton. As this predation leaves no visible evidence of damage, the potential effects that polyp-feeding fishes have on prey corals has typically been overlooked by reef ecologists whose focus has been on the relatively large and obvious effects of skeletal-feeders (Cole et al. 2008, Rotjan and Lewis 2008). Furthermore, the amount of coral tissue consumed by these polyp-feeders is likely to have been underestimated (Harmelin-Vivian and Bouchon-Navaro 1982, 1983, Cole et al. 2011) which has lead to the assumption that these fishes are of no significance to energy pathways, and thus polyp-feeding corallivores have generally been assigned a minimal role in the trophodynamics of reef systems (e.g. Hatcher 1988, Hixon 1997, but see Glynn 2004, Cole et al. 2011). Despite this, small-bodied corallivores feed continuously and at very high rates (400-700 bites per hour), are widely abundant on reefs throughout the Indo-Pacific and are ecologically similar to many small herbivores (Tricas 1985, Findlay and Findlay 2001, Gochfeld 2004, Cole et al. 2010). Both consume a nutritionally poor food source, are small relative to the size of their prey, have high dietary selectivity and consume only a small fraction of (and rarely kill) potential prey organisms (Gochfeld 2004, Cole et al. 2008). These fishes also forage over relatively small home ranges (*circa* 20-100m^2), meaning the same coral colonies are repeatedly consumed (Tricas 1985, 1989b, Wrathall et al. 1991, Righton et al. 1998, Berumen and Pratchett 2006). As such, polyp-feeding corallivores are likely to play a significant role in coral reef trophodynamics and we expect that the effects of continual tissue loss on scleractinian corals from polyp-feeding corallivores to be comparable to that of small herbivores on plants in terrestrial systems.

Predation by polyp-feeding corallivorous fishes rarely results in direct coral mortality, but rather represents a long term chronic stress on coral populations (Tricas 1985, Pratchett

2007). For example, a recent study found that each adult butterflyfish consumes up to 3g of coral tissue each day, suggesting that these fishes represent an important trophic link between corals and higher consumers (Cole et al. 2011). Moreover, most species show highly convergent patterns of prey use, feeding disproportionately upon species of tabular acroporid corals (e.g. *Acropora cytherea* and *Acropora hyacinthus*) (Figure 1b) (Irons 1989, Pratchett 2005, 2007, Berumen etal. 2005, Cole and Pratchett 2011). For example, the chevron butterflyfish, *Chaetodon trifascialis*, feeds almost exclusively upon these table corals regardless of their abundance (Irons 1989, Pratchett 2005, 2007, Berumen and Pratchett 2008). Even when tabular acroporids comprised only 0.32% of the coral community, this species still took 82.7% of its bites from these colonies (Irons 1989). The ecological significance of this highly selective tissue loss is currently unknown. However, we expect that the constant loss of coral tissue to act as a drain on energy reserves, where investment in regeneration of lost tissue occurs at the expense of growth and reproduction. But before the ecosystem effects of chronic tissue consumption can be assessed, the magnitude of tissue loss relative to the rate of production first needs to be estimated (e.g. Harmelin-Vivien and Bouchon-Navaro 1983, Hay 1997).

The aim of this study is to expand on the findings from Cole et al. (2011) which assessed the amount of coral tissue consumed by individual butterflyfishes and used estimates of corallivore abundances to estimate the amount of coral tissue consumed from the reef at the population level. In the current study we extend these findings by determining the proportion of this consumption directed towards tabular acroporid corals and estimating the proportion of both the standing biomass and potential productivity that this consumption represents. Tabular acroporids are a functionally important group of corals on reef crest habitats, providing much of the topographic complexity which plays a key role in enhancing the diversity of reef fish assemblages (reviewed by Pratchett et al. 2008). Likewise these corals are an important food resource and support the high diversity and abundance of *Chaetodon* butterflyfishes that occupy these reef habitats (Pratchett 2005). The potential impacts of chronic tissue consumption on coral colonies and reef trophodynamics will be explored using existing knowledge of plant-herbivore interactions from terrestrial ecosystems.

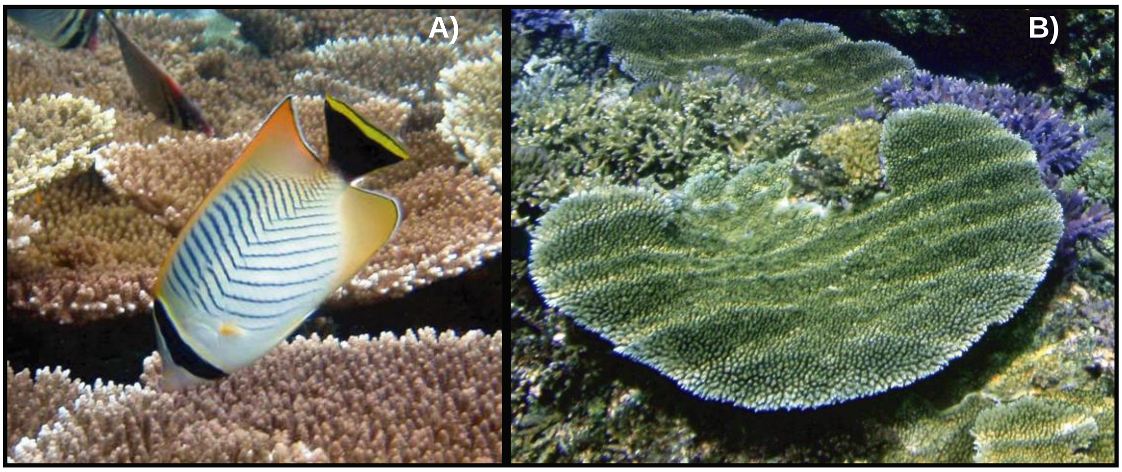

Figure 6.1: A) An adult corallivorous butterflyfish *Chaetodon trifascialis* (foreground) and *C. baronessa* (background) and B) a colony of a tabular acroporid coral (*Acropora hyacinthus*).

6.3 Methods

6.3.1 Study sites

This study was conducted at Lizard Island (14°409 S, 145°279 E), a continental island on the northern Great Barrier Reef (GBR), 35 km off the eastern coast of Australia. Sampling was conducted at three locations on the Northern, Eastern and Southern sides of Lizard Island: North Reef, South Island and South West Palfrey's. These three locations are separated by distances of 2–8 km but are all characterized by extensive contiguous fringing reef. In order to estimate the amount of live tissue removed from tabular acroporid corals, data was collected on the size and density of all coral-feeding fishes, their feeding rates, and the amount of tissue removed per bite by fishes of different size. Estimates of the total annual biomass of live coral tissue removed by coral-feeding fishes were then compared to estimates of net accumulation (proxy for productivity) for tabular Acroporid corals, to determine the proportion of live coral growth removed by coral-feeding fishes.

6.3.2 Corallivore abundance and coral community structure

Absolute densities and total lengths of all obligate coral-feeding butterflyfishes were quantified using underwater visual census, with ten replicate 50 x 4m belt transects surveyed at each site. Replicate transects were laid parallel to and approximately 3m from the edge of the reef crest. For all fishes recorded on transects, total length was visually estimated. Size estimations were validated by catching a subset of fish and comparing estimated versus actual length; all cases were found to be accurate to within 5mm.

The composition of the coral community on each of the ten transects used for fish census was assessed using the line point transect methodology. Line point transects have recently been assessed as the preferred method in sampling coral communities, giving the highest accuracy and precision when comparing between sites, they also have the advantage of sampling the coral community at the same scale as the fish community (Nadon and Stirling 2006). On these transects the substrate directly underneath the tape was recorded to species level for scleractinian corals and to broad categories (e.g. sand, rubble, pavement, macroalgae) for all other substrate types every 25cm, providing 200 sample points per transect. This data was used to determine the proportional cover of tabular acroporid corals at each site (Table 6.1, step 1).

6.3.3 Diet composition

To determine the proportional consumption of different coral species, 3 minute feeding observations were performed on 40 individuals of each of the three most abundant obligate corallivorous butterflyfishes at each site: *Chaetodon baronessa, C. lunulatus* and *C. trifascialis*, following Pratchett (2005). These three species accounted for 90% (313/348 individuals) of the obligate coral-feeding butterflyfishes recorded on the reef crest at these three sites. During feeding observations each individual was observed from a distance of 3m and the substrate upon which all bites were taken was recorded (following Pratchett 2005). A total of at least 40 observations were conducted for each of the three species at each site. This data was used to determine the proportion of bites taken by each of the three species at each site on tabular acroporids (Table 6.1, step 5).

6.3.4 Proportion of tabular acroporid tissue biomass consumed

To assess the proportion of tabular acroporid biomass that is consumed annually by corallivorous butterflyfishes we combined estimates of the amount of coral tissue eaten by fishes with the total available coral tissue biomass at each of the three sites. Firstly, we converted the proportional cover of tabular acroporids into an equivalent planar surface area on a 200m^2 transect (Table 6.1, step 2). This is an appropriate conversion as tabular acroporids have a relatively flat 2-dimensional table shape. As such the top down proportional cover will have only minor deviations from the equivalent planar surface area of substrate that is covered. Secondly, to assess the amount of coral tissue biomass avilable on a coral colony we calculated coral tissue mass-to-surface area ratios and a conversion factor which enabled the actual 3-dimensional skeletal surface area to be converted to an equivalent 2-dimensional planar surface area. These ratios enabled us to accurately estimate the amount of coral tissue available as it incorporates coral tissue from all surfaces of the coral colony. To calculate these ratios, one large branch section (10-15cm in length) was removed from 15 randomly chosen colonies of tabular acroporids. Each of these branches was given five abrupt shakes and then drip dried upside down on absorbent paper for 5 minutes to remove surface water. Each branch was then wet weighed with and without live tissue; coral tissue was removed by immersion in chlorine solution. The difference in weight between the two measurements corresponded to the amount of coral tissue on each branch. Top down digital photographs were taken of each branch which allowed the planar surface area to be calculated using the CPCe software (Kohler and Gill 2006). The 3-dimensional skeletal surface area of each branch was determined using the parafin wax technique following Vytopil and Willis (2001). To relate the increase in mass (g) between wax coatings to surface area a calibration relationship was determined using 15 PVC cylinders of known surface area ranging from 2.21 to 589.59cm^2. The regression relationship between increases in mass (x) and surface area (y) of the cylinders ($y = 45.212\mathrm{x} - 0.6756$, r^2=0.97) was then used to calculate the 3-dimensional skeletal surface area of each coral branch. To calculate the tissue mass-to-surface area ratio of each branch we divided the 3-dimensional skeletal surface area by the tissue weight for each branch. This gave a mean tissue mass-to-surface area ratio of 1g coral tissue to 36.68cm^2 (± 1.68 SE). Likewise, the 3-dimensional skeletal surface area of each branch was divided by its planar surface area to provide a mean conversion factor of 1cm^2 of 2-dimensional planar area equates to 4.94cm^2 (± 0.46 SE) of 3-dimensional surface area. This conversion factor was multiplied by the planar surface area of tabular acroporid corals (calcuated in step 2) for each of the three sites to provide the equivalent 3-dimensional surface area of tabular acroporid coral tissue available at each site (Table 6.1, step 3).

To assess the amount of coral tissue consumed by corallivorous butterflyfishes we used size specific regression equations determined in a previous study (Cole et al. 2011) which link the total length of individual butterflyfishes of each species with their daily coral consumption (Table 6.2). These regression equations were used to calculate the amount of coral tissue removed per day by each coral-feeding butterflyfish observed on each transect to provide an overall estimate of the total amount of coral tissue removed by all coral-feeding butterflyfishes per day per 200m^2 at each of the three study sites (Table 6.1, step 4). Two butterflyfish species (*C. rainfordi* and *C. trifascialis*) were detected on these transects for which size specific regression equations are not available. In these cases, regression equations of the closest related species were used (*C. aureofasciatus* and *C. baronessa* respectively) (Bellwood et al. 2010). The total amount of coral tissue removed per day by coral-feeding butterflyfishes at each site (Table 6.1, step 4) was then multiplied by the proportion of bites taken by each species on tabular acroporids (*A. hyacinthus* and *A. cytherea)* at each of the three sites based on our feeding observation data (Table 6.1, step 5) to determine the total amount of tissue removed from tabular acroporids per 200m^2 per day (Table 6.1, step 6). *Chaetodon aureofasciatus, C. rainfordi* and *C. plebeius* are generally rare on the reef crest habitat and accounted for less than 10% (31/344) of the total abundance of obligate corallivores in our study. As such we did not perform feeding observations on these species but rather used previously published estimates on the proportion of their diet that is focused on tabular acroporids, with these values ranging between 15 and 20% (Pratchett 2005, Berumen and Pratchett 2008).

The tissue mass-to-surface area ratio was multiplied by the daily amount (g) of coral tissue removed from tabular *Acropora* colonies (Table 6.1, step 6) to convert the total amount of coral tissue consumed per day to an equivalent 3-dimensional surface area (cm^2) of coral (Table 6.1, step 7). To calculate the proportion of tabular acroporid tissue consumed annually by corallivorous butterflyfishes we multiplied the areal equivalents of daily coral consumption estimates by 365 (Table 6.1, step 8) and divided by the actual 3-dimensional surface area of tabular acroporids tissue that was available at each site (Table 6.1, step 9). To calculate the error around our estimate of annual consumption we repeated these calculations three times; once using the mean value for each variable in all calculations, once using the mean plus one standard error in all calculations and once using the mean minus one standard error, with our final error values representing the deviation from the mean in our three calculations. We do not expect the extrapolation from daily to yearly consumption estimates to be distorted by seasonal differences in feeding rates. Unlike herbivorous fishes corallivorous butterflyfishes are surprisingly consistent and no study has documented a significant effect of season on the feeding rates of these fishes (e.g. Cox 1986, Hourigan, Tricas and Reese 1988, Irons 1989, Pratchett 2005, Gregson et al. 2008).

5.3.5 Proportion of coral productivity consumed

To estimate of the proportion of primary productivity of tabular acroporids that is consumed by corallivorous fishes we used the annual increase in proportional cover as a proxy for productivity. To calculate the average annual increase in proportional cover of the family Acroporidae, Thompson and Dolman (2010) used data collected annually (1985-2007) from 36 near shore reefs of the GBR (between 16°S and 23°S) by the Australian Institute of Marine Sciences long term monitoring program. Thompson and Dolman (2011) used data only during periods that had no major disturbance events (e.g. cyclones, crown-of-thorns starfish, coral bleaching events) to calculate the proportional increase of the coral community. The Acroporidae increased in proportional cover at an average annual rate of 16.9% (Thompson and Dolman 2010). While this estimate of annual growth does not include estimates from mid-shelf reefs, it does represent a wide spatial and temporal dataset of growth rates and there are no other estimates of annual areal increase available for acroporid corals on the GBR. As such it is the best available estimate for determining the potential productivity of tabular acroporids at Lizard Island. To calculate the net accumulation and potential productivity of tabular acroporid corals at Lizard Island, the average proportional increase (16.9% per annum) was multiplied by the current proportional cover of tabular acroporids at each of the 3 sites (Table

6.1, step 10). This amount was then converted to a 2D planar surface area per 200m2 (Table 6.1, step 11). The annual change in planar surface area of tabular acroporids was calculated based on the growth rates reported in Thompson and Doman (2010) (Table 6.1, step 12), and then converted to an equivalent 3-dimensional skeletal surface area (Table 6.1, step 13). To calculate the annual amount of potential productivity that is consumed by coral-feeding butterflyfishes (Table 6.1, step 14), the total area of tabular acroporid tissue consumed annually by corallivorous butterflyfishes (Table 6.1, step 8) was divided by the total annual increase in acroporid tissue due to growth (Table 6.1, step 13).

While the approach of using net accumulation as a proxy for productivity is not ideal and will result in an overestimation relative to the consumption of actual net primary productivity (which is measured as gross primary productivity minus respiration), it does represents a comparable method to previous studies which have typically used some aspect of biomass increase between caged and uncaged plots as a proxy for productivity (Cargill and Jefferies 1984, McNaughton 1985, Pandey and Singh 1992, McNaughton et al. 1998, 1996, Russ and McCook 1999, Russ 2003, Vanderklift et al. 2009, Stein et al. 2009 etc.). In our study we have used the term ‘potential productivity’ and acknowledge that true net primary productivity will be higher than measured here.

6.4 Results

6.4.1 Corallivore abundance and coral community structure

A total of 348 obligate coral-feeding butterflyfishes were detected across the three sites with 90% of these belonging to just 3 species, *C. baronessa, C. trifascialis* and *C. lunulatus*. The mean density of obligate coral-feeding butterflyfishes differed significantly (ANOVA, $F_{2,27}$=6.96, $p<0.01$) among the three sites with North Reef (13.2 ± 0.9 per 200m^2) and South West Palfrey’s (12.4 ± 0.7 per 200m^2) having a significantly (Tukey’s HSD, $p<0.05$) higher density compared to South Island (9.2 ± 0.8 per 200m^2). The community composition differed slightly between the three sites, with North Reef having a significantly (Tukey’s HSD, $p<0.05$) higher density of *C. baronessa* than either of the other sites, with a mean density of just over double South Island (Figure 6.2).

Total hard coral cover was significantly higher at South West Palfrey's (52% ± 2.2), than South Island (38% ± 2.9) or North Reef (38.2% ± 3.4) (ANOVA, $F_{2,27}$=7.96, p<0.01). Coral community structure varied little between the three sites with corals from the *Acropora* genus accounting for 70-80% of the live coral cover. Tabular acroporids were the single most abundant group within this genera accounting for 18-25% of the proportional cover among sites. The remaining coral community was made up of 25 species from seven families with these species having a low relative cover. Of these other corals, no individual species ever accounted for more than 3% of the total cover (Figure 6.3).

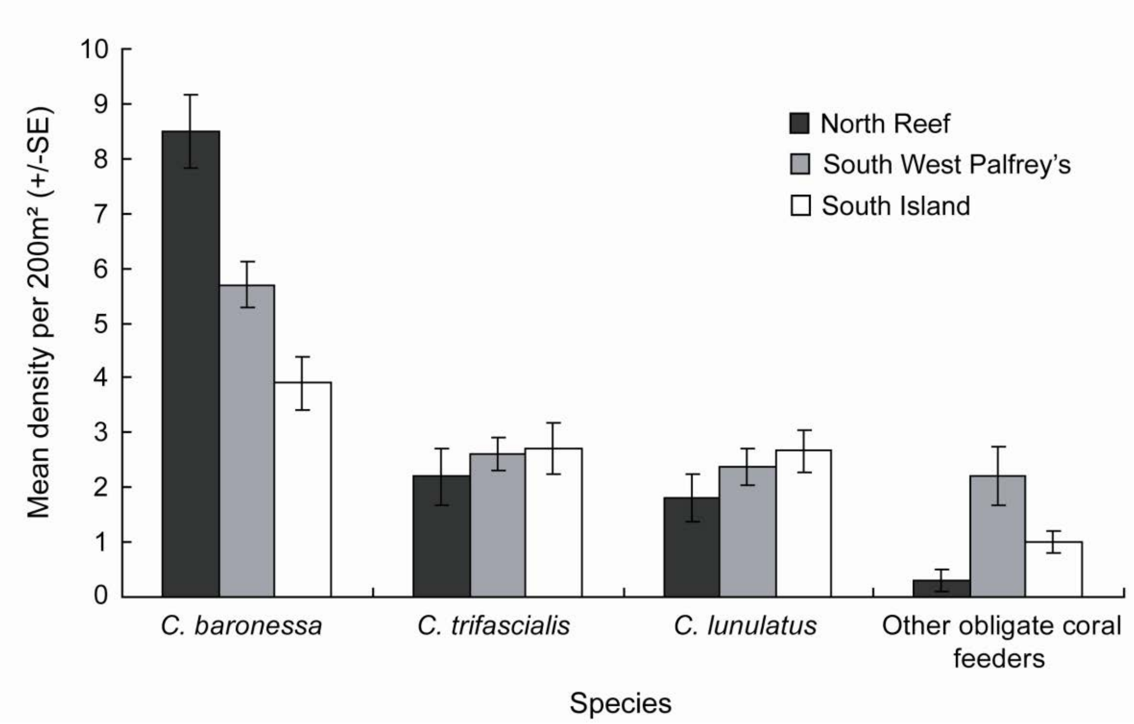

Figure 6.2: Mean density of corallivorous butterflyfishes at three exposed reef crests: North reef, South-West Palfrey's and South Island. Other obligate coral-feeders included *Chaetodon plebeius*, *Chaetodon aureofasciatus* and *Chaetodon rainfordi*. Values are the means and standard errors of the number of fish counted on ten 50 by 4m transects at each site.

6.4.2 Diet composition

Among the three study species a total of 14,113 bites were observed with 63% (8914/14113) of these taken on colonies of tabular acroporids. Diet composition varied little between the three study sites for each species. *Chaetodon trifascialis* was the most selective, taking between 83.9% and 91.6% of bites from tabular acroporids with the remaining bites focused primarily on other *Acropora* spp. *Chaetodon baronessa* was also highly selective in its feeding and took between 68.3% and 80.3% of bites from tabular acroporids with its remaining diet evenly dispersed between other *Acropora* spp. and *Pocillopora* spp. *Chaetodon lunulatus* had a generalist diet and dispersed its feeding relatively evenly across all available corals. Tabular acroporids accounted for 28.4% and 34.5% of *C. lunulatus* bites at South Island and North Reef respectively, but at Palfrey's the main dietary item was other *Acropora* spp. (50.7% of observed bites) and tabular acroporids only accounted for 25.7% of bites (Figure 6.3).

6.4.3 Total biomass and annual consumption of productivity of tabular acroporids

Total daily coral consumption by all obligate corallivores varied significantly (ANOVA, F2,27=13.42, p<0.001) between the three reefs and ranged from a low of 18.63 (± 1.6) g.200m-2.day-1 at South Island to highs of 26.9 (± 1.3) g.200m-2.day-1 and 27.4 (± 1.5) g.200m-2.day-1 at South West Palfrey's and North Reef respectively. Approximately 60% of total coral consumption by obligate coral-feeding butterflyfishes is on tabular corals which relates to an annual consumption of 8.9-13.5% of the tabular acroporid tissue biomass available at the three sites (Table 6.1). If tabular acroporids are increasing in proportional cover at a rate of 17% per annum this would increase the areal cover of tabular acroporids by 6-8.5m2 which means corallivorous butterflyfish consume approximately 52-79% of the annual potential productivity of tabular acroporid corals (Table 6.1).

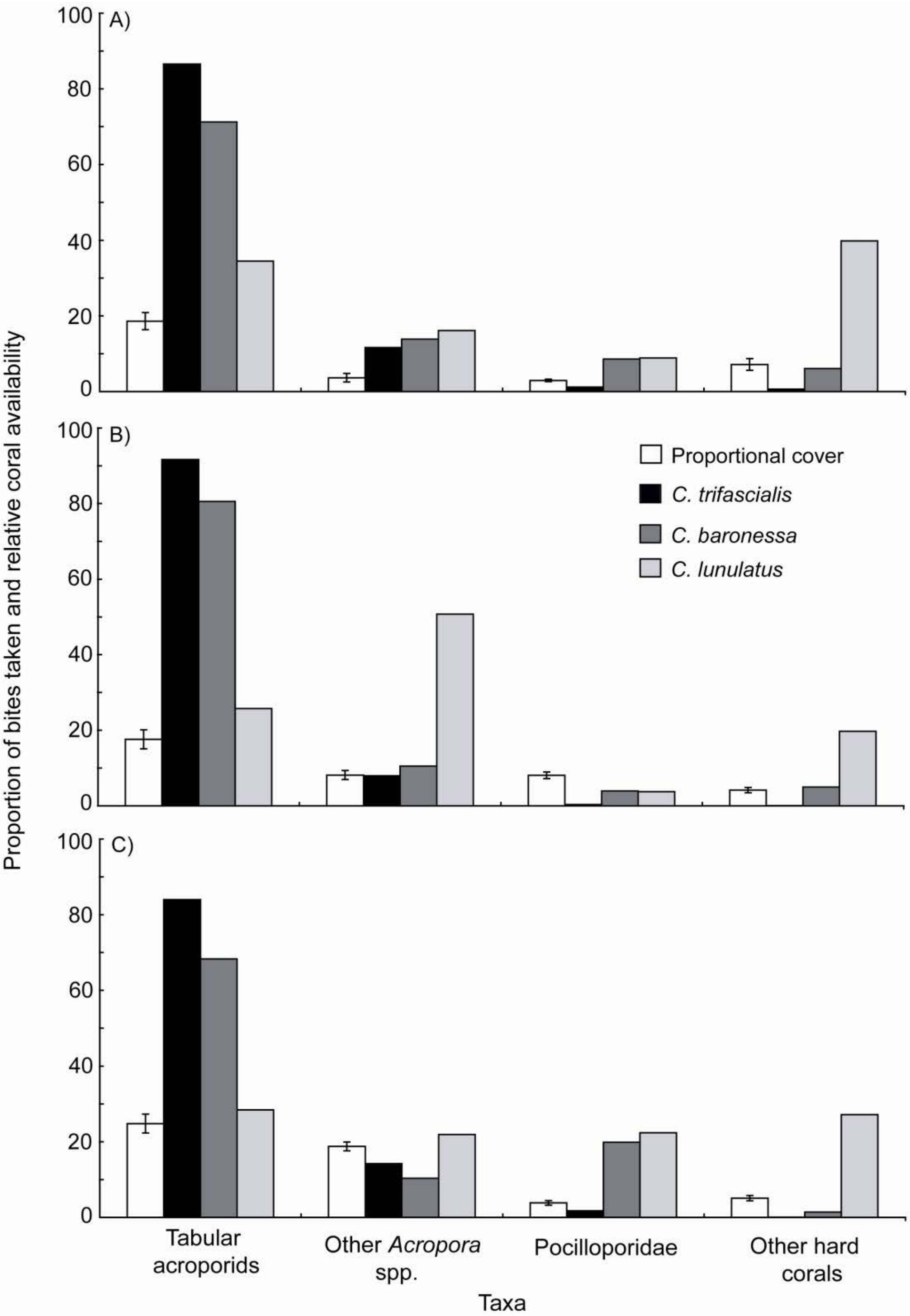

Figure 6.3: Diet composition of the three most abundant corallivorous butterflyfish; *Chaetodon trifascialis*, *C. baronessa* and *C. lunulatus*, and coral availability at the three exposed reef crest habitats: A) North Reef, B) South West Palfrey's and C) South Island. Values are the proportion of the total bites taken on each coral resource category during three minute observations of 40 individuals of each species at each site. Coral availability is presented as the mean (±SE) of the proportional cover of each coral resource averaged across ten, 50m point-intercept transects at each site

Table 6.1: Calculation of the proportion of tabular acroporid coral tissue biomass and productivity consumed annually by obligate coral-feeding butterflyfishes. Values are the site means with standard error in parenthesis.

Coral availability	**North Reef**	**South Island**	**South-West Palfrey's**
1. Proportional cover of tabular acroporids (%)	18.6 (2.3)	17.6 (2.5)	24.8 (2.5)
2. Planar surface area of tabular acroporids ($m^2/200m^2$)	37.2 (4.5)	35.2 (5.1)	49.6 (5.0)
3. Equivalent 3D surface area ($m^2/200m^2$) **(A)**	183.8 (22.3)	173.9 (25.0)	245.0 (24.7)
Proportion of tissue biomass consumed			
4. Mean coral tissue consumed ($g.200m^{-2}.day^{-1}$)	27.4 (1.5)	18.6 (1.6)	26.9 (1.3)
5. Proportion (%) of bites taken from tabular acroporids	67.6	61.6	66.9
6. Total tissue removed from tabular acroporids ($g.200m^{-2}.day^{-1}$)	18.5 (1.2)	11.5 (0.9)	18.0 (1.2)
7. Total 3D area of tissue removed ($cm^2/200m^2/day$) **(B)**	678.6 (43.0)	421.8 (32.9)	660.2 (42.3)
8. Total area of tissue removed annually ($m^2.200m^{-2}.yr^{-1}$) (step 7 x 365 ÷10000)	24.8 (1.6)	15.4 (1.2)	24.1 (1.5)
9. Proportion (%) of tabular acroporid tissue consumed annually (step 8 ÷ by step 3.)	13.5 (0.7)	8.9 (0.5)	9.8 (0.4)
Proportion of productivity consumed			
10. Increase in the proportional cover of tabular acroporids (%) (step 1 multiplied by 117%)	21.8 (2.6)	20.6 (3.0)	29.0 (2.9)
11. Planar surface area of tabular acroporids ($m^2/200m^2$)	43.5 (5.3)	41.2 (5.9)	58 (5.8)
12. Change in planar surface area of tabular acroporids ($m^2/200m^2$) (step 11 – step 2)	6.3 (0.8)	6 (0.9)	8.4 (0.8)
13. Equivalent 3D surface area ($m^2/200m^2$) **(A)**	31.1 (4.5)	29.6 (5.1)	41.5 (5.0)
14. Proportion of tabular acroporid productivity consumed annually (%) (step 8 ÷ by step 13)	79.7 (3.3)	52.0 (2.4)	58.1 (2.7)

A. Converted using a 2D planar area to 3D skeletal surface area ratio of 1 cm2 : 4.94 cm2

B. Converted using a tissue mass to surface area ratio of 1g : 36.68 cm2

Table 6.2: Size specific regression equations determining the amount of coral tissue (y) removed for a fish of a given size (x) for four species of corallivorous chaetodontids, based on data from Cole et al (2011, chapter 4).

Species	**Consumption equation**
C. baronessa	$y = 0.0348x - 1.2645$
C. lunulatus	$y = 0.0308x - 1.1813$
C. aureofasciatus	$y = 0.0313x - 1.1401$
C. plebeius	$y = 0.03x - 1.3947$

6.5 Discussion

This study demonstrates that coral-feeding butterflyfishes consume a significant proportion of both the standing biomass and annual potential productivity of tabular acroporid corals. This challenges the idea that coral-feeding butterflyfishes consume only minor amounts of coral tissue and subsequently have negligible effects on coral health (e.g. Harmelin-Vivian and Bouchon-Navaro 1982, 1983, Hixon 1997). Further, these estimates are likely to be conservative as there are many other corallivorous fishes that feed on corals whose consumption rates were not considered in our calculations. For example, at our study sites the facultative corallivore *Chaetodon citrinellus* was also relatively abundant with a mean density of between 3-5 individuals per transect and tabular acroporids account for approximately 20% of the diet of this species (Pratchett 2005). Likewise, many reefs throughout the Indo-Pacific also have obligate polyp-feeders from other families (e.g. Labridae) (Cole et al. 2010). In the present study we could not assess the contribution of these corallivores as we do not have any data on bite size and daily coral consumption rates. With these limitations in mind, if the corallivore guild is considered as a whole, the total biomass consumed will be considerably larger than the amount estimated here, calling into question the assumption that chronic tissue loss will have only minor impacts on coral populations.

In terrestrial systems, herbivores are often highly selective in the range of plant species that they consume and, generally, the smaller the herbivore the higher the level of dietary specialisation (Crawley 1983, 1989, 1997). Similarly, coral-feeding fishes are highly selective in their feeding behaviour and consume preferred coral prey disproportionately to their abundance (Irons 1989, Berumen, Pratchett and McCormick 2005, Pratchett 2005, 2007). At Lizard Island the proportional cover of tabular acroporids ranged from 17-25% of the total benthos, but 63% (8914/14113) of the observed bites by the three most abundant corallivores (*C. baronessa, C. lunulatus* and *C. trifascialis*) were taken on these corals. This selective predation translates to an annual consumption of between 9-13.5% of the standing biomass of tabular acroporid colonies in reef crest habitats. These total consumption estimates are within the range observed in terrestrial systems where herbivores typically consume between 3-30% of the total leaf area in an ecosystem annually (reviewed by Crawley 1983, 1997). In terrestrial systems even relatively low levels of defoliation can have significant effects on the fitness of certain plant species. For example, persistent low levels of insect herbivory on oak trees removed 8-12% of the total leaf area annually; this tissue loss resulted in significantly reduced seed production relative to control trees (Crawley 1985). As such, it is likely that a corresponding level of tissue loss through corallivory will have comparable impacts upon corals.

While the total biomass consumed by corallivorous fishes is similar to terrestrial herbivores, our estimate that between 52-79% of the potential productivity of tabular acroporids is consumed by corallivorous butterflyfishes annually is much higher than similar studies in terrestrial systems. Herbivores, on average, consume only 10-20% of the annual productivity (Crawley 1983, 1997, Cyr and Pace 1993, Bigger and Marvier 1998). Within these estimates, though there is considerable variation between habitats, and the amount of productivity consumed can range as high as 60% for highly productive grazing lawns in the Serengeti (McNaughton 1985, Frank et al. 1998). Marine herbivores consume a much higher proportion of productivity than their equivalents in terrestrial ecosystems (Carpenter 1986, Cyr and Pace 1993, Hay 1997). Herbivorous fishes (F: Scaridae, Acanthuridae), for example, consume between 40-100% of the daily productivity of turf algal communities on coral reefs, with this consumption highest on the reef crest (Carpenter 1986, Russ 1987, Klumpp and Polunin 1990, Van Rooij et al. 1998). Intense grazing by these fishes maintains turf algal communities in a highly productive but low standing biomass state with these fishes representing the largest energy flux on coral reefs (Carpenter 1986, Russ 2003). In both marine and terrestrial systems fast growing, highly productive algal/plant species are frequently eaten while slower growing species are generally avoided or consumed in low proportions as a consequence of chemical or physical defences which make them unpalatable (Tricas 1989a, Augustine and McNaughton 1998, Endara and Coley 2011). In a meta-analysis that related terrestrial plant growth rates to the proportion of photosynthetic biomass consumed daily by herbivores, Cebrian and Duarte (1994) demonstrated that herbivory increased with plant turnover rate and fast growing species supported a disproportionately larger herbivore pressure than slower growing counterparts. They concluded that herbivory is likely to be an important mechanism depressing plant biomass in fast growing plant communities (Cebrian and Duarte 1994). A similar result is likely occurring on coral reefs in which the biomass of herbivorous fishes correlates more strongly with algal productivity than alga biomass (e.g. Russ 2003). Likewise, a similar relationship with productivity may explain why corallivorous fishes reach their highest densities on the reef crest where the fast growing *Acropora* corals also reach their highest densities (Pratchett and Berumen 2008).

The combined proportion of productivity that enters the foodweb through corallivorous and herbivorous fishes is much higher than terrestrial ecosystems (with the exception of highly productive grasslands) and raises the question of why such a high proportion of the primary productivity is consumed on coral reefs. The answer remains unclear but is likely related to the oligotrophic state of coral reefs. Under these conditions, efficient nutrient cycling and turnover of primary productivity is necessary to maintain the high consumer biomass characteristic of coral reefs. In terrestrial ecosystems the majority (80-90%) of the biomass produced by plants is not consumed by herbivores. Rather fallen leaves enter the foodweb through decomposers (Crawley 1983, Lowman 1992). Although primary consumers on coral reefs remove a much higher proportion of the productivity of coral and turf algal communities, it is unlikely that much of this consumption enters higher trophic levels directly. Predation rates upon adults of both polyp-feeding corallivores and larger herbivores (e.g. scarids, acanthuroids) are extremely low and these fish are rarely found in the stomachs of predators (e.g. Hiatt and Strasburg 1960, St John 1999, Mumby et al. 2006, Farmer and Wilson 2011, but see Kingsford 1992). Furthermore, butterflyfishes are relatively long lived (10-14yrs) (Berumen 2005, Zekeria et al. 2006) and much of the primary productivity consumed by these fishes will be used to meet the fishes' growth and metabolic demands and will be effectively held static in this trophic level until they die through natural causes (e.g. disease, senescence, etc.). After this, the productivity consumed will be released through the detrital foodweb. Between 50-80% of the primary productivity on coral reefs is processed by detritivores (Hatcher 1983, Arias-Gonzalez et al. 1997). The importance of both the detrital pathway and small detritivores (e.g. gobies, blennies) in recycling and transferring primary productivity to higher consumers in the coral reef food chain has only recently been recognized (Wilson et al. 2003, Depczynski and Bellwood 2003, Wilson 2004, Depczynski et al. 2007). This similar dependence upon the detrital foodweb in both marine and terrestrial ecosystems indicates that these systems broadly function in similar ways. The main difference is the relatively large proportion of primary productivity that is consumed and incorporated into the standing biomass of corallivorous and herbivorous fishes before cycling through the detrital foodweb, whereas in terrestrial systems the majority of productivity is consumed directly by decomposers (Crawley 1983).

It is likely that our study overestimates the proportion of primary productivity lost through corallivory; there are two main areas in our study that could contribute to this overestimation. Firstly, increases in proportional cover represent growth in both coral tissue and skeleton, whereas the proportion of productivity consumed is only based on the tissue component. This assumption will result in productivity being underestimated as energy used to produce the carbonate skeleton of corals is not incorporated in our calculations. However we do not expect this to be a major error in our study as skeletal growth is energetically cheap and the growth of most branching corals is tissue dominated (Barnes and Chalker 1990, Anthony et al. 2002). For example, a model developed by Anthony et al. (2002) indicated that for every 100J of energy used in growth only 2-4% of this is spent in calcification. Secondly, a more important source of error is that the annual growth rate estimates used in our study were calculated from healthy reefs which will have resident populations of corallivorous fishes, meaning that the estimated proportional increase of 17% is a net increase after some level of predation (Thompson and Dolman 2010). Consequently, our estimate of coral productivity is not a direct measure of net primary productivity (which is measured as gross primary productivity minus respiration); rather, we have used growth as a proxy for productivity. There are currently no estimates of coral growth rates on reefs without corallivorous fishes; likewise aquarium based estimates are lacking and their relevance to field based estimates are questionable. To account for some of these limitations we can recalculate the estimate of productivity consumed using a higher proportional increase per annum. If we double the increase in proportional cover of the tabular acroporids to 34% per annum, corallivorous butterflyfishes consume 31-44% of the productivity of these corals, which is still high when compared to similar sized consumers in terrestrial ecosystems. When more accurate data on coral primary productivity becomes available our estimates of productivity consumed by corallivorous butterflyfishes can be recalculated. However, as a first step, our study has demonstrated that corallivorous butterflyfish have the potential to consume a significant proportion of both the standing biomass and potential productivity of tabular acroporid corals.

The response of corals to the chronic grazing pressure exerted by small-bodied corallivores is currently unknown. Unlike the acute effects of the periodically abundant invertebrate corallivores such as *A. planci* or *Druppella* spp., which can dramatically reduce live coral cover over a relatively short period of time (Carpenter 1997), polyp-feeding fishes are a long term, chronic stressor on coral populations and predation only results in partial mortality of coral colonies. On healthy reef systems this predation will most likely impact corals through sublethal effects, such as reduced growth and energy reserves, lowered fecundity and overall condition, rather than direct overgrazing and eventual death of a coral colony. The magnitude of these sublethal effects will depend upon the expense incurred by a coral from regenerating grazed tissue. Tissue regeneration is an energetically expensive process. For example, a 32% reduction in the growth rate of the coral *Montastrea annularis* occurred over a two month period following the creation of 1cm^2 lesions, and growth remained suppressed for a further 30 days after tissue regeneration had stopped (Meesters et al. 1994). Our study has demonstrated that the consumption side of the coral-corallivore relationship is considerably higher than previously thought. As such, we expect that this consumption will be a significant drain on energy reserves of tabular acroporid corals, although manipulative experiments are needed to determine whether the exclusion of coral-predators results in corresponding increases in growth, condition and reproductive output of these heavily consumed coral species.

Partial predation is a common feature of virtually all ecosystems, but it is in terrestrial systems that plant-herbivore interactions have been most extensively studied. These studies have created a general acceptance that herbivory can have major effects on plant communities, reducing growth rates, fitness and limiting the distribution and abundance of frequently consumed prey organisms (reviewed by Crawley 1989, 1997, Maron and Crone 2006). These studies have forced a rephrasing of the research question from "do herbivores have an effect?" to "under what conditions do consumers have meaningful effects on plant dynamics?" (Olf and Ritchie 1998, Maron and Crone 2006). In contrast, the equivalent relationship on coral reefs has been dismissed as largely unimportant to reef processes on the assumption that the amount of coral tissue consumed by corallivorous fishes is too low to have any meaningful effects on prey corals (e.g. Harmelin-Vivian and Bouchon-Navaro 1982, 1983, Hixon 1997). However, our study demonstrates that corallivorous fishes consume a major proportion of the standing biomass (9-13.5%) and potential productivity (52-71%) of tabular acroporid corals. Considering the large effects that can occur in plant communities from even relatively small annual defoliation rates (e.g. Marquis 1984, 1992, Crawley 1985), it is extremely likely that polyp-feeding corallivores will have similar effects to those seen in plants following herbivory. These grazing fishes are likely to limit the energy available for growth, reproduction and maintenance in potential prey organisms, such that grazing will have significant long-term consequences and may even reduce resilience of corals to other significant disturbances like climate-induced coral bleaching (e.g. Bellwood et al. 2006, Cole et al. 2009b, Gochfeld 2010).

Chapter 7: Limited effects of chronic fish predation on common reef-building corals[7]

7.1 Abstract

On coral reefs, polyp-feeding fishes feed almost continuously upon scleractinian corals, however the effect of chronic tissue loss on individual coral colonies has never been quantified. In this study we removed coral-feeding fishes from two reefs to test whether chronic feeding by these predators significantly affects condition, growth and/or fecundity of individual coral colonies. Following removals, the predation rate on individual corals of *Acropora hyacinthus* was 8 times lower on experimental reefs (2.03 ± 0.39 bites.colony^{-1}.20 minutes^{-1}) compared to control reefs (15.73 ± 1.79 bites.colony^{-1}.20 minutes^{-1}). Similarly, there was a 6 fold difference in predation for *Pocillopora damicornis* (1.75 ± 0.37 vs 10.55 ± 1.79 bites.colony^{-1}.20 minutes^{-1}) and a 3 fold reduction upon *Acropora millepora* (0.85 ± 0.23 vs 2.30 ± 0.49 bites.20 minutes^{-1}). Whole colony growth rates, tissue mass per unit area, total lipid content and fecundity were all higher for corals on experimental reefs with reduced predation, however these differences were small and only significant for the total lipid content of *Acropora hyacinthus*, which was 9.3% higher (52.6% ± 0.8 vs 48.1% ± 0.7) on reefs with reduced predation relative to controls. Our results indicate that on healthy reef systems, where photosynthesis and energy acquisition is not impaired, corals have a high tolerance to the chronic damage caused by polyp-feeding fishes and the energy used to regenerate lost tissue does not result in an energy trade-off with other life history functions. However, on reefs already stressed by other factors which impair energy acquisition (e.g. coral bleaching), chronic predation can be more important and may ultimately effect the survivorship of highly preferred prey corals.

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[7] A manuscript of this chapter is in preparation for submission to the journal *Marine Ecology Progress Series*.

7.2 Introduction

All ecosystems are dependent upon a key group of autotrophic organisms which provide the habitat structure and often the energy that facilitates the high diversity and biomass of productive ecosystems (Jones and Lawton 1995, Jones et al. 1997). These autogenic engineers range from vascular plants in terrestrial ecosystems, to kelp forests on temperate rocky reefs and scleractinian corals on tropical reefs (Jones et al. 1997). In all habitats, organisms have evolved to utilise these habitat-forming primary producers as a food source. Trophic interactions between primary producers and consumers typically involve modular organisms, where predation results in only partial consumption and partial mortality of the prey organisms. In these situations the prey is capable of regenerating itself, with the resultant effect on the organism a function of both the amount of tissue consumed and the energetic cost of tissue regeneration (Lubchenco and Gaines 1981). Energy is a finite resource that must be allocated between several competing biological processes such as tissue maintenance costs, somatic growth and reproduction. As the energy invested in regeneration increases, a corresponding decline in growth or reproduction is expected to occur (Meesters et al. 1994, Henry and Hart 2005). These sub-lethal effects have been well documented in terrestrial systems where tissue loss through herbivory can influence both individual plants and overall community structure (reviewed by Crawley 1983, 1989, 1997, Maron and Crone 2006). Sub-lethal effects can arise through reductions in growth rates, reduced seed production and viability, impaired photosynthetic potential and increased investment of energy in tissue maintenance and regeneration (Crawley 1989, 1997, Huntly 1991), which all combine to reduce a plant’s overall fitness (reviewed by Maron and Crone 2006). Despite this, grazing is not always detrimental to plants. For example, some fast growing plant species have developed a tolerance strategy to damage, which enables these plants to rapidly regenerate injured tissue with minimal fitness consequences (e.g. McNaughton 1983, Paige and Whitham 1987, Belsky et al. 1993).

On coral reefs an important, but often overlooked, group of grazing organisms are coral-feeding fishes. There are at least 130 species from 11 reef fish families that feed on live scleractinian corals (Cole et al. 2008, Rotjan and Lewis 2008, Berumen and Rotjan 2010). Within the corallivore guild there are two broad functional groups: skeletal- and polyp-feeders. Skeletal-feeding corallivores (e.g. Tetradontidae, Scaridae) are the most destructive and physically damage the coral skeleton when feeding (e.g. Guzman and Lopez 1991, Jayewardene 2006, Rotjan et al. 2006, Bonaldo et al. 2011). This damage can have significant effects upon the structure of the coral community and can reduce colony growth rates and influence the abundance and distribution patterns of preferred coral prey species (e.g. Neudecker 1979, Wellington 1982, Cox 1986, Littler et al. 1989, Grottoli-Everett and Wellington 1997, Miller and Hay 1998). For example, selective predation by the skeletal-feeding butterflyfish *Chaetodon unimaculatus* upon its preferred coral prey, *Montipora verrucosa*, significantly reduced this coral's vertical growth rate, restricted its distribution away from reef margins and decreased the ability of *M. verrucosa* to compete for space (Cox 1986). The large effects of predation from skeletal-feeding corallivores on individual colonies have been well established (e.g. Cox 1986, Jayewardene 2009). However, on most reefs throughout the Indo-Pacific these skeletal-feeding corallivores are relatively rare or move over large areas (Cole et al. 2008). In contrast, the majority of the corallivore functional group on these reefs are polyp-feeding corallivores from the Labridae and Chaetodontidae families, which move over relatively small home ranges and feed continuously upon the same subset of coral colonies (Reese 1989, Tricas 1989b, Wrathal et al. 1992, Cole et al. 2008). This chronic loss of tissue is expected to be a net drain on a coral colony's energy reserves, whereby more energy will be spent on tissue regeneration costs at the expense of other life history processes such as growth or reproduction.

Previous studies have dismissed polyp-feeders as playing only a minor role in coral reef dynamics (e.g. Harmelin-Vivien and Bouchon-Navaro 1982, 1983, Hixon 1997), assuming that the total amount of coral tissue removed from the reef is too small, relative to the amount of coral tissue available, to have any meaningful effect. Implicit in this belief is an assumption that corals are a homogenous resource and predation will be relatively evenly dispersed amongst different coral colonies on the reef, such that the amount of tissue consumed from any one colony is very low. However, recent studies have demonstrated that both the total amount of coral tissue consumed by these fishes and their level of dietary selectivity is significantly higher than previously thought (Berumen et al. 2005, Pratchett 2005, 2007, Cole et al. 2011). Each adult butterflyfish removes between 2-3g of coral tissue each day, which translates to a population level removal rate of between 14.6g – 28.3g of coral tissue per 200m^2 per day (Cole et al. 2011, Cole et al. *in review*). Further, this consumption is highly targeted, with most polyp-feeders feeding disproportionately upon colonies of fast growing *Acropora* and *Pocillopora* corals (Berumen et al. 2005, Pratchett 2007, Berumen and Pratchett 2008, Cole and Pratchett 2011a, Lawton et al. *In press* a, b). For example, average predation rates on individual coral colonies differed by a factor of 17 between four common reef corals; slow growing *Porites* colonies received the lowest rate with an average of 2.85 bites.hr^{-1} compared to 50.1 bites.hr^{-1} for the highly preferred coral *Acropora hyacinthus* (Cole and Pratchett 2011a). Corals which are most frequently eaten will need to invest a higher proportion of their daily energy budgets into regeneration of lost tissue, which will result in an energy trade-off effect whereby less energy is available for other life history processes such as growth and reproduction (reviewed by Henry and Hart 2005). Likewise, the corals which are most heavily consumed by corallivorous fishes (*Acropora* and *Pocillopora* corals) are also the corals which are most susceptible to climate-induced coral bleaching events (Marshall and Baird 2000). As such, the effect of tissue loss through corallivory may become more important during periods of increased stress (e.g. during climate-induced bleaching events), when available energy reserves to regenerate lost tissue are reduced, potentially resulting in an overall increased level of coral mortality (e.g. Bellwood et al. 2006, Cole et al. 2009)

The overall aim of this study was to assess the functional role that polyp-feeding corallivores have on coral reef dynamics by quantifying the energetic cost of chronic tissue consumption on prey corals. Specifically, we removed corallivorous fishes from two reefs, resulting in reduced levels of coral predation for 19 months. During this time the growth, condition and fecundity of individual coral colonies were monitored. Our *a priori* hypothesis was that a reduction in the amount of tissue lost to predation would result in more energy available for other life history processes and result in increased growth rates, condition and fecundity of these corals. However this hypothesis was not supported.

7.3 Methods

7.3.1 Study site and corallivore removal

This study was conducted between September 2008 and April 2010 on four platform reefs on the western side of Kimbe Bay (5°25'S, 150°05'E), a large sheltered bay on the northern coast of New Britain Island, Papua New Guinea. The four study reefs (Lady Di, No Name, Puk Puk and Maya's) are all isolated platform reefs with steep slopes and shallow reef tops, located <1km from the main island of New Britain. This study was confined to the reef flat and crests of these platform reefs, an area which provided comparable environmental exposure among the four study reefs. This habitat is also where densities of coral-feeding fishes reach their peak (Pratchett and Berumen 2008, Cole et al. 2010). Coral-feeding fishes were removed from two reefs, Puk Puk and Maya's in September 2008, with reduced densities maintained until April 2010. Adult coral-feeders were removed using hand spears and barrier nets and killed to prevent them returning to the study reefs. After the initial removal, densities of adult corallivores were maintained with little further effort. However, on each sampling trip reefs were checked for juvenile corallivores and if present these juveniles were removed and relocated to a nearby reef. The remaining two reefs (Lady Di and No Name) were used as controls, with corallivore densities unmanipulated.

7.3.2 Coral, corallivore abundance and predation frequency

To assess the variation in abundance and composition of coral-feeding fishes on each of the four reefs, 6 replicate 50 x 4m belt transects were used on each reef. These reefs were sampled 4 times: September 2008, April 2009, September 2009 and April 2010. On each transect all coral-feeding fishes observed were recorded to species level and classed as either obligate or facultative coral-feeders, based on the classification in Cole et al. (2008). On each of these transects coral community composition was assessed using point-intercept transects, with the substrate directly under the tape recorded to species level at 50cm intervals, providing 100 sample points per transect. Separate, two-way analysis of variance (ANOVA) were used to test for differences in corallivore abundance and total coral cover between the two treatments over the four sampling periods. Coral cover was arcsine transformed and residual plots were examined to confirm that ANOVA assumptions of normality and homogeneity of variance were satisfied. Variation in the structure of the coral community among the four reefs through time was examined using a multivariate analysis of variance (MANOVA) using 5 resource categories (*Acropora hyacinthus*, *Acropora millepora*, *Pocillopora damicornis*, other *Acropora* spp., and other hard corals). Pillai's trace statistic was used to determine the significance of the MANOVA and residual plots were used to examine univariate and multivariate assumptions of homogeneity and normality.

To quantify differences in predation frequency between the four reefs, 20 minute colony observations were undertaken at each reef on 20 haphazardly chosen colonies of *Acropora hyacinthus*, *Acropora millepora* and *Pocillopora damicornis*. Colonies used in these observations had a diameter of between 20 and 60cm, with this size corresponding to that used for our estimates of colony energetics. During these observations the coral colony was watched from a distance of 5m with all bites taken by corallivorous fishes during this time recorded, following Cole and Pratchett (2011a). A two way ANOVA was used to test for differences in the frequency of predation among coral species and between corallivore predation treatments. Residual plots were examined to ensure ANOVA assumptions were met. Tukey's HSD post hoc test was then used to identify where differences among group means occurred.

7.3.3 Energetic cost of predation

7.3.3.1 Colony growth rates

Twenty colonies of *Acropora hyacinthus* and *Acropora millepora* (minimum size 20cm diameter longest side) were tagged on each of the four reefs in September 2008. This minimum size was used to standardise the intensity of predation received; colonies which are smaller than 20cm diameter are rarely consumed by corallivorous fishes and subsequently are not expected to exhibit any effects of chronic tissue loss (Cole and Pratchett 2011). A top down digital photograph, which included a scale bar was taken of each colony on each sampling trip (September 2008, April 2009, September 2009 and April 2010) providing a time-series of colony growth. The planar surface area of each colony was then determined using the CPCe software (Kohler and Gill 2006). Any tagged colony that died during the experiment was replaced with an alternative colony of a similar size and, where discernable, notes on the cause of mortality were recorded. Growth rates are presented as the percentage increase in planar surface area per month, which allowed the comparison of differently sized coral colonies and colonies that were monitored for differing lengths of time. A two way ANOVA was used to test for differences in the monthly growth rate between coral species and between corallivore predation treatments. Colony growth rates were arcsine transformed and residual plots were examined to ensure ANOVA assumptions were satisfied. Whole colony growth was not assessed for *Pocillopora damicornis* as it has a 3-dimensional branching structure. Increases in planar surface area (our measurement of whole colony growth) are only appropriate for species which have a relatively flat 2-dimensional growth form (e.g. plate or corymbose growh forms).

7.3.3.2 Tissue biomass and total lipid content

In April 2010, four branches were taken from each of 20 haphazardly chosen colonies of *Acropora hyacinthus*, *Acropora millepora* and *Pocillopora damicornis* from each of the four reefs. Two of the four sampled branches were fixed in 10% phosphate-buffered formalin immediately after collection and were used to determine total lipid content. These branches were decalcified in 2% hydrochloric acid (HCL) solution for 24 hours, followed by 5% HCL solution until all skeletal material had been dissolved. Samples were dried for 24 hours at 55°C and weighed to the nearest milligram. These dried samples were then immersed in a 2:1 chloroform:methanol solution for a further 24 hours to extract lipids. These samples were then redried at 55°C overnight and then re-weighed. Total lipid content was taken as the weight lost during the extraction, with total lipid content presented as a percentage of the original tissue biomass with the two branches averaged to give a colony mean (following Ward 1995).

The remaining two branches taken from each colony were used to determine tissue biomass per unit area. After collection these branches were given 5 abrupt shakes and air dried on absorbant paper for 5 minutes to remove excess moisture and then weighed to the nearest milligram. Branches were then placed in a concentrated bleach solution to remove all organic material. The branches were washed in freshwater and again air-dried for five minutes before re-weighing, with the change in weight corresponding to the tissue biomass on each branch. The skeletal surface area of each branch was then determined using the paraffin wax technique following Vytopil and Willis (2001). To relate the increase in mass between the two wax coatings to skeletal surface area a calibration curve was determined using 10 PVC cylinders of known surface area ranging from 1.51 to 166.59cm^2 and provided a regression equation of $y = 42.498x + 2.7462$, r^2 =0.94, where y is the skeletal surface area and x is the increase in the weight of wax between the two wax coatings. Tissue biomass per unit area was then calculated by dividing the wet weight of coral tissue on each branch by the skeletal surface area. Separate, two-way ANOVAs were used to test for differences in tissue biomass and total lipid content among coral species and between reefs with and without manipulated corallivore densities. Total lipid content was arcsine transformed to satisfy ANOVA assumptions. Tukey's HSD post hoc test was used to identify where differences in group means occurred. A consequence of calculating tissue mass per unit area using the wet, rather than the dry weight of coral tissue is that our estimates of tissue mass will be higher and not directly comparable to other studies (e.g. Anthony and Fabricus 2000, Cole and Pratchett 2011b).

7.3.3.3 Reproductive output

To assess whether predation affects polyp fecundity of *Acropora hyacinthus* and *Acropora millepora*, the number of oocytes (eggs) per polyp was quantified for the first 15 colonies of each species on each reef that had visible oocytes when branches were broken below the expected sterile zone (following Baird et al. 2002). Two branches were removed from each of these colonies and fixed in 10% phosphate buffered formalin before decalcification in HCL as above. Using a dissecting microscope the number of oocytes present in five randomly chosen polyps from each branch was counted and averaged to give a colony mean. As these oocytes were unpigmented at the time of sampling (and therefore not mature), differences in oocyte size between treatments were not compared. A two-way ANOVA was used to test whether polyp fecundity (mean density of oocytes per polyp) differed between coral species and between corallivore density treatments. Residual plots were used to ensure that ANOVA assumptions were not violated.

7.4 Results

7.4.1 Coral cover, corallivore abundance and predation intensity

Total coral cover did not differ significantly (ANOVA, $F_{3,60}$ = 0.83, p > 0.05) among the four reefs, nor was the interaction between reef and sampling period significant (ANOVA, $F_{3,60}$=0.7, p>0.05). However, total coral cover did increase significantly (ANOVA, $F_{2,60}$=8.95 p<0.001) on all reefs over the course of this experiment. In August 2008 total coral cover averaged 41.6% (± 2.3 SE) on control reefs and 43.8% (± 1.7 SE) on experimental reefs, increasing to 50.7% (± 3.5 SE) and 49.3% (± 2.3 SE) respectively in April 2010. Relative abundances of *Acropora hyacinthus, Acropora millepora* and *Pocillopora damicornis* were not significantly different among the four reefs (MANOVA, Pillai's trace=2.3, df=15, p>0.05), with these three coral species accounting for approximately 20-30% of the cover on each of the 4 reefs.

A total of six species of obligate corallivores (*Chaetodon baronessa*, *Chaetodon trifascialis*, *Chaetodon lunulatus*, *Chaetodon octofasciatus*, *Labrichthys unilineatus* and *Diproctacanthus xanthurus*) and four facultative corallivores (*Chaetodon kleinii*, *Chaetodon rafflesi*, *Chaetodon vagabundus* and *Chaetodon citrinellus*) were detected on the four study reefs. However, 75% (503/666) of observed fishes were either *C. baronessa* or *L. unilineatus*. Prior to the removal corallivore populations did not vary between reefs (Tukey's HSD, p>0.05) with an average density of obligate corallivores on experimental reefs of 24.3 (± 1.9 SE) individuals.200m^{-2} and 23.6 (± 1.7 SE) individuals.200m^{-2} on control reefs. However, there was a significant interaction effect between sampling period and treatment (ANOVA, $F_{3,84}$=42.06, p<0.0001) which corresponds to the 5-fold reduction in the abundance of polyp-feeding corallivores on experimental reefs (Figure 7.1).

During removals a total of 183 and 219 fishes were removed from Puk Puk and Maya's reefs, respectively. As a consequence of the reduced abundance of corallivorous fishes, predation rates were lower for all coral species on experimental reefs relative to controls, with a significant interaction between coral species and treatment (ANOVA, $F_{2,234}$=16.19, p<0.0001). There was an 8-fold reduction in the mean (± S.E) number of bites taken upon colonies of *Acropora hyacinthus* (15.7 ± 1.8 vs 2.0 ± 0.39 bites.20 minutes^{-1}.colony^{-1}), a 6-fold reduction for *Pocillopora damicornis* (10.55 ± 1.79 vs 1.75 ± 0.37 bites.20 minutes^{-1}.colony^{-1}) and a 3-fold reduction in the number of bites taken upon *Acropora millepora* (2.30 ± 0.49 vs 0.85 ± 0.23 bites.20 minutes^{-1}.colony^{-1}) between control and experimental reefs respectively (Figure 7.2).

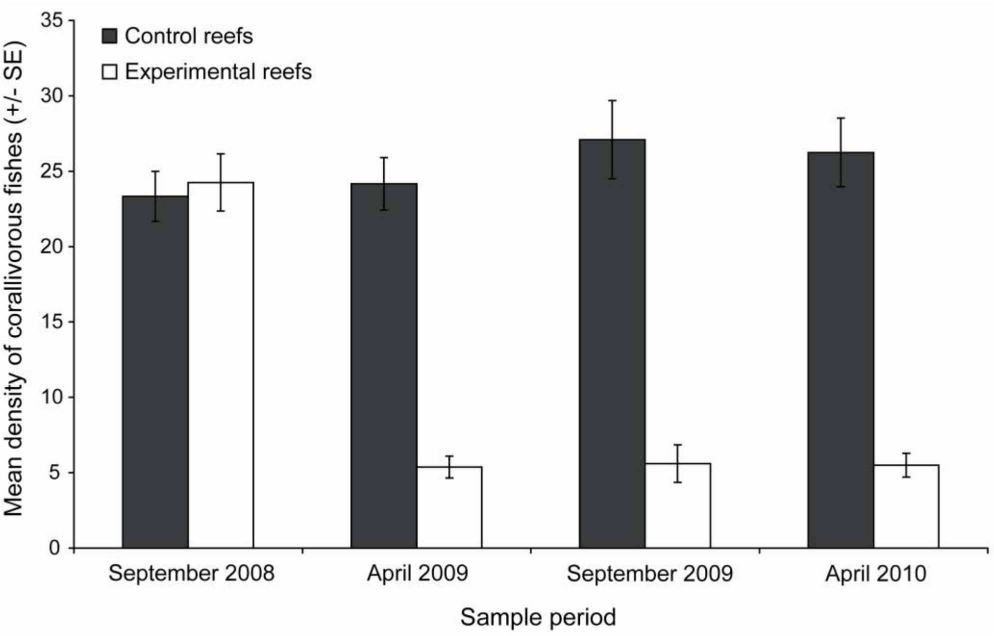

Figure 7.1: Mean density of corallivorous fishes on experimental and control reefs at four census periods between September 2008 and April 2010. Values are the mean and standard error of the number of fish counted on 6, 50x 4m belt transects averaged across the two reefs in each treatment.

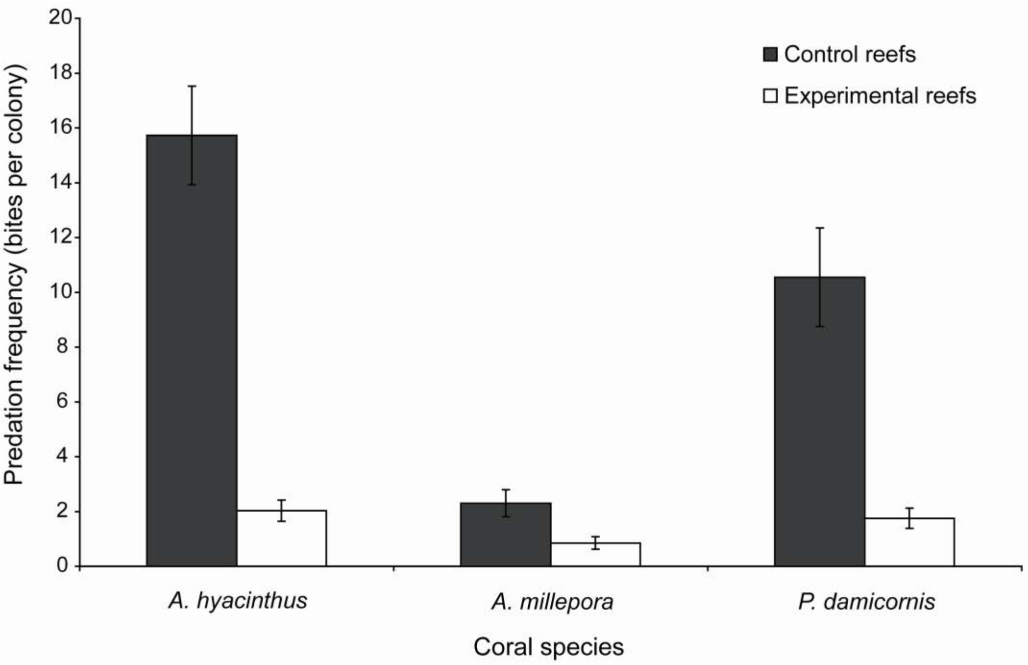

Figure 7.2: Mean (± SE) number of bites taken on colonies of *Acropora hyacinthus*, *Acropora millepora* and *Pocillopora damicornis* during 20 minute observations on experimental and control reefs (n=40 observations per species). Observations were performed after the removal of corallivorous fishes on experimental reefs.

7.4.2 Effect of predation on coral colony growth rates

Coral colony growth rates did not differ significantly (ANOVA, $F_{1,161}$=2.66, *p*>0.05) between experimental and control reefs and the interaction between predation treatment and coral species was also not significant (ANOVA, $F_{1,161}$=2.01, *p*>0.05). Although colony growth rates did differ significantly (ANOVA, $F_{1,161}$=13.582, *p*<0.001) between the two coral species, with *Acropora hyacinthus* growing faster than *Acropora millepora*. Whilst predation was not found to be a significant factor influencing colony growth rates, colonies of *A. hyacinthus* did increase in planar surface area at a 10.9% higher rate each month (7.1% ± 0.9 vs 6.4% ± 0.7 month^{-1}) on reefs with reduced densities of coral-feeding fishes relative to control reefs. Likewise, the relative growth rate of *A. millepora* was also 5.1% higher (6.2% ± 0.6 vs 5.9% ± 0.5 month^{-1}) on reefs with reduced predation relative to controls. The corals tagged during this study had very high rates of mortality. Of the 160 colonies originally tagged in August 2008 only 45% (36/80) of *A. hyacinthus* and 74% (59/80) of *A. millepora* colonies were still alive in April 2010. Despite the high mortality rate observed, colonies that did survive generally doubled in size during a 12 month period. In terms of the absolute growth rates for all reefs combined, colonies of *A. hyacinthus* increased in planar surface area by an average rate of 96.1 (± 3.9) $cm^2.month^{-1}$ which was four times faster than *A. millepora* (23.8 ± 1.8 $cm^2.month^{-1}$).

7.4.3 Effect of predation on tissue biomass, lipid reserves and polyp fecundity

Tissue biomass per unit area differed significantly among the three coral species (ANOVA, $F_{2,194}$=121.64, p<0.0001), however predation had no significant (ANOVA, $F_{1,194}$=3.33, p>0.05) effect on coral tissue biomass per unit area and the interaction between coral species and treatment was also non-significant (ANOVA, $F_{2,194}$=0.19, p>0.05). Despite this, coral tissue biomass of all species was higher on reefs without predation, although the magnitude of this difference was small (Figure 7.3). Coral tissue biomass on experimental reefs with reduced densities of corallivorous fishes was 3.5% higher for *Acropora hyacinthus* (61.7 ± 2.38 vs 59.6 ± 2.0 mg^{-1}), 3.6% for *Acropora millepora* (57.1 ± 1.5 vs 55.1 ± 1.9 $mg.cm^{-1}$) and 2.1% for *Pocillopora damicornis* (44.1 ± 1.9 vs 43.2 ± 2.2 $mg.cm^{-1}$) relative to control reefs. Likewise, total lipid content of all coral species was higher on reefs with reduced densities of corallivores (Figure 7.3) and there was a significant interaction (ANOVA, $F_{2,194}$=4.53, p<0.05) effect between coral species and predation treatment. This interaction was driven by *A. hyacinthus* (Tukey's HSD p<0.0001) which received the highest rates of predation. Total lipid content of this species was 9.3% (52.6% ± 0.8 vs 48.1 % ± 0.7) higher on experimental reefs relative to controls (Figure 7.3). In contrast, total lipid content of *P. damicornis* and *A. millepora* was only 3.6% (49.2% ± 0.8 vs 47.5% ± 0.9) and 1.1% (53.2% ± 0.8 vs 52.7% ± 0.9) higher on experimental reefs, and these differences were not significant (Tukey's HSD p>0.05). Predation did not significantly affect coral fecundity (ANOVA, $F_{1,116}$=0.12, p>0.05) and the interaction between coral species and predation was also not significant (ANOVA, $F_{1,116}$=0.03, p>0.05). The mean density of oocytes per polyp was marginally higher on experimental reefs for colonies of *A. hyacinthus* (5.9 ± 0.2 vs 5.8 ± 0.1) and *A. millepora* (5.5 ± 0.2 vs 5.4 ± 0.1) relative to control reefs.

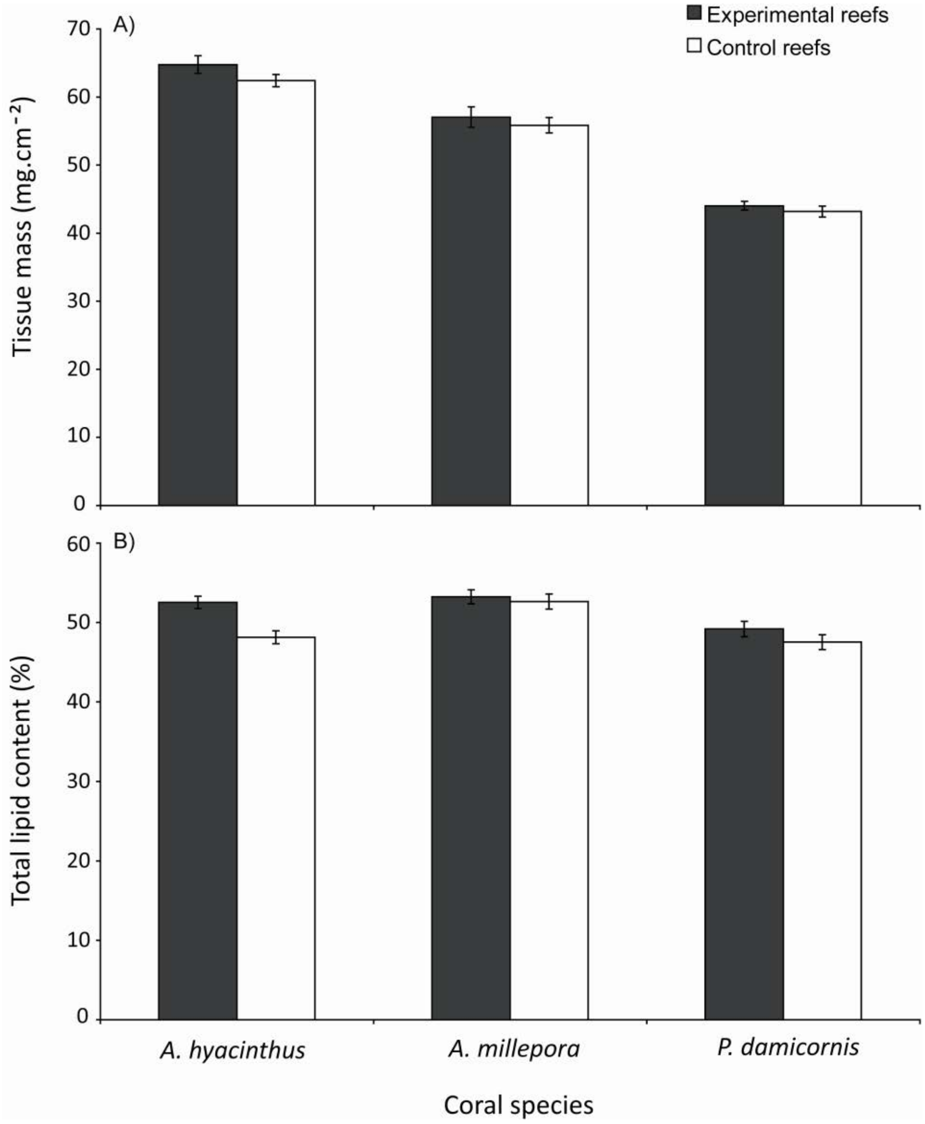

Figure 7.3: Differences in A) tissue biomass (mg.cm^2) and B) total lipid content (%) for 3 species of scleractinian corals on reefs with experimentally reduced densities of corallivorous fishes and control reefs with natural densities of corallivores.

7.5 Discussion

In this study we manipulated the densities of polyp-feeding corallivorous fishes at the scale of individual reefs to quantify the effect that chronic tissue consumption has on coral communities. All coral response variables, such as whole colony growth rates, tissue biomass, lipid reserves and fecundity were higher on reefs which had reduced densities of polyp-feeders, although the magnitude of these differences was often small and only the total lipid content of colonies of *Acropora hyacinthus* was significantly influenced by corallivore predation. For most organisms, energy is a limiting factor that must be allocated between competing biological processes, such as growth, reproduction and tissue regeneration, all of which are energetically expensive processes (Rinkevich 1996). Consequently, the lack of a strong effect of predation is surprising given the large tissue biomass removed by polyp-feeding fishes. At Lizard Island, corallivorous butterflyfishes remove between 15-28g coral tissue per 200m^2, with this consumption representing between 52-79% of the potential productivity of tabular acroporids (Cole et al. 2011: chapter 4, 6). In Kimbe Bay the densities of corallivorous fishes and the availability of heavily consumed corals (e.g. *A. hycainthus*) are comparable to Lizard Island indicating a similar biomass of coral tissue is being consumed annually. As such, we expected that by significantly reducing the total amount of tissue lost to predation to have resulted in these colonies having more energy available to invest in other life history processess and ultimately would have increased the fitness of these colonies relative to controls.

The lack of a strong effect of predation in this study indicates that regenerating lost tissue does not represent a large energetic cost to coral colonies. The size and shape of an injury can have a large influence on the energetic cost of tissue regeneration, with small lesions healing faster than larger ones (Henry and Hart 2005). Polyp-feeding corallivores continuosly pick at the surface of prey corals, which results in multiple small wounds dispersed across the colony surface. These polyp-sized injuries are estimated to take only 7-10 days to regenerate (Gochfeld 2004), which is 4-6 times faster than corallivore injuries that damage the skeleton itself (Jayewardene 2006). As such, the energetic cost of regenerating tissue removed by polyp-feeders may be relatively low and only become significant when predation intensity is either unusually high or when energy reserves are reduced due to more significant stressors like coral bleaching (e.g. Bellwood et al. 2006, Cole et al. 2009b, Gochfeld 2010).

Many studies have demonstrated that under normal, sunny conditions, the energy fixed through photosynthesis exceeds the daily energy requirements of corals (e.g. Muscatine 1984, Crossland 1987, Edmunds and Davies 1986, Davies 1984, 1991). For example, *Pocillopora damicornis, Montipora verrucosa* and *Porites lobata* were all found to produce a surplus of photosynthetic fixed energy during both optimal (sunny and cloud free) and normal conditions (intermittant cloud cover). However, under overcast conditions (heavy cloud cover) all three species went into deficit and energy reserves were consumed to meet metabolic costs (Davies 1991). It is likely that the minimal effects of tissue loss observed in our study are in part linked to the small number of days in Kimbe Bay when shallow water corals do not exceed their energy demands through photosythesis. Kimbe Bay lies within the coral triangle and represents an ideal location for coral growth, characterised by clear water, high light intensity and relatively high year round temperatures (28-31°C) (*pers obs.*). All coral colonies in our study on both experimental and control reefs were very healthy, growing at fast rates and maintaining very high energy reserves. Total lipid content ranged from 47-53%, which is higher than estimates for corals from other locations which typically range between 20-40% (Stimson 1987, Harland et al.1992, 1993, Ward 1995, Yamashiro et al. 1999, Cole and Pratchett 2011b: chapter 5). The high total lipid content, tissue biomass per unit area and the low variability between colonies supports the view that on shallow reef tops in Kimbe Bay, energy is not a limiting factor in colony growth or condition. Even though we did detect a significant effect of predation on the total lipid content of *Acropora hyacinthus*, this difference was relatively small (Figure 7.3) and did not result in any corresponding increase in growth or fecundity for this species.

An unexpected result of our study was the high mortality of coral colonies that were tagged. This high mortality rate is not expected to be unique to Kimbe Bay, but may be more pronounced on the shallow reeftops, compared to deeper or more sheltered locations (Hughes and Connell 1999). A similar mortality rate was observed on reef crest habitats at Heron Island, where 26% of monitored colonies died over a 12 month period (Hughes and Connell 1987). In our study, the majority of mortality was whole colony death, and appeared to be independent of colony condition. Rather, these colonies were killed by direct acute stressors. The exact causes of mortality varied but included bleaching stress (both salinity and thermal bleaching), storm damage, coral diseases and invertebrate predation although not all deaths could be attributed to a single direct cause. Partial mortality was generally rare on these reefs but when it did occur it generally lead to total mortality by the next sampling trip. Considering the fast growth rates and energy reserves of the coral colonies living in the shallow habitats sampled in our study, it is surprising that the colony turnover rate is so high. It suggests that this shallow environment is not suitable for long term coral growth and that these platform reefs have reached their vertical limit in terms of reef accretion. As such, the coral populations living on these shallow reef tops are likely to represent an ephemeral population which is characterised by a live fast, die young demographic.

The effects of partial predation have been most extensively studied in terrestrial systems, where the majority of studies have demonstrated that tissue loss through herbivory has negative effects on both individual plants as well as community structure (reviewed by Crawley 1983, 1997, Maron and Crone 2006). However, other studies have found contradictory results, where herbivory has either no apparent effects or can even benefit grazed plants by increasing relative growth rates and reproductive output (Paige and Whitham 1987, Belsky et al. 1993). In terrestrial systems, plants have two broad strategies for minimising the effects of herbivory: they may avoid damage through investment in chemical and physical defences which make tissue unpalatable (Coley et al. 1985, Endara and Coley 2011), or they can develop fast regrowth strategies which enable them to tolerate a relatively large amount of damage (Belsky et al.1993, Rosenthal and Kotanen 1994, Strauss and Agrawal 1999). Plants, like corals, are exposed to many forms of damage throughout their lifetime and the strategy of tolerance depends on plants possessing traits that, rather than protecting from damage, allow them to rapidly regrow damaged tissue with minimal fitness consequences (Belsky et al. 1993, Strauss and Agrawal 1999). For example, the wild radish *Raphanus raphanistrum* can experience a 25% loss of leaf area without any corresponding decrease in growth or seed production (Lehtilä and Strauss 1999). The coral species used in our study are all fast growing corals that are amongst the first species to recolonise shallow reef habitats following major disturbance events (e.g. Pratchett et al. 2010). The fastest growing and most frequently eaten coral, *Acropora hyacinthus*, forms robust and relatively large tables which enable this species to overtop and shade neighbouring corals. The fast growth rates and the indirect competitive strategy used by *A. hyacinthus* suggests that it has evolved a similar tolerance strategy to terrestrial plants, whereby it is capable of absorbing a large amount of damage before negative effects become apparent (Belsky et al. 1993).

Predation from polyp-feeders is a natural part of the dynamics of coral reef systems and our study demonstrates that on healthy reef systems where energy is not a limiting factor predation from polyp-feeding fishes does not have a major influence on coral growth, condition or community composition. However, as the total amount of stressors acting on a reef system increases corallivore predation can become more important. During a disturbance event that results in coral mortality, the balance between tissue regeneration and consumption can become skewed towards consumption, whereby the relative intensity of predation increases as the same amount of predation is directed towards fewer corals. Under these conditions coral predation can become an important covariate influencing the mortality rates of corals (e.g. Bellwood et al. 2006, Cole et al. 2009, Gochfeld 2010).

Chapter 8: General Discussion

Identifying and understanding ecological processes that maintain, promote or prevent coral reef growth are fundamental in assessing the resilience of coral reef ecosystems (Hughes et al. 2003, 2005, 2010, Bellwood et al. 2003, 2004, Nyström et al. 2008). Coral predation by fishes is one process that has been largely overlooked, but is potentially very important in determining the population and community dynamics of scleractinian corals (reviewed by Cole et al. 2008, Rotjan and Lewis 2008). Coral-feeding fishes occupy a relatively unique niche on reef systems and represent the closest link between corals and fishes, and an important link between primary productivity and higher trophic levels (e.g. Glynn 2004). Previous research has suggested that only a limited number of fishes were actually capable of feeding directly upon hard corals (Robertson 1970, Connell 1973, Goldman and Talbot 1976, Huston 1985, but see Randall 1974). It is also often considered that the total amount of coral tissue consumed by these corallivores was too small, relative to the total amount of coral tissue available, to have any meaningful effects upon the coral community (e.g. Harmelin-Vivien and Bouchon-Navaro 1982, 1983, Hixon 1997). However, this thesis has demonstrated that the corallivore guild is considerably larger than previously thought. At least 130 species from 11 different reef fish families have been documented to feed at least in part upon live coral (Cole et al. 2008: chapter 2).

The potential influence of coral-feeding fishes on corals, depends not only on the total level of feeding activity, but also the way that feeding is distributed among coral colonies, species, and types. Not only does the relative frequency and intensity of predation change among different coral species, but also varies greatly within a species depending on colony size (Cole and Pratchett 2011: chapter 3). Likewise, I have shown that the total amount of coral tissue consumed by corallivorous butterflyfishes is much larger than previously thought (Cole et al. 2011: chapter 4) and that this consumption represents a relatively large proportion of both the standing biomass and potential productivity of heavily consumed coral species (e.g. *Acropora hyacinthus*) (chapter 6). This high consumption rate indicates that polyp-feeding corallivores are an important trophic link in the storage of energy fixed by reef-building corals.

Subsequently, these fishes are expected to play a more important role in reef trophodynamics than previously assumed (e.g. Hatcher 1988, but see Glynn 2004)(chapter 6). Despite this, the large amount of coral tissue consumed by corallivores did not translate into any meaningful effects on coral growth rates, condition or reproductive output on a reef-wide scale when these coral predators were removed (chapter 7), indicating that this interaction is more complex than a simple cause and effect relationship.

Over the last 30 years, considerable research has been conducted on the feeding behaviours and dietary preferences of corallivorous fishes, with these studies demonstrating that corallivorous fishes exhibit clear patterns of prey use and preferentially select *Acropora* and *Pocillopora* corals over all other taxa (chapter 2, Reece 1981, Irons 1989, Cox 1994, Alwany et al. 2003 Pratchett 2005,2007, Berumen et al. 2006, Cole et al. 2010: appendix, Lawton et al. *In press* b: appendix). These findings have been extended in this thesis (chapter 3). I have demonstrated that colonies of highly preferred corals species (e.g. *Acropora hyacinthus*, *Pocillopora damicornis*) receive between 4-15 times the rate of predation of less frequently consumed corals (e.g. *Acropora millepora*, massive *Porites*). Likewise, I have also demonstrated that the amount and intensity of predation received by a colony varies greatly within a species depending on colony size. Very small corals (<200cm^2) were effectively avoided by coral predators, however the slightly larger intermediate sized colonies (200-600cm^2) receive the highest intensity of predation. This pattern was highly consistent between the two corals investigated, despite relative differences in the total magnitude of predation received. This indicates that the size-specific refuge from predation is likely to be a consistent feature of all coral species and predation from polyp-feeders is unlikely to have any effects. This is an important finding and suggests that predation from polyp-feeders will not have significant effects on coral recovery rates following disturbance events, as long as there are enough larger colonies to feed from nearby.

Despite the large amount of tissue consumed and the highly selective nature of this tissue consumption, I was unable to identify consistent effects of corallivore predation on coral growth and condition. Juvenile butterflyfishes which settle directly into live coral and consume this coral exclusively for 6 to 8 weeks had a substantial negative effect on the tissue biomass per unit area of colonies, although they were not found to influence energy reserves (chapter 5). This result was consistent between a manipulative experiment and a comparison of colonies that were naturally occupied by juveniles and nearby controls that did not host juveniles. In contrast, a larger scale reef-wide manipulation of corallivore densities resulted in only minor effects of corallivore predation on the growth and condition of corals (chapter 7). Only the total lipid content of *A. hyacinthus* was significantly affected by predation, however this difference was relatively small and did not correspond to any meaningful increases in colony growth rates, tissue biomass or reproductive output. The differential effects of juvenile and adult corallivores may be a consequence of the relative intensity of predation and subsequent tissue loss. While the actual bite size of juveniles is much smaller than adults (chapter 4), all of their feeding effort is directed towards just one colony for an extended period of time. In comparison, adult corallivores generally take only a few bites from any individual colony before moving on to feed from the next colony in its home range, a pattern that is repeated continuously throughout the day (e.g. Tricas 1985, 1989a, b). As such, over a period of weeks, colonies that host juveniles may experience a greater net loss of coral tissue compared to a colony that is only preyed on by adult corallivores. Even though predation from juvenile butterflyfishes resulted in a significant reduction in tissue biomass, it did not affect the total lipid content of these colonies, meaning these colonies have a high capacity to regenerate lost tissue. The longer term effects of juvenile predation are currently unknown. However, it is possible the observed reduction in tissue biomass may be an adaptation to minimise the energy lost through predation. That is the coral minimises tissue regeneration until after the juvenile butterflyfish has outgrown the host and begins to forage across multiple colonies.

When the results from these two experiments are combined (chapter 5, 7), it appears that the effect of predation from polyp-feeding fishes was obscured in PNG by the high growth and rapid turnover among coral colonies studied. However this does raise the question of why the abundances of coral-feeding fishes are not higher, considering that the coral prey could support a higher level of tissue loss before negative effects occur. Several factors potentially interact to create this paradox, including larval supply, post recruitment processes (e.g.

Doherty and Fowler 1994, Caley et al. 1996, Schmitt et al. 1999, Booth et al. 2000, Holbrook et al. 2000, Vallès et al. 2009) and inter-specific competition (e.g. Tricas 1989b, Righton et al. 1998, Hobbs and Munday 2004, Berumen and Pratchett 2006a), among others. Differences in adult abundance have been shown to closely follow prior levels of recruitment by reef fishes (e.g. Schmitt and Holbrook 1999, Holbrook et al. 2000). In general, larval butterflyfishes are poorly represented in the plankton (Leis 1989), with many species requiring specific coral microhabitats for successful recruitment. Further, many of these juveniles settle predominantly into the habitat occupied by adults. Consequently, they may initially recruit successfully to a coral colony but not be able to establish a feeding territory in these habitats where adults have monopolized available space.

Alternatively, the behavioural response of corals to predation may also influence the carrying capacity of corallivores. Following predation corals retract their polyps and repeated feeding upon the same colony must be delayed long enough for polyps to once again become fully extended (Tricas 1989a, Gochfeld 2004). While colonies can be fed from during periods of polyp retraction, the amount of tissue removed per bite is expected to be reduced. At higher fish densities, the feeding efficiency of corallivores is expected to decline as a greater proportion of coral polyps are in a retracted state. This could lead to higher rates of inter-specific competition and the formation of feeding territories (e.g. Tricas 1989b, Roberts and Ormand 1992, Wrathal 1992, Righton et al. 1998, Berumen and Pratchett 2006a). For example, Tricas (1989b) manipulated coral availability and found that as food resources declined the territory size of the corallivorous butterflyfish, *Chaetodon multicinctus*, increased, but the level of aggression needed to defend these resources also increased. Likewise he found that territories increased in area by up to 350% if competitors were removed. The demographics of corallivorous fishes are currently not well understood and factors like larval supply and recruitment, post recruitment processes and inter-specific competition should all be examined to try to explain the observed deviation between corallivore abundance and potential carrying capacity of the environment.

A limitation of our experiment to examine the reef-wide effects of corallivore predation was that only corals which looked healthy (e.g. no disease, brightly coloured, etc.)

and were not in direct competition with other organisms were sampled. As such, these colonies are likely to have the highest energy reserves on the reef. Consequently the energetic cost to these corals of regenerating grazed tissue did not result in energy limitation of other life history processes. Likewise, this experiment was conducted in Kimbe Bay, a region which has ideal environmental parameters (high sunlight, high year round temperatures, clear water, etc.) for fast growing coral colonies. All the colonies sampled in our experiment had an unusually high total lipid content and growth rates relative to comparable studies at lower latitude reefs (chapter 7). Even in this region, which is ideal for coral growth, total lipid content of *A. hyacinthus* was 10% higher on reefs with reduced densities of predators. As such, it is possible that polyp-feeders will have larger effects on other reef systems at lower latitudes which have more variable environmental parameters. Under these conditions energy is more likely to be a limiting factor and the cost of tissue regeneration may have more meaningful effects on coral growth, condition and reproductive output. Likewise, if our study had included colonies that were living in suboptimal microhabitats or those that were in direct competition with other colonies we may have detected more of an effect and these colonies should be investigated by future studies.

The results from our study demonstrate that under normal healthy reef conditions (especially high light), most coral colonies grow very quickly. However, the impact of chronic tissue loss is more pronounced under conditions where coral has been depleted or stressed as a result of other disturbances (Glynn 1988, Knowlton et al. 1988, Rotjan et al. 2006, Gochfeld 2010). Moreover, polyp-feeding fishes respond to damaged, diseased and stressed colonies with increased feeding effort (McIlwain and Jones 1997, Cole et al. 2009b, 2010: appendix, Chong-Seng et al. 2011: appendix). This increased feeding intensity during periods of coral stress is likely to be a significant compounding factor, and represent a much larger energetic impact than that felt by healthy colonies. Under these stressed conditions the resource to consumer ratio can be skewed towards the consumer, and results in an increased utilization of these diminished prey resources leading to the possibility of over-consumption and colony death (Glynn 1996, Baker et al. 2008, Jayewardene et al. 2009, Gochfeld 2010). For example, the extent of coral mortality following the 1998 mass bleaching event was exacerbated by the concentration of feeding effort from remaining fish corallivores upon remnant *Acropora* colonies (Bellwood et al. 2006). Likewise, following a long history of disturbances on reefs in Guam and Moorea, the distribution of *Acropora* and *Pocillopora* colonies have become restricted to refuges inside herbivorous damselfish territories (Gochfeld 2010, White and O'Donnell 2010). When colonies of *Pocillopora damicornis* were experimentally transplanted away from these territories, rapid and intense predation occurred and resulted in these colonies being overgrazed, with up to 85% of accessible tissue being removed within 88 hours (Gochfeld 2010). The combination of recurrent disturbances and corallivore predation has resulted in the coral community on these reefs transitioning from *Acropora*-dominated to *Porites*-dominated reefs (Gochfeld 2010, White and O'Donnell 2010, Trapon et al. 2011, Pratchett et al. 2011b). Coral-feeding fishes are rarely, if ever, the direct cause of mortality for healthy colonies, however they may be an important covariate in coral mortality for colonies that are already stressed by other anthroprogenic factors (e.g. Bellwood et al. 2006, Cole et al. 2009b, Chong-Seng et al. 2011).

Finally, care should be taken before discounting the importance of corallivory to reef systems based on the outcomes of the long term corallivore removal experiment presented in chapter 7. This thesis has been predominantly focused on corallivorous butterflyfishes. However there are many more species of polyp-feeding corallivores (e.g. tubelip wrasses, pomacentrids, filefishes, etc.) that contribute to coral predation on Indo-Pacific reefs (Cole et al. 2008: chapter 2, Rotjan and Lewis 2008, Cole et al. 2010: appendix). While these fishes are also unlikely to influence the coral community on healthy systems they will contribute to the overall background level of stress, with their subtle effects only becoming apparent when compounded by anthropogenic impacts (e.g. Bellwood et al. 2006). Likewise, skeletal-feeding corallivores are an important component of many reef systems and can be important determinants of coral abundance, condition and distribution patterns (Neudecker 1979, Wellington 1982, Cox 1986, Miller and Hay 1989, Littler et al. 1998, Rotjan et al. 2006). A recent paper by Bonaldo et al. (2011) has suggested that coral-grazing by parrotfish is also more important on Indo-Pacific reefs. They estimated 78% of the total surface area of massive *Porites* spp. is consumed annually from reef flats at Lizard Island, Great Barrier Reef. When this figure is combined with my estimate that between 9-13.5% of the standing biomass of tabular acroporids is consumed by butterflyfishes on reef crest sites at Lizard Island (chapter 6), the total amount of coral primary productivity that enters the foodweb through the entire corallivore guild is much larger than previously expected (e.g. Hatcher 1988). Consequently, corallivores may be an important component of the way energy cycles through coral reef systems (e.g. Glynn 2004). While this thesis found that corallivores have minimal direct effects on healthy reefs, the importance of coral consumption increases rapidly following major disturbance events. As such, a concerted effort is needed to reduce the overall level of anthropogenic stressors acting on coral reef systems if the long term regional decline of live coral cover is to be reversed.

8.1 Areas of future work

This thesis has demonstrated that corals lose a considerable amount of tissue through predation on a daily basis. As this tissue loss was found to have minimal effects when corals and coral reefs are in a healthy state it raises the question of what mechanisms have developed to enable this paradox. Many ecological theories have been developed for terrestrial plant-herbivore interactions (e.g. Coley 1985, Hartley and Jones 1997, Stamp 2003). For example the resource availability hypothesis predicts that species with inherently slow growth rates should try to avoid predation by investing energy in chemical or physical defences which make the tissue unpalatable to herbivores or results in a higher handling time per unit of food. The cost of investing in these defences is expected to be less than the cost of regrowing grazed tissue for slow growing species. The same amount of tissue removed from a slow growing species will have a greater net effect, as the proportion of productivity removed will be high. In contrast, inherently fast growing species can rapidly regrow damaged tissue with little effect on primary productivity (Coley 1985, van der Meijden et al. 1988, Del-Val and Crawley 2005, Massey et al. 2007, Endara and Coley 2011). Moreover, when resources are limited, growth is slow for all species and the environment will favour those species which can minimise tissue loss. Resource rich environments, though, favour fast growing species as the cost of investing in defences is higher than the energy needed to rapidly regrow lost biomass

(Coley 1985, Endara and Coley 2011). Corals and corallivorous fishes represent an ideal system to test the generalities of this and other plant-herbivore based theories. For instance, many of the slower growing massive or encrusting coral species which are not consume by corallivorous fishes have a more diverse range and a higher density of defensive nematocysts within their tissues (e.g. sweeper tentacles) (e.g. Lang 1973, Thomson and Brown 1986, Lang and Chornesky 1990). In contrast, fast growing, weedy coral species (e.g. *Acropora hyacinthus*) which have an indirect competitive strategy of overtopping and shading neighbouring corals are the main dietary prey of most corallivorous fishes throughout the Indo-Pacific (Cole et al. 2008).

This thesis has demonstrated that on healthy reef systems, the balance between corallivore predation and tissue regeneration favours the regenerative capacity of corals. However, a constant theme of past and present studies on corallivorous fishes is that the potential effect of corallivore predation is related to the intensity of predation received by a colony and generally becomes more significant when corals are already stressed by other factors (Glynn 1996, Rotjan et al. 2006, Bellwood et al. 2006, Cole et al. 2009a, b: appendix, Gochfeld 2010). During a disturbance (e.g. climate-induced bleaching event) that results in coral mortality, the relative resource to consumer ratio moves to favour the consumer, at least in the short term (weeks-months), whereby the same amount of coral consumption is dispersed amongst fewer and fewer corals. A pressing question for coral reef managers is what level of background pressure is needed before the stress imposed by corallivores becomes too much for these corals. At what point do chronic stressors begin to influence coral mortality rates (e.g. Bellwood et al. 2006), prevent coral recovery (e.g. Jayewardene et al. 2009) or contribute to long term changes to the structure of the coral community (e.g. Gochfeld 2010)?

The question of how much stress corals can withstand also extends to which coral colonies receive predation. In our study small coral colonies (<200cm^2) received an effective size-refuge from predation (chapter 3). However this refuge is unlikely to be maintained if the availability of larger colonies declines. Under the future predictions of climate change the frequency and severity of disturbances are expected to increase, which may result in the size distribution of corals being skewed towards smaller sized colonies (e.g. Bak and Meester 1998, 1999, McClanahan et al. 2008). Chapter 3 indicates that these small sized colonies are unlikely to have evolved under a history of high predation. As such, any future increases in the amount of predation received by these colonies could have more significant effects on growth and condition than those seen on larger colonies on today's reefs (chapter 7). Future experimental studies are needed which assess how changes in the intensity of predation effect the growth rates, condition and size at first reproduction of these small-sized colonies under a range of environmental conditions. Likewise the effects of corallivore predation should also be investigated on recently disturbed reefs to examine whether predation can slow coral reef recovery rates if the total coral cover drops below a critical threshold (e.g. Jayewardene et. al. 2009).

Finally, corallivores may also be important in influencing other reef processes. Coral diseases are currently a major threat to future reef systems. The geographic distribution and incidence of coral disease outbreaks has steadily increased over the last 20 years. The role that corallivorous fishes play in coral disease transmission is as yet unknown. It has been suggested that polyp-feeders contribute to the spread of diseases by acting as a transmission vector of infectious material (e.g. Aeby and Santavy 2006, Raymundo et al. 2009). A recent study has demonstrated that numerous corallivores (and non-corallivores) feed directly on the diseased band of both Brown- and Black-band diseases (Chong-Seng et al. 2011: appendix). Under aquarium conditions the corallivorous butterflyfish *Chaetodon plebeius* fed intensively upon diseased nubbins and actually reduced the speed at which this disease progressed through experimental nubbins of the staghorn coral, *Acropora muricata* (Cole et al. 2009c: appendix). Despite these studies, the interaction between coral-feeding fishes and coral diseases remains unclear and controlled experiments are needed which assess whether corallivore predation has any beneficial aspects for diseased colonies or whether these fishes contribute to the observed patterns of disease transmission.

8.2 Conclusion

Throughout the tropical indo-Pacific, coral reef development has remained in a state of positive growth despite predation from corallivorous fishes being a constant feature of these reefs since the late Miocine period (Bellwood et al. 2010). Most reefs within the Indo-Pacific are dominated by the *Acroporidae* and *Pocilloporidae*, two families heavily consumed by polyp-feeding fishes. For these corals to maintain reef development through evolutionary time, the balance between tissue loss and regeneration must favour regeneration. As such, it is likely that these heavily consumed corals have developed a similar tolerance strategy to those seen in fast growing species of terrestrial plants (e.g. Belsky et al. 1993). This is not to say that chronic tissue consumption does not influence colony condition and mortality when additional stressors are acting on the system (e.g. Rotjan et al. 2006, Bellwood et al. 2006, Cole et al. 2009b: appendix, Gochfeld 2010). The results of this thesis indicate that on healthy reef systems, predation by polyp-feeding corallivores is unlikely to negatively affect corals at the population level; however predation may be a significant contributing factor in the mortality of stressed individuals within the population. This will have important implications for future reefs, where predicted increases in anthropogenic pressures (e.g. climate-induced bleaching, ocean acidification, etc.) are expected to lead to an overall increased level of stress on most reef systems and potentially a reduced capacity for coral colonies to regenerate and tolerate chronic tissue loss from polyp-feeding fishes.

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Appendix:

Other papers published during my candidature:

Lawton, R.J., Cole, A.J., Berumen, M.L., Pratchett, M.S. (*In press b*) Detecting local versus regional specialisation: dietary versatility reduces vulnerability to climate change among coral-feeding butterflyfishes. *Ecography,* doi: 10.1111/j.1600-0587.2011.07326.x

Chong-Seng, K.M., Cole, A.J., Pratchett, M.S, Willis, B.L. (2011) Selective feeding by coral reef fishes on coral lesions associated with brown band and black band disease. *Coral Reefs*, 30:473-481.

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Geographical variation in resource use by specialist versus generalist butterflyfishes

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ABSTRACT

Localised patterns of resource use can be constrained by multiple factors. Comparison of resource use at multiple locations with differing resource availability can allow fundamental specialists to be distinguished from species that simply feed predominantly on prey types that are locally abundant. This study investigates geographic variation in the feeding ecology of coral-feeding butterflyfishes to examine whether patterns of resource use and levels of dietary specialisation vary among distinct locations, corresponding with changes in resource availability. Our specific aims were to investigate whether the dietary niche breadth of four butterflyfishes varies among five geographically separated locations and assess whether each species utilises similar resources in each location. Resource availability and dietary composition of four butterflyfishes were quantified at three sites across each of five geographic locations throughout the Pacific. Niche breadth, niche overlap, and resource selection functions were calculated for each species at each site and compared among locations. Availability of dietary resources varied significantly among locations and sites. *Chaetodon vagabundus, C. citrinellus* and *C. lunulatus* had low levels of dietary specialisation and used different resources in each location. *Chaetodon trifascialis* had high levels of dietary specialisation and used the same few resources in each location. Our results indicate that relative levels of dietary specialisation among different butterflyfishes do hold at larger spatial scales, however, geographical variation in the dietary composition of all butterflyfishes indicates that prey availability has a fundamental influence on dietary composition. Highly specialised species such as *C. trifascialis* will be highly vulnerable to coral loss as they appear to be largely inflexible in their dietary composition. However, the increased feeding plasticity observed here for *C. trifascialis* suggests this species may have a greater capacity to respond to coral loss than previously assumed.

Key words: dietary specialisation, coral reef, Chaetodontidae, fundamental niche, realised niche, geographic variation, resource selectivity

INTRODUCTION

Many studies have shown that the range of resources used by an organism can be considerably smaller than the range of resources they are physiologically capable of using (Colwell and Fuentes 1975, Fox and Morrow 1981). Localised patterns of resource use can be constrained by a number of factors. Access to resources may be restricted by interactions with other organisms such as competition and predation (Colwell and Fuentes 1975). Local patterns of resource use can be also limited by resource availability at these local scales. A species may use a narrow range of resources because they are highly abundant and widely available, or because there are no alternative resources available (Lawton et al. In press). Thus, on a local scale, some species may appear to be functioning as specialists, but across their entire geographic range they have generalised ecologies (Fox and Morrow 1981). Despite recognition that niche breadth may vary with spatial scale (Brown 1984, Gaston et al. 1997), species are often considered to be equally specialised across all spatial scales (Devictor et al. 2010). Very few studies have compared local and regional patterns of specialisation (e.g. Hughes 2000, Krasnov et al. 2008) and only a small number have specifically compared spatial variation in resource use to variation in resource availability (e.g. Kuussaari et al. 2000, Stachowicz and Hay 2000, Flesch and Steidl 2010). This incomplete understanding of species' global ecology may result in inaccurate characterisations of vulnerability and extinction risk and hinder conservation efforts.

Ideally, a species' niche breadth should be determined experimentally by measuring their performance separately across several resources, or along a controlled resource gradient (Devictor et al. 2010). Unfortunately, these types of experiments are difficult to conduct for many species, so an alternative approach is to record patterns of resource use across multiple locations with differing resource availability and compare local and regional patterns of specialisation. This can allow species that are fundamental specialists to be distinguished from those that are local specialists as a result of constraining factors (Hughes 2000). A fundamental specialist will use the same narrow range of resources across multiple locations, regardless of their availability. For example, the parasitic flea *Tarsopsylla octodicemdentata* almost exclusively exploits the red squirrel *Sciurus vulgaris* across its entire geographic range (Krasnov et al. 2008). In contrast, a local specialist will use a narrow range of resources on a local scale, but the particular resources that are used will vary regionally and/or with resource availability. For example, the checkerspot butterfly (*Euphydryas editha*) uses a single host plant genus locally, but the particular host plant species that is used varies regionally (Hughes 2000).

Here we compare the dietary niche breadth of coral-feeding butterflyfishes (Family Chaetodontidae) across multiple geographic locations with differing resource availability. Butterflyfishes provide an ideal model in which to investigate local and regional patterns of dietary specialisation. Species within this diverse family vary significantly in their dietary preferences and level of dietary specialisation (Reese 1981, Harmelin-Vivien and Bouchon-Navaro 1983, Pratchett 2005, Pratchett 2007). Some species, such as *Chaetodon trifascialis,* only feed on a small number of hard coral species; while other species, such as *C. citrinellus*, feed across a broad range of dietary items including hard corals, soft corals and other reef macro-invertebrates (Pratchett 2005). There is also anecdotal evidence that dietary composition varies geographically for some species. For example, based on stomach content analysis hard corals account for over 82% of the diet of *C. vagabundus* at locations in the Indian Ocean (Harmelin-Vivien 1989), but in the Pacific Ocean they comprise less than 20% of its diet (Harmelin-Vivien 1989, Pratchett 2005). Importantly, the feeding behaviour of butterflyfishes is readily observable in the field and the availability of dietary resources can be directly measured at the same time and place (Berumen et al. 2005, Lawton et al. In press). These characters allow us to establish patterns of dietary preference and specialisation in a group of closely related species and determine whether species are fundamentally specialised or simply feeding predominantly on prey types that are locally abundant.

Coral-feeding butterflyfishes have been identified as one of the most vulnerable groups of reef fishes to the combined effects of ongoing global coral loss and habitat degradation on reefs (Wilson et al. 2006, Pratchett et al. 2008). Characterising their local and regional patterns of dietary specialisation has important implications for understanding how butterflyfishes are being impacted by climate change (Wilson et al. 2010). Specialist coral feeders, such as *C. trifascialis*, are thought to be most vulnerable as the *Acropora* corals they preferentially feed on are highly sensitive to climate induced coral bleaching (Pratchett et al. 2008). The resilience of coral-feeding butterflyfishes to any future coral loss will be determined by their ability to use alternative resources if the abundance of preferred corals declines (Pratchett et al. 2004); however, this is currently unknown for most specialist coral-feeders. Although in-situ feeding observations have provided detailed estimates of dietary composition and specialisation (at high taxonomic resolution) only a small number have compared resource use to resource availability and these studies have been confined to a few isolated locations (e.g. Johnston Atoll: Irons 1989, Hawaiian Islands: Cox 1994, Great Barrier Reef: Berumen et al. 2005, Pratchett 2007, Seychelles: Graham 2007). As yet, there have been no systematic comparisons of resource availability and butterflyfish dietary specialisation across multiple geographic locations using the same methodology. Consequently, the degree that particular butterflyfish species are truly specialised or generalised is unknown, and therefore their vulnerability to global climate change is not fully appreciated.

The objective of this study is to investigate geographic variation in the feeding ecology of coral-feeding butterflyfishes and examine whether patterns of resource use and levels of dietary specialisation vary among distinct locations, corresponding with changes in resource availability. Our specific aims were to (i) investigate whether the dietary niche breadth of four butterflyfishes varies among five geographically separated locations; and (ii) assess whether each species utilises similar resources in each location. If dietary specialisation is high but resource use varies among locations, then local resource use is likely to be constrained. In contrast, if dietary specialisation is high and the same resources are used in each location, then patterns of resource use most likely reflect fundamental specialisation rather than local constraints.

METHODS

Study sites

Feeding observations were conducted at five geographically separated locations throughout the Pacific - Lizard Island, Northern Great Barrier Reef; Heron Island, Southern Great Barrier Reef; Kimbe Bay, Papua New Guinea; Noumea, New Caledonia and Moorea, French Polynesia (Fig 1). These five locations are situated along known diversity gradients, with pairwise distances between 1100km and 6600km apart. Species diversity of both corals and reef fish is highest in a region which includes Papua New Guinea, known as the Indo-Australian Archipelago (IAA) and declines with increasing distance from this region, being lowest in the eastern Pacific (Bellwood and Hughes 2001). Among scleractinian corals, species richness in Papua New Guinea is approximately double that of French Polynesia (Karlson et al. 2004). At each location, three distinct sites were chosen for feeding observations. Sites were standardised for habitat type and depth. At each site sampling was conducted along the exposed to semi-exposed reef crest to eliminate potential effects of variable exposure (e.g. Berumen et al. 2005).

Resource availability

Variation in the availability of coral prey was assessed using 50m point intercept transects. At each site, five replicate transects were laid consecutively, following the contour of the reef crest, in the same area where feeding observations took place. For each transect, the substrate directly beneath 200 uniform sampling points (spaced every 25cm) was recorded to species level for corals, and to broad categories for all other substrate types (e.g. non-coral substrate, macroalgae). Variation in total coral cover among locations and sites (nested within locations) was assessed using a nested ANOVA. Variation in proportional cover of dietary resources (grouped into 12 resource categories, listed in Table 1) among locations and sites (nested within locations) was compared using a nested multivariate analysis of variance (MANOVA). Availability of individual resource categories was compared among locations and sites (nested within locations) using univariate analyses of variance. Alpha values were adjusted for multiple tests using a Bonferroni correction (Miller 1981). Data were arc-sin transformed to satisfy assumptions of homogeneity and normality. Residual plots, homogeneity tests and sphericity tests were used to ensure assumptions were met. Pillai's trace statistic was used to determine the significance of MANOVA results. All statistical analyses were conducted using SPSS Statistics 18.0.

Feeding observations

Feeding observations were conducted for four common and widespread species of butterflyfishes - *Chaetodon vagabundus, C. citrinellus*, *C. lunulatus* and *C. trifascialis.* All four species have been documented to consume hard (scleractinian) corals as part of their diet in at least some locations throughout their geographic range (Cole et al. 2008). Both *C. vagabundus* and *C. citrinellus* have been previously reported as facultative corallivores – consuming hard corals as well as other macro-invertebrates and soft corals; while *C. lunulatus* and *C. trifascialis* are both reported as obligate corallivores, feeding almost exclusively on hard corals (Pratchett 2005, Cole et al. 2008). Dietary composition was determined for each species from field observations of feeding behaviour at each site. Individual adult butterflyfishes were randomly selected and followed at a distance of 2 - 5 metres for a 3-minute period. Every effort was made to ensure individual fish were not observed more than once. The total number of bites taken from each species of coral, other non-coral macro-invertebrates, and non-coral substrates during each observation was recorded, following Pratchett (2005). At least twenty observations for each species were conducted throughout the day at each site, giving a total of at least 60 observations at each location for each species.

Dietary specialisation and selectivity

Due to the large geographic scale of this study, the specific coral species present in each location varied. Therefore, all dietary resources were grouped into 12 categories (listed in Table 1) to enable comparisons of dietary specialisation and selectivity to be made between locations. Variation in overall dietary composition among locations and sites (nested within locations) for each species was analysed using MANOVAs, which simultaneously compared the proportion of bites taken by each species on each of the 12 resource categories. Variation in proportional composition of individual resource categories was compared among locations and sites (nested within locations) for each species using univariate analyses of variance. Alpha values were adjusted for multiple tests using a Bonferroni correction (Miller 1981). Residual plots, homogeneity tests and sphericity tests were used to ensure assumptions were met. Pillai's trace statistic was used to determine the significance of results.

Smith's measure of niche breadth (*FT)* was used to determine the relative degree of dietary specialisation for each species on each of the 12 resource categories at each site (Smith 1982). This measure takes into account resource availability and is less sensitive to the use of rare resources compared to other niche breadth measures (Krebs 1999). *FT* is a standardised measure, ranging from 0 (most specialised) to 1 (least specialised), therefore allowing comparison of the level of specialisation between sites and locations for each species. Niche breadth was compared among locations using separate one way ANOVAs for each species. Data were arcsin transformed and residual plots and homogeneity tests were used to ensure ANOVA assumptions were met.

Niche overlap between locations was measured for each species using Morista's similarity index. This index reduces bias due to small sample sizes and is least affected by the number of resource categories compared to other niche overlap measures (Krebs 1999). Morista's similarity index (C_λ) ranges from 0 (no similarity) to 1 (complete similarity) and was calculated following Krebs (1999). The total number of bites taken by each species on each of the 12 resource categories was pooled across the three sites for each location and these pooled values were used in calculations.

Resource selection functions were used to investigate variation in dietary selectivity between locations and determine which resources were used significantly more or less frequently than expected based on their availability. Resource selection functions were calculated for the 12 resource categories for each species at each site following Manly et al.'s (2002) Model Design II, Sampling Protocol A. These functions allow for sampling of resource use at the individual level and resource availability at the population level (Manly et al. 2002). Bonferroni corrected 95% confidence intervals were calculated around each selection function such that the use of a particular prey was deemed to be significantly disproportionate to its availability if the 95% confidence interval did not encompass one (Manly et al. 2002). Selection functions significantly greater than one indicated selection (i.e. resource was consumed significantly more than expected based on availability); selection functions significantly less than one indicated avoidance (i.e. resource was consumed significantly less than expected based on availability).

RESULTS

Resource availability

Total coral cover was highest at sites in New Caledonia (41% ±4.2 S.E. to 80% ±8.4 S.E.) and Papua New Guinea (48% ±5.2 S.E. to 63% ±3.2 S.E.) and lowest at sites in French Polynesia (26% ±2.9 S.E. to

37% ±6.1 S.E.). Differences in total coral cover among locations were not significant (nested ANOVA, $F_{4,10}=3.009$, $P=0.072$), however there were significant differences among sites nested within locations (nested ANOVA, $F_{10,60}=6.888$, $P<0.001$). Availability of dietary resources varied significantly among locations (nested MANOVA, Pillai's trace=3.401, df = 48,208 $P<0.001$) and sites nested within locations (nested MANOVA, Pillai's trace=3.775, df = 120,580 $P<0.001$). The Heron Island coral assemblage was dominated by *Acropora* corals, with *Acropora hyacinthus,* 'Staghorn *Acropora*' and 'Other *Acropora*' resource categories comprising more than 55% of the total coral cover at this location (Fig 2). Lizard Island was the only location where soft corals were available in any meaningful quantity (10.5% ±0.6 S.E. cover compared to <1% cover in all other locations (Fig 2). Cover of *A. hyacinthus* was highest in Papua New Guinea (14.3% ±1.0 S.E., all other locations <10%), while New Caledonia sites had a much higher cover of Staghorn *Acropora* (25.9% ±0.8 S.E.) compared to all other locations (<5%) (Fig 2). French Polynesia sites were dominated by *Porites sp.* and *Montipora sp.* – these two resource categories accounting for >80% of the total coral cover in this location (Fig 2). The availability of all individual resource categories except 'Other hard corals' varied significantly among locations (Table 1). Post hoc tests indicated that percentage cover of *A. hyacinthus* was significantly higher in Papua New Guinea compared to Lizard Island, Heron Island and French Polynesia, cover of *A. hyacinthus* was also significantly higher in New Caledonia compared to French Polynesia (Tukey's HSD $p<0.01$). Percentage cover of 'Staghorn *Acropora'* was significantly higher in New Caledonia compared to all other locations (Tukey's HSD $p<0.001$), while percentage cover of 'Other *Acropora*' was significantly lower in French Polynesia and higher at Lizard Island, Heron Island and New Caledonia relative to all other locations (Tukey's HSD $p<0.01$). Lizard Island and Papua New Guinea had significantly higher cover of *Pocillopora sp.* compared to all other locations (Tukey's HSD $p<0.001$). Percentage cover of *Porites sp.* was significantly lower in Lizard Island, Heron Island and New Caledonia compared to Papua New Guinea and French Polynesia (Tukey's HSD $p<0.001$). Percentage cover of *Montipora sp.* was significantly higher in French Polynesia compared to Lizard Island and Heron Island (Tukey's HSD $p<0.01$), while percentage cover of soft corals was significantly higher at Lizard Island compared to all other locations (Tukey's HSD $p<0.001$).The availability of all individual resource categories except *A. hyacinthus, Montipora sp., Porites sp*, Soft Corals and 'Other' also varied significantly among sites nested within locations (Table 1).

Dietary composition and specialisation

Chaetodon vagabundus

Chaetodon vagabundus took at least 90% of all bites on non-coral substrates at Lizard Island, Heron Island and French Polynesia, but in New Caledonia and Papua New Guinea this figure dropped to 72.4% (±14 S.E.) and 61.1% (±6 S.E.) respectively (Supplementary information, Appendix S1). A large number of bites were taken on hard corals in Papua New Guinea (32.0% ±5.2 S.E.) compared to other locations (less than 15%). Dietary composition varied significantly among locations (nested MANOVA, Pillai's trace=0.633, df = 48,1204 $P<0.001$) and sites nested within locations (nested MANOVA, Pillai's trace=0.681, df = 120,3070 $P<0.001$). Proportional consumption of non-coral substrates, *Pocillopora sp., Montipora sp., Porites sp.,* Favidae and 'Other' varied significantly among locations and proportional consumption of non-coral substrates, *Montipora sp.* and 'Other' also varied significantly among sites nested within locations (Supporting information, Appendix S2). Dietary niche breadth was relatively high, ranging from 0.66 (±0.14 S.E.) in New Caledonia to 0.92 (±0.03) in French Polynesia (Fig 3), and did vary not significantly among locations (one way ANOVA, $F_{4,10}=2.606$, $P=0.10$). Niche overlap between locations was also high, ranging from 0.89 to 1.00 (Table 2). Resource selections functions indicated that non-coral substrates were positively selected at all but one site, but selectivity for other dietary resources was much more variable among locations (Table 3). Different resource categories were selected or avoided in each location and, in some cases, selectivity for particular resource categories differed among sites within a location (e.g. *Porties sp.* in New Caledonia).

Chaetodon citrinellus

Chaetodon citrinellus fed predominantly on hard corals at Lizard Island and Papua New Guinea (68.7% ±6 S.E. and 60.3% ±15 S.E. of all bites respectively), while in New Caledonia and French Polynesia the majority of bites were taken on non-coral substrates (53.3% ±9 S.E. and 60.4% ±18 S.E. respectively) (Supplementary Information, Appendix S1). *Chaetodon citrinellus* fed across a range of different hard coral resource categories in all locations. Roughly half of all bites on hard corals were taken on *Montipora sp.* in French Polynesia and 'Other *Acropora'* in Heron Island, while at Lizard Island *Pocillopora sp*. accounted for nearly 40% of all bites on hard corals on average. In contrast, in both New Caledonia and Papua New Guinea, bites were spread reasonably evenly between all hard coral resource categories. Dietary composition varied significantly among locations (nested MANOVA, Pillai's trace=1.109, df = 48,1144 $P<0.001$) and sites nested within locations (nested MANOVA, Pillai's trace=1.453, df = 120,2920 $P<0.001$). Proportional consumption of all individual resource categories except other hard corals and 'other' varied significantly among locations, while proportional consumption of non-coral substrates, 'Staghorn *Acropora', Pocillopora sp., Montipora sp., Porites sp.* and 'Other' varied significantly among sites nested within locations (Supporting information, Appendix S2). Niche breadth ranged from 0.89 (±0.04 S.E.) in New Caledonia to 0.93 (±0.01) in Heron Island (Fig 3) and did not vary significantly among locations (one way ANOVA, $F_{4,10}=0.285$, $P=0.88$). Niche overlap was variable between locations, ranging from 0.65 to 0.94, however there was no clear pattern in similarity between locations (Table 2). Resource selection functions indicated that *C. citrinellus* was a highly generalised feeder at local and regional scales. Significant selectivity or avoidance was only shown for a few resource categories and most categories were consumed in proportion to their availability across all locations (Table 3).

Chaetodon lunulatus

Chaetodon lunulatus fed almost exclusively on hard corals, taking at least 97% of all bites on hard corals at all locations (Supplementary Information, Appendix S1). Bites were taken on at least 7 of the 9 hard coral resource categories in each location, with the majority of bites taken on 'Staghorn *Acropora*',' Other *Acropora*', *Pocillopora sp.* or *Montipora sp.*. Dietary composition varied significantly among locations (nested MANOVA, Pillai's trace=1.334, df = 48,1184 P<0.001) and sites nested within locations (nested MANOVA, Pillai's trace=1.464, df = 120,3020 P<0.001). Proportional consumption of all individual resource categories except non-coral substrates, soft corals and 'Other' varied significantly among locations and sites nested within locations; proportional consumption of Favidae and Other *Acropora* also varied significantly among sites nested within locations (Supporting information, Appendix S2). Dietary niche breadth ranged from 0.64 (±0.10 S.E.) in Papua New Guinea to 0.73 (±0.05 S.E.) in New Caledonia (Fig 3), and did not vary significantly among locations (one way ANOVA, $F_{4,10}$=0.403, P=0.80). However, niche overlap was highly variable between locations (Table 2). Dietary composition was most similar between Heron Island and Lizard Island (overlap: 0.85) and least similar between French Polynesia and all other sites except Papua New Guinea (overlap of 0.28, 0.24 and 0.37 for Heron Island, Lizard Island and New Caledonia respectively). Resource selection functions indicated that *C. lunulatus* had very generalised feeding preferences across all locations, with most resource categories consumed in proportion to their availability (Table 3).

Chaetodon trifascialis

Chaetodon trifascialis also fed exclusively on hard corals, taking 100% of bites on hard corals at all locations (Supplementary Information, Appendix S1). With the exception of French Polynesia, over 90% of all bites were taken on *Acropora* coral resource categories (*A. hyacinthus,* 'Staghorn *Acropora'* and 'Other *Acropora'*) in each location on average, and between 42.6% (±0.9 S.E., New Caledonia) and 82.0% (±0.2 S.E., Papua New Guinea) of all bites were taken on *A. hyacinthus* (Supplementary Information, Appendix S1). In French Polynesia only 56.6% (±4.0 S.E.) of all bites were taken on *Acropora* coral resource categories, and instead *C. trifascialis* also fed on *Montipora sp.* and *Pocillopora sp.* corals. Dietary composition varied significantly among locations (nested MANOVA, Pillai's trace=1.016, df = 40,1164 P<0.001) and sites nested within locations (nested MANOVA, Pillai's trace=0.70, df = 100,2970 P<0.001). Proportional consumption of *A. hyacinthus, '*Staghorn *Acropora'* and 'Other *Acropora'* varied significantly among locations and sites nested within locations; proportional consumption of *Pocillopora sp., Porites sp.* and *Montipora sp.* also varied significantly among sites nested within locations (Supporting information, Appendix S2). Dietary niche breadth varied significantly among locations (one way ANOVA, $F_{4,10}$=8.375, P=0.03), ranging from 0.33 (±0.03 S.E.) in French Polynesia to 0.64 (±0.06 S.E.) in New Caledonia (Fig 3). Niche overlap was reasonably high between all locations (Table 2) except French Polynesia and Lizard Island, and French Polynesia and Papua New Guinea (overlap of 0.29 and 0.38 respectively). Resource selection functions indicated that *C. trifascialis* was a highly specialised feeder, with similar patterns of selectivity recorded in each location (Table 3). *Acropora hyacinthus* was positively selected at all sites where it was available, except one site (North Wistari) at Heron island where it was consumed in proportion to availability. Furthermore, with the exception of two sites in French Polynesia, significant selectivity was only shown for *Acropora* coral resource categories.

DISCUSSION

Despite varying resource availability, we found that the level of dietary specialisation shown by each of the four species of butterflyfishes varied little among geographically separated locations. Species using a high number of resources locally did so across all locations and varied patterns of resource use with varying resource availability. In contrast, species using a low number of resources locally used the same resources in each location, regardless of their availability. Similarities between local and regional patterns of dietary specialisation suggest that the dietary niche of coral-feeding butterflyfishes is not constrained at the locations studied here.

Our analyses indicated that *C. vagabundus, C. citrinellus* and *C. lunulatus* had low levels of dietary specialisation and varying patterns of resource use in each location. These findings are in agreement with previous studies showing that these species feed on a large range of dietary resources across multiple locations (e.g. Motta 1988, Harmelin-Vivien 1989, Cox 1994, Pratchett 2007) and suggest that they have wide dietary niche breadths. Most likely, the same factors that allow these species to use a wide range of dietary resources locally also allow them to substitute those resources between locations (Krasnov et al. 2008). In contrast, *C. trifascialis* used very similar resources and had high levels of dietary specialisation in each location. *Acropora* corals dominated its diet, accounting for 57% of dietary composition in French Polynesia, despite very low availability (<2% total cover), and >90% of dietary composition at all other locations. *Chaetodon trifascialis* is widely known to preferentially feed on *Acropora* corals throughout its geographic range, showing high selectivity for these corals regardless of their availability (Reese 1981, Alwany et al. 2003, Graham 2007, Pratchett 2007). For example, even though *Acropora* corals comprised less than 0.5% of the total cover at Johnston Atoll, *C. trifascialis* still took 83% of all bites on these corals (Irons 1989). This high dietary specialisation, and selective use of the same resources across locations despite varying resource availability, suggests that *C. trifascialis* has a very narrow dietary niche breadth.

Our inferred dietary niche breadths for these species are supported by their response to localised coral loss on reefs. Consistent with our conclusion of wide dietary niche breadths, multiple studies have shown that *C. vagabundus, C. citrinellus* and *C. lunulatus* do not decline in abundance following moderate coral loss (e.g. Williams 1986, Halford et al. 2004, Pratchett et al. 2006), or have smaller relative declines in abundance compared to other more specialised species (e.g. Bouchon-Navaro et al. 1985, Berumen and Pratchett 2006b). Furthermore, *C. lunulatus* has also been shown to alter its diet and increase feeding on previously non-preferred coral species following a bleaching event resulting in a 55% decline in total coral cover and a loss of some coral taxa (Pratchett et al. 2004). In contrast, *C. trifascialis* is often one of the worst affected of all coral-feeding butterflyfishes by coral loss (Wilson et al. 2006, Pratchett et al. 2008). Consistent with our conclusion of narrow dietary niche breadth, the abundance of *C. trifascialis* has declined severely following coral loss across multiple locations (e.g. Halford et al. 2004, Graham et al. 2006, Pratchett et al. 2006, Wilson et al. 2006) and at some sites possible local extinctions of this species have been recorded (Berumen and Pratchett 2006b).

Although *C. trifascialis* is undoubtedly vulnerable to coral loss, our results suggest that it is more versatile and thus, less vulnerable to coral loss than has been previously suggested. *Chaetodon trifascialis* has been characterised as an extreme specialist (e.g. Pratchett et al. 2008) as it feeds almost exclusively on tabular *Acropora* corals, such as *A. hyacinthus*, in a number of locations (Reese 1981, Irons 1989, Pratchett 2005, Berumen and Pratchett 2008). In the current study, *A. hyacinthus* accounted for less than 50% of dietary composition at some sites (e.g. Ilot Nge, Seche Croissant, North Wistari), and at many sites staghorn *Acropora* and other *Acropora* corals were also consumed in significant quantities. Furthermore, as was apparent in French Polynesia in the current study, there is some evidence that *C. trifascialis* increases consumption of other coral taxa when abundance of

*Acropora c*orals is very low. *Chaetodon trifascialis* has also been observed to increase feeding on *Pocillopora* corals at sites in the Seychelles where *Acropora* corals were scarce (Graham 2007). These recent demonstrations of feeding plasticity suggest that *C. trifascialis* may have a lower dependence on *Acropora* corals, and *A. hyacinthus* in particular, than has previously been assumed. But while increased use of alternative coral taxa may enable *C. trifascialis* to persist through periods of coral loss in the short term, it may also have significant sub-lethal effects on growth and condition. In a tank experiment, *C. trifascialis* juveniles maintained on an exclusive diet of non-preferred corals rapidly lost weight, despite actively feeding each day (Berumen and Pratchett 2008). Likewise, liver lipid reserves (an indicator of physiological condition) of *C. lunulatus* and *C. baronessa* were found to be significantly lower at sites where the abundance of preferred corals was low, even though feeding rates were maintained (Berumen et al. 2005). If use of non-preferred coral resources is continuous or prolonged, then sub-lethal effects may accumulate over time, potentially decreasing reproductive output and reducing survival. Such a situation may already have occurred at some sites in Moorea, French Polynesia, where the abundance of *C. trifascialis* has declined by almost 100% following a shift in coral composition from assemblages dominated by *Acropora* spp. to assemblages dominated by *Pocillopora* spp. as a result of recurrent disturbances (Berumen and Pratchett 2006b).

Interspecific interactions such as competition and predation are often cited as a key constraint on resource use (Colwell and Fuentes 1975). Competitive interactions between species can restrict the use of mutually preferred resources by subordinate competitors (Connell 1983, Abramsky et al. 1990, Young 2004, Bonin et al. 2009). Clear dominance hierarchies have been demonstrated for butterflyfishes and some species are known to aggressively defend territories containing the coral *A. hyacinthus* (Berumen and Pratchett 2006a). However, the only species in this study with locally restricted use of resources, *C. trifascialis*, is competitively dominant (Berumen and Pratchett 2006a). Consequently, coral resource use by *C. trifascialis* is unlikely to be restricted by competitive interactions with other butterflyfish species. An alternative possibility is that competitive interactions may actually result in an expansion of dietary niche breadth for some subordinate butterflyfishes, whereby dominant competitors limit access to reef habitats with high abundance of preferred coral resources but are unable to completely monopolise specific prey types (Pratchett 2005). Aside from competition, predation (or more specifically, the risk of predation) can moderate patterns of prey and habitat use (Werner et al. 1983, Gotceitas and Colgan 1990, Creel et al. 2005). Predation is generally thought to be very low for coral-feeding butterflyfishes (Cole et al. 2008), although further research is needed to explicitly quantify predation risk for adult butterflyfishes and the influence of predation risk on patterns of prey and habitat use. It is possible that resource availability was limiting resource use at some sites. However, despite varying resource availability among both sites and locations, *C. trifascialis* used the same restricted range of resources (mostly *Acropora* corals) across all sites and locations. This finding reinforces experimental studies conducted by Berumen and Pratchett (2008) showing that *C. trifascialis* is a fundamental dietary specialist. In contrast, *C. vagabundus, C. citrinellus* and *C. lunulatus* all varied patterns of resource use in each location and used a wide range of resources across all locations.

It has long been assumed that localised patterns of resource use are constrained for many organisms (Hutchinson 1957). This assumption is supported by numerous studies which have experimentally demonstrated an expansion of niche breadth for a wide range of organisms following a release from interspecific competition or predation pressure (reviewed by Colwell and Fuentes 1975). However, in combination with recent studies failing to detect an expansion of niche breadth in the absence of competition (Arlettaz et al. 1997, Mesquita et al. 2007, but see Costa et al. 2008), our findings question this assumption and suggest that interspecific interactions may not be the primary determinant of niche breadth for some species (Manthey et al. 2011). Furthermore, our results suggest that the dietary niche breadth of coral feeding butterflyfishes is unlikely to be much wider if considered on a regional rather than a local scale. A similar conclusion can be inferred from a recent study of host specificity in parasitic fleas, which found that host specialisation was scale invariant, such that species that were either specialised or generalised at a local scale, were also specialised or generalised across their entire geographic range (Krasnov et al. 2008). These findings suggest that local resource use will not always be constrained. As a result, researchers should be wary of expecting the niche breadth of organisms to expand if the spatial scale of analysis is increased.

Conclusions

Although previous studies have emphasized the vulnerability of specialised coral feeding fishes to coral loss based on their inability to use non-preferred resources (e.g. Pratchett et al. 2008), there has been little understanding of whether particular butterflyfish species are fundamentally specialised or locally adapted to take advantage of dominant coral taxa. Our results indicate that relative levels of dietary specialisation among different butterflyfishes do hold at larger spatial scales, but we found geographical variation in the dietary composition of all butterflyfishes, showing that prey availability has a fundamental influence on dietary composition. The similarity between local versus regional patterns of prey use was highest for *C. trifascialis*, which relies on coral taxa (mostly *Acropora* spp) that are highly vulnerable to an increasing array of different disturbances (Pratchett et al. 2008). With coral loss and degradation of reef ecosystems predicted to increase (Hoegh-Guldberg et al. 2007), this species is likely to be at a high risk of extinction. However, the increased feeding plasticity observed here suggests that *C. trifascialis* may have a greater capacity to respond to coral loss than previously assumed from single region assessments. These findings reinforce the importance of considering patterns of specialisation across a broad geographic scale when assessing vulnerability.

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Table 1: ANOVA results for variation in availability of dietary resource categories between nine sites nested within five locations. Significant values at Bonferroni corrected α=0.004 are shown in bold.

Source	Variable	SS	d.f.	MS	*F*	*P*
Location	Non-coral substrate	1.199	4	0.300	31.756	**<0.001**
	Soft coral	0.128	4	0.032	98.718	**<0.001**
	Acroproa hyacinthus	0.169	4	0.042	9.808	**<0.001**
	Staghorn *Acropora*	0.786	4	0.196	22.441	**<0.001**
	Other *Acropora*	0.311	4	0.078	33.983	**<0.001**
	Pocillopora sp.	0.051	4	0.013	51.402	**<0.001**
	Montipora sp.	0.026	4	0.006	5.680	**0.001**
	Porites sp.	0.383	4	0.096	49.658	**<0.001**
	Favidae	0.022	4	0.005	10.138	**<0.001**
	Isopora sp.	0.103	4	0.026	35.378	**<0.001**
	Other hard corals	0.001	4	0.000	2.213	0.078
	Other	0.012	4	0.003	4.084	**0.005**
Site(Location)	Non-coral substrate	0.642	10	0.064	6.808	**<0.001**
	Soft coral	0.008	10	0.001	2.320	0.022
	Acroproa hyacinthus	0.076	10	0.008	1.762	0.088
	Staghorn *Acropora*	1.060	10	0.106	12.105	**<0.001**
	Other *Acropora*	0.269	10	0.027	11.771	**<0.001**
	Pocillopora sp.	0.031	10	0.003	12.554	**<0.001**
	Montipora sp.	0.095	10	0.010	8.400	**<0.001**
	Porites sp.	0.028	10	0.003	1.443	0.184
	Favidae	0.009	10	0.001	1.715	0.098
	Isopora sp.	0.038	10	0.004	5.206	**<0.001**
	Other hard corals	0.004	10	0.000	3.371	**0.002**
	Other	0.007	10	0.001	.926	0.516

Table 2: Niche overlap (C_λ) among five locations of four butterflyfish species.

	Lizard Island	Papua New Guinea	New Caledonia	French Polynesia
C. vagabundus				
Heron Island	1.00	0.89	0.98	1.00
Lizard Island		0.89	0.98	1.00
Papua New Guinea			0.94	0.90
New Caledonia				0.98
C. citrinellus				
Heron Island	0.74	0.69	0.90	0.78
Lizard Island		0.93	0.71	0.65
Papua New Guinea			0.69	0.68
New Caledonia				0.94
C. lunulatus				
Heron Island	0.85	0.66	0.78	0.28
Lizard Island		0.64	0.75	0.24
Papua New Guinea			0.64	0.71
New Caledonia				0.37
C. trifascialis				
Heron Island	0.84	0.77	0.96	0.70
Lizard Island		0.99	0.82	0.38
Papua New Guinea			0.74	0.29
New Caledonia				0.66

Table 3: Dietary selectivity of four butterflyfishes at five locations on 12 resource categories. +: category used significantly more than expected (selected); =: category used in proportion to availabilty; -: category used significantly less than expected (avoided); 0: category unused (strongly avoided); NA: category not available. HI: Heron Island, LI: Lizard Island, PNG: Papua New Guinea, NC: New Caledonia, FP: French Polynesia.

Location	Site	Non-coral substrate	Soft coral	*A. hyacinthus*	*Staghorn Acropora*	*Other Acropora*	*Pocillopora sp.*	*Montipora sp.*	*Porites sp.*	*Favidae*	*Isopora sp.*	Other hard corals	Other
C. vagabundus													
HI	Blue Pools	+	0	0	0	0	-	0	0	0	0	=	=
	North Wistari	+	NA	0	0	=	-	0	=	0	0	0	=
	2nd Point	+	NA	0	0	0	=	0	0	=	-	0	0
LI	Bird Islet	+	0	=	-	=	0	0	0	=	0	0	0
	Lizard Head	+	-	=	0	-	-	0	-	-	0	0	=
	South Island	+	0	-	-	0	0	0	0	-	0	=	=
PNG	Christines	+	0	-	0	-	=	=	=	=	0	0	+
	Lubaluba	+	NA	-	0	0	=	=	=	=	0	=	=
	Susans	=	NA	-	0	-	=	=	=	=	-	=	+
NC	Ilot Nge	+	0	-	-	=	=	+	+	0	0	=	+
	Recif Senez	+	NA	0	0	0	0	=	0	NA	NA	NA	=
	Seche Croissant	+	0	0	-	-	=	0	=	NA	0	=	+
FP	Motu Ahi	+	NA	NA	NA	0	=	-	-	0	NA	0	=
	Temea	+	NA	0	0	0	=	=	-	0	NA	0	0
	Tiahura	+	NA	NA	0	0	0	-	-	0	NA	0	0
C. citrinellus													
HI	Blue Pools	=	0	=	=	=	=	=	=	=	=	-	-
	North Wistari	=	NA	=	=	=	=	=	=	0	=	=	=
	2nd Point	+	NA	=	=	-	=	=	=	=	=	=	=
LI	Bird Islet	-	-	=	=	=	+	=	=	=	=	=	=
	Lizard Head	=	=	=	0	=	+	=	-	-	=	=	=
	South Island	-	-	=	=	=	+	=	-	=	=	=	=
PNG	Christines	-	0	-	0	=	+	=	=	=	=	0	=
	Lubaluba	=	NA	=	0	=	=	=	=	=	0	=	-
	Susans	-	NA	=	0	=	+	+	-	=	-	=	0
NC	Ilot Nge	+	0	=	=	=	=	=	=	=	0	=	0
	Recif Senez	+	NA	=	=	-	=	=	0	NA	NA	NA	=
	Seche Croissant	+	0	=	=	=	=	=	=	NA	0	=	=
FP	Motu Ahi	-	NA	NA	NA	=	+	+	-	0	NA	=	0
	Temea	=	NA	=	0	0	=	=	-	=	NA	0	=
	Tiahura	+	NA	NA	0	=	=	=	-	=	NA	=	0

C. lunulatus													
HI	Blue Pools	-	0	=	=	=	+	=	=	=	=	=	=
	North Wistari	-	NA	+	=	=	=	=	=	=	=	=	=
	2nd Point	=	NA	=	=	+	=	+	=	=	=	+	-
LI	Bird Islet	-	-	+	=	=	+	=	=	=	=	=	-
	Lizard Head	-	0	=	0	+	+	=	=	=	=	=	0
	South Island	-	-	+	=	=	+	=	=	=	=	=	0
PNG	Christines	0	0	=	=	=	=	+	+	=	=	=	=
	Lubaluba	-	NA	0	=	=	-	=	+	=	=	+	-
	Susans	0	NA	=	=	=	+	=	=	=	=	=	0
NC	Ilot Nge	-	0	+	=	=	+	=	+	=	0	=	0
	Recif Senez	-	NA	+	=	=	=	=	0	NA	NA	NA	0
	Seche Croissant	-	0	+	=	=	=	+	+	NA	0	=	0
FP	Motu Ahi	-	NA	NA	NA	=	=	+	+	0	NA	=	0
	Temea	-	NA	=	0	0	=	+	+	0	NA	0	0
	Tiahura	-	NA	NA	0	0	-	+	+	=	NA	=	0
C. trifascialis													
HI	Blue Pools	0	0	+	=	+	0	-	0	-	=	0	0
	North Wistari	0	NA	=	=	=	-	0	0	-	0	0	0
	2nd Point	0	NA	+	=	+	0	=	0	0	-	0	0
LI	Bird Islet	0	0	+	=	=	=	0	0	0	0	0	0
	Lizard Head	0	0	+	-	=	=	0	0	0	0	0	0
	South Island	0	0	+	=	=	=	0	0	0	0	0	0
PNG	Christines	0	0	+	=	=	=	-	-	0	-	0	0
	Lubaluba	0	NA	+	0	=	=	0	-	0	0	0	0
	Susans	0	NA	+	0	=	=	-	-	0	0	0	0
NC	Ilot Nge	0	0	+	+	+	0	=	0	0	=	0	0
	Recif Senez	0	NA	+	=	+	=	0	0	NA	NA	NA	0
	Seche Croissant	0	0	+	+	+	0	-	0	NA	0	0	0
FP	Motu Ahi	0	NA	NA	NA	+	+	=	=	0	NA	0	0
	Temea	0	NA	+	=	+	+	=	-	0	NA	0	0
	Tiahura	0	NA	NA	=	+	=	=	-	0	NA	=	0

FIGURE LEGENDS

Fig 1: Map of the five locations sampled in this study: Heron Island, Great Barrier Reef (HI); Lizard Island, Great Barrier Reef (LI); Kimbe Bay, Papua New Guinea (PNG); Noumea, New Caledonia (NC); and Moorea, French Polynesia (FP).

Fig 2: Mean (± S.E.) percent cover of twelve resource categories at Heron Island (HI), Lizard Island (LI), Papua New Guinea (PNG), New Caledonia (NC), and French Polynesia (FP). NCS: non-coral substrate, SC: soft coral, AHY: *Acropora hyacinthus*; AST: Staghorn *Acropora*, AOT: Other *Acropora*, POC: *Pocillopora sp.*; MON: *Montipora sp.;* POR: *Porites sp.*; FAV: Favidae; ISO: *Isopora sp.;* OHC: Other hard corals; OTH: Other.

Fig 3: Mean (± S.E.) dietary niche breadth (*FT)* of four butterflyfish species at Heron Island (HI), Lizard Island (LI), Papua New Guinea (PNG), New Caledonia (NC), and French Polynesia (FP).

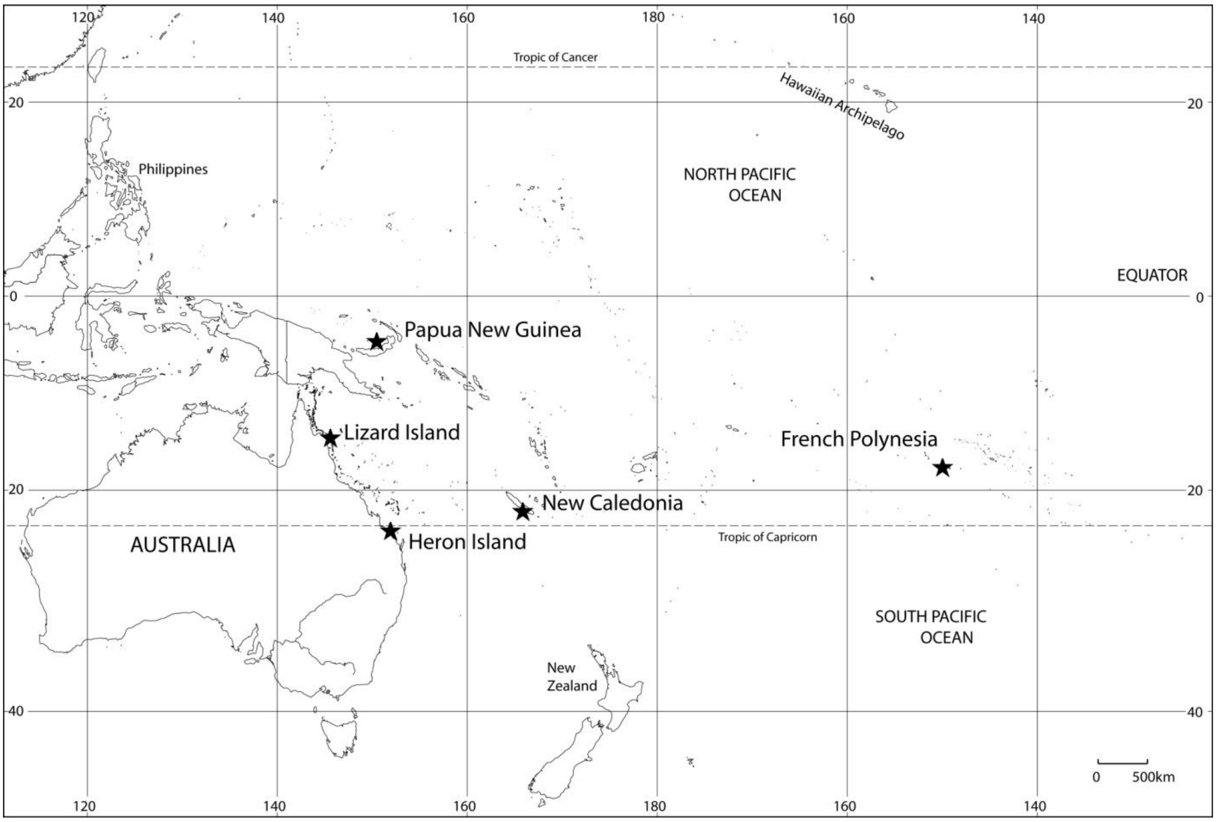

Fig 1

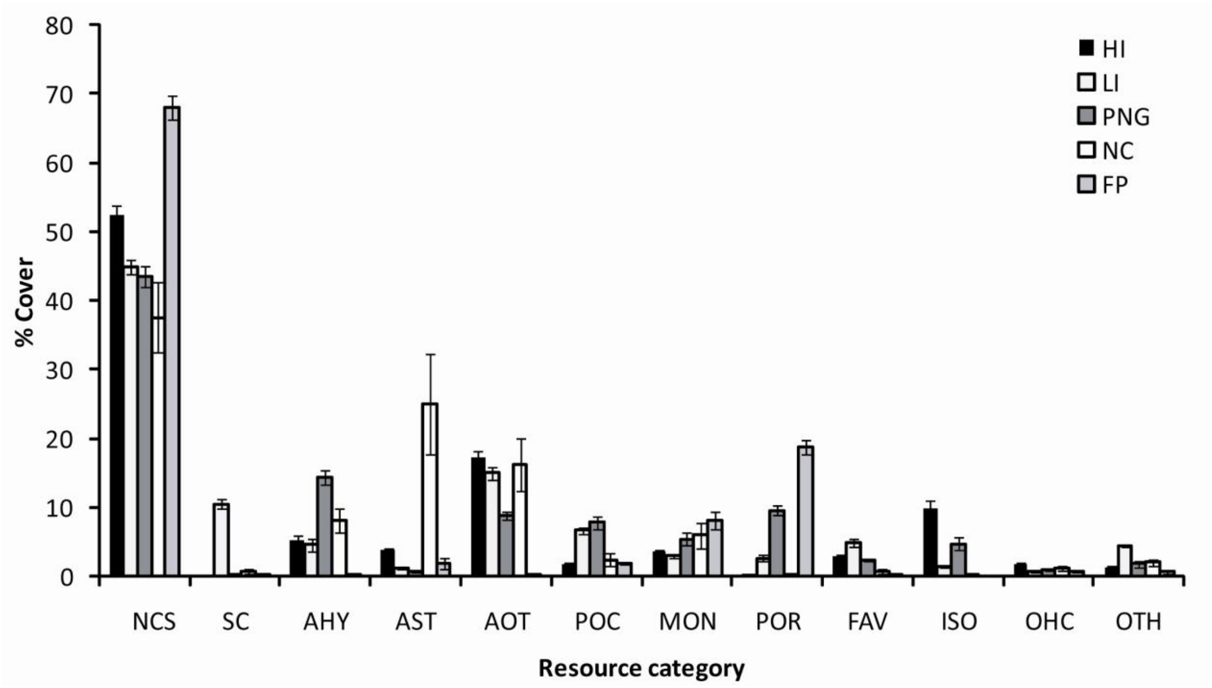
% Cover
80
70
60
50
40
30
20
10
0
HI
LI
PNG
NC
FP
NCS
SC
AHY
AST
AOT
POC
MON
POR
FAV
ISO
OHC
OTH
Resource category

Fig 2

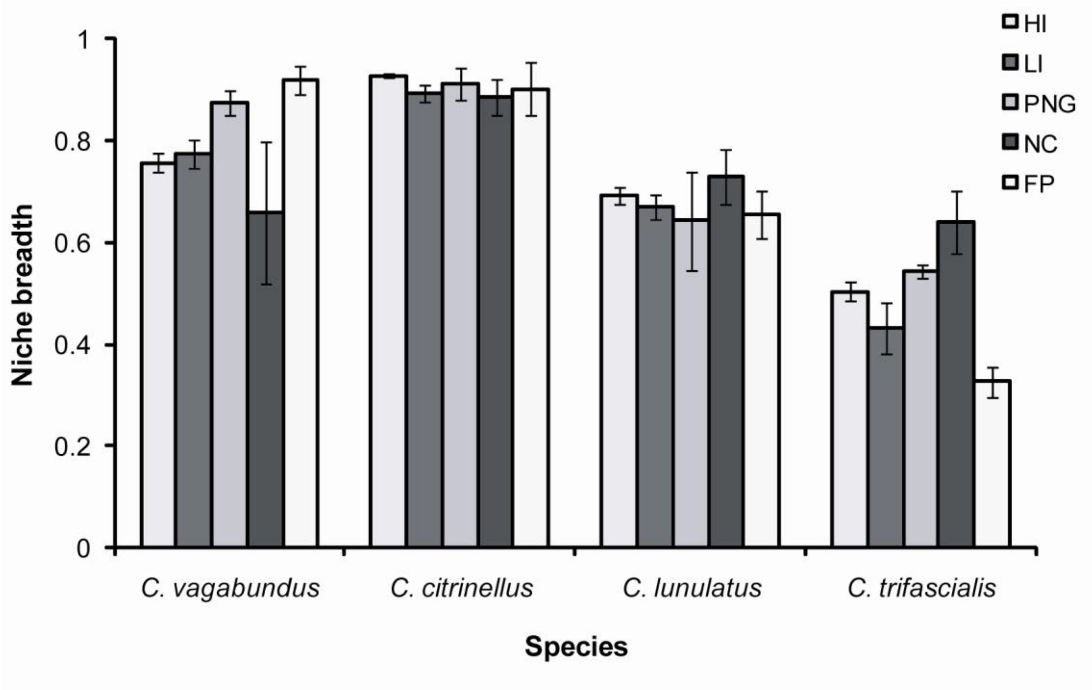
Niche breadth
1
0.8
0.6
0.4
0.2
0
HI
LI
PNG
NC
FP
C. vagabundus
C. citrinellus
C. lunulatus
C. trifascialis
Species

Fig 3

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REPORT

Selective feeding by coral reef fishes on coral lesions associated with brown band and black band disease

K. M. Chong-Seng · A. J. Cole · M. S. Pratchett · B. L. Willis

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NOTE

Cleaning to corallivory: ontogenetic shifts in feeding ecology of tubelip wrasse

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Corallivory in tubelip wrasses: diet, feeding and trophic importance

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Effects of coral bleaching on the feeding response of two species of coral-feeding fish

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Reef sites

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